THE EFFECT OF LOCATION ON NATURAL SELECTION IN BULK POPULATIONS OF BARLEY HORDEUM VULGARE L.

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A thesis submitted to the Faculty of Graduate
Studies and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

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March 1976

Short title

NATURAL SELECTION IN BARLEY

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ABSTRACT

Ph.D. CHOO THIN-MEIW Agronomy

THE EFFECT OF LOCATION ON NATURAL SELECTION IN BULK POPULATIONS OF BARLEY (<u>HORDEUM</u> <u>VULGARE</u> L.)

The effect of alternating bulk populations between two locations, Macdonald College and La Pocatière, on natural selection in segregating generations of a barley cross was evaluated in F_6, F_{10} and F_{15}. One population was grown year after year at each location, while others were alternated either annually or after two to eight years at one location. Materials for study and further propagation were harvested at random from each population.

There was no significant effect of alternating the segregating populations on natural selection with regard to segregation for awn type, aleurone colour, rachilla hair length, spike density, hairiness of rachis edges, collar type or shape of basal rachis internode. Similarly, there was no effect on the trait means for grain yield, number of heads per plot, number of kernels per head, 1000-kernel weight, awn length, head length, flag leaf width, length or area, or plant height. Equally, stability parameters and frequency of superior genotypes were not affected.

By F_{15} almost all populations had shifted towards plants with rough awns, yellow aleurone, short-haired rachillas and hairy rachis edges. Short-statured genotypes were eliminated. Selection for grain yield appeared to stabilize.

Wider environmental diversity is apparently needed in order to evaluate effectively the usefulness of a procedure involving the alternation of segregating populations.

It appears, from this limited study, that little would be gained in barley breeding programs by adopting a procedure involving the exchange of bulk populations, during segregating generations, between locations environmentally as similar as Macdonald College and La Pocatière.

RESUME

Ph.D. CHOO THIN-MEIW Phytotechnie

EFFET DU LIEU SUR LA SELECTION NATURELLE DE POPULATION BULK D'ORGE (HORDEUM VULGARE L.)

Ce travail a consisté à évaluer l'effet d'alterner des populations bulk entre deux lieux, La Pocatière et Macdonald College, sur la sélection naturelle dans des générations en disjonction d'un croisement d'orge. On a choisi les générations F_6, F_{10} et F_{15} aux fins de cette étude. Une des populations a été ensemencée année après année à chaque endroit pendant que d'autres ont été alternées annuellement ou de deux à huit ans après avoir été cultivées à un endroit.

Les semences utilisées pour fin d'analyse et de propagation ont été récoltées aléatoirement à partir de chaque population.

Aucun effet significatif causé par le fait d'alterner les populations en disjonction, n'a pu être observé sur la sélection naturelle en ce qui a trait à la disjonction des caractères suivants, le type de barbe du lemma, la couleur de l'aleurone, la pubescence du rachillet, la densité de l'épis, la pubescence des bords du rachis, le type et la forme de collet à la base de l'épis. Même, on n'a pu observer aucun effet sur les caractères responsables du rendement en grain, soit le nombre d'épis par parcelle, le nombre de grains par épis, le poids de 1000 grains, la longueur de la barbe du lemma, la longueur de l'épis, la longueur, la largeur et l'aire foliaire de la feuille apicale et la hauteur de la plante. Les composantes responsables de la stabilité et de la fréquence des genotypes supérieurs n'ont pas été affectées.

A la F_{15} presque toutes les populations ont produit des plantes avec une barbe de lemma hirsute, une aleurone jaune, des poils de rachillet courts et un rachis avec bords pubescents. Les génotypes donnant des plantes courtes ont été éliminés. Il semble y avoir eu stabilisation de la variation du rendement en grain.

Une plus grande diversité de l'environement apparait nécessaire afin d'évaluer de façon efficace et utile dans toute procédure impliquant le fait d'alterner des populations en disjonction. Cette étude limitée indique qu'il y a peu à gagner dans un programme d'amélioration de l'orge par l'alternance des populations bulk en disjonction entre des endroits aussi similaires que Macdonald et La Pocatière.

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. H. R. Klinck for his guidance, advice and assistance during the course of this study; to Dr. H. A. Steppler for his valuable suggestions and critical reviews during the preparation of the manuscript; and to Dr. C. A. St-Pierre for his assistance in various ways. Appreciation is extended to Mrs. M. Couture for the excellent typing of this manuscript.

Thanks are due to my parents and uncles, to Mr. Lau, Yoke-Choi and Miss Monica Wu for their support and encouragement during the period of my post-graduate study.

The financial support from the Brewing and Malting Barley Research Institute, a Max Binz Bursary for Foreign Students, a David Stewart Memorial Fellowship, a Malaysian Hakka Association Scholarship and a Kampar Hakka Association Scholarship are gratefully acknowledged.

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I. INTRODUCTION

The interactions of genotypes with environments have been observed by plant breeders for many years. However, there have been only a few attempts to exploit them in practical plant breeding programs. St-Pierre _et al_. (1967) carried out pedigree selection from a segregating population of barley under the environmental conditions of Macdonald College and La Pocatière. They found that strains selected at alternate locations in successive years, starting at La Pocatière in F_2, possessed the widest adaptation. Borlaug (1968) claimed that the process, used in the Mexican wheat breeding programs, of moving segregating populations back and forth between two diverse locations, with two generations in one year, not only reduced by half the time required to develop a new variety, but also simultaneously permitted the identification of lines and the development of varieties having wide adaptation. Differential selection in varietal mixtures and hybrid bulk populations of cereal crops at different locations has been investigated by several workers. To the best of my knowledge, no one has studied the effect of this "alternating segregating population" procedure on natural selection in any hybrid bulk populations.

Suppose a desirable plant type were eliminated by natural selection at one location, and another desirable plant type were eliminated at another location, could this procedure preserve a sufficiently high proportion of desirable plant types in a population? If a population were alternated between two locations in which a desirable plant type was selected against at one and selected for at the other, what would be the outcome in this population for the desirable plant type? When a particular generation is considered, alternated populations are grown less frequently at one location than those grown continuously at that location. The changes in any character in the alternated populations, then, will be slower than, or at most equal to, those in latter populations. Thus, this alternating segregating population procedure seems to provide a means to maintain maximum genetic variability in our breeding material or mass reservoirs.

5 There is considerable evidence showing that natural selection would eliminate the non-adapted genotypes. Could this procedure bring the population into wider adaptation? If so, should someone wish to maximize the effect of alternation, what is the ideal alternating frequency? Should we alternate our population annually or every two, three or more years? Should we grow the population more years at one location than at the other? What kinds of location should be used in this procedure? How many locations are needed? What are the characters that are most likely to be affected by this procedure?

This study was designed to answer some of these questions. For practical purposes, two locations within the province of Quebec were chosen. These two locations, Macdonald College and La Pocatière, are about 250 miles apart and are situated at almost the same altitude. However, they differ by two degrees in latitude. Daylength at the two locations differs by about half an hour on 21 June. Average monthly bright sunshine is approximately 200 hours at each location. On the average of the propagation period (1959-1972) monthly temperature at the early growing season is about 3°C higher at Macdonald College; it is about 2°C higher at the late growing season. However, monthly rainfall is about 1 cm lower at Macdonald College (Table 2). They also differ in soil texture; the La Pocatière clay has a higher water-retention capacity. Barley usually yields more at Macdonald College, although maturing is about one to two weeks earlier than at La Pocatière.

The effect of natural selection on varietal mixtures and composite populations has been reported elsewhere, but there are relatively few and inadequate data clearly showing changes in single hybrid populations in response to the pressures of natural selection. The population structure of a single hybrid population can be expected to differ from that of varietal mixtures and composite populations. Thus, the results obtained in the studies from the latter populations may or may not be applicable to a single hybrid population. It is believed that studies on changes brought about by natural selection in a single hybrid population should provide some valuable information for a breeding program.

The objectives of the present investigation were to study

(1) the effect of a procedure called alternation of segregating populations at two locations on unselected barley populations,

(2) the effect of alternating frequency on several agronomic characters, and

(3) the effect of natural selection on several agronomic characters in a single hybrid population.

II. REVIEW OF LITERATURE

A. The effect of natural selection

1. Changes in varietal mixtures

Several investigators have studied the effects of natural selection and competition in changing the composition of bulk populations made up by artificially mixing equal quantities of small grain varieties. A mixture of durum and hard red spring wheat was grown by Klages (1936) for a single season. A very large increase in the durum component of the mixture was explained by the occurrence of a severe stem rust epidemic.

Laude and Swanson (1942) mixed equal numbers of seeds of the winter wheat varieties, Kanred, Harvest Queen and Currell, and grew the mixture at two locations in Kansas over a nine-year period. Shifts in the varietal ratios resulted in nearly pure stands of Kanred, the better adapted variety, by the end of the experiment. The changes in the varietal ratio were attributed both to competition among plants which resulted in greater survival of the better adapted variety and to production of more seeds per plant by Kanred.

Two different barley varietal mixtures and a mixture of five wheat varieties were grown by Suneson and Wiebe (1942) for periods of five to nine years. They found that the survival of the varieties in a mixture bore no relationship to the yields of component varieties when grown in pure stands. Vaughn barley and Ramona wheat were well adapted and high yielding when grown in pure stands but proved to be very poor competitors in the mixtures. They suggested a decided limitation to the bulk method of breeding as plants that survive best in the hybrid mixture may not be the types that would yield best when grown alone.

Suneson (1949) grew a mixture of equal quantities of four barley varieties for a total period of 16 years. At the end of that time, the proportions of varieties in the mixtures were Atlas 88.0 per cent, Club Mariout 10.5 per cent, Hero 0.7 per cent, and Vaughn 0.4 per cent. During this same period Vaughn averaged significantly higher than any of the other varieties in yield when tested in pure stands and Hero was second in yield. Vaughn and Hero also were considerably more resistant to the leaf diseases which were serious in some years of the study. The only marked difference noticed for growth habit was a somewhat more erect early growth for Atlas that might have given it a competitive advantage. On the basis of these results, he suggested that the bulk method of breeding would not necessarily perpetuate either the highest yielding or the more disease resistant progenies, but rather those with an intangible character of competitive ability.

Sakai (1955) provided results of a competition study of Dr. Oka. A mixed population of two rice varieties, Taichung No. 65 and O-Chiam, were grown for four crops in Taiwan. The mixing was made in three initial proportions: 0.05:0.95, 0.50:0.50, and 0.95:0.05. The results showed that the proportion of Taichung No.65 decreased generation after generation without regard to the initial proportions, although Taichung No.65 yields higher than O-Chiam.

Mumaw and Weber (1957) reported that marked varietal changes occurred in soybean varietal composites which were grown at one location for five seasons. Varieties having greater height, later maturity, more lodging and greater branching habit increased in proportion.

Suneson and Ramage (1962) mixed awned and awnless Onas wheat isogenics from backcrosses in a 2:1 ratio, then grew them progressively for seven years. No significant population shift resulted. However, rough awns increased by 20 per cent in a 1:1 mixture of rough and smooth-awned Atlas barleys for the same period. Hooded barley was strikingly inferior under both yield and survival assays. They concluded that yield and survival relations for hybrids and varieties are generally but not universally in accord.

Early and Qualset (1971) reported that complementary competition was observed in all mixed populations in which the barley variety, Tenn. 60.34 occurred. Its yield was suppressed in mixtures by about 20 per cent, while the other two varieties increased a like amount, so that the total mixed population yield was equal to that expected from pure stand performance. The reduced yield of Tenn. 60-34 in mixed stands was due entirely to a decreased number of spikes produced per unit area.

Blijenburg and Sneep (1975) studied competitive interactions in a mixture of eight barley varieties and examined the relationship between the competitive ability of these varieties and their yield in monoculture. They found that the frequencies of the varieties in the mixture changed rapidly, one of the varieties increased up to 86 per cent by the end of the six-year study. Yield in monoculture of seven of the eight varieties appeared to be in agreement with their competitive ability in mixture.

All of these investigators, working with different crops or different varieties, come to the same conclusion; that is, that natural selection did operate in their varietal mixtures.

2. Changes in composite populations

The "evolutionary plant breeding method" with composite cross populations, as Suneson (1969) stated, was begun by Harlan and his associates (1940). They mixed equal amounts of 28 varieties of barley crossed in all possible combinations except one, and this stock was called Composite Cross II (C.C.II.). With several objectives in mind, the composite and the individual crosses were grown for seven generations and were tested. They concluded that growing a number of crosses in a composite mixture was apparently equal to the method of pedigree culture. A number of plant characters were also studied. Smooth-awned types averaged greater floret sterility and slightly lower yields. Blue colour in the aleurone probably was not related to capacity to yield.

Segregation studies of C.C.II have been carried out. Middleton and Chapman (1941), working from F_3 to F_5 generations, showed the smooth-awned types to be rather rapidly disappearing at both locations, though possibly somewhat faster at one location than at the other. Three years of yield trials with bulked segregates gave results significantly in favor of rough-awned types as compared with either smooth-awned or hooded types. Yield trials with true-breeding lines from the single cross of two selections of the composite were also significantly in favor of the rough-awned types. An association was found to exist between factors for spring growth habit and smooth awnedness. They suggested that this association was one factor in the lack of adaptation generally observed in smooth-awned strains when fall-sown at the two locations. Suneson and Stevens (1953) recorded four plant census enumerations involving the F_4, F_{12} and F_{23} generations of this composite. It was found that the percentage of smooth-awned types decreased with advancing generation.

The yielding ability of C.C.II was studied by Suneson (1956). The composite was grown at Davis, California, for 29 generations in bulk. During the early segregating generations, the composite was conspicuously inferior to Atlas, a check variety, in yielding ability and general agronomic appearance. It was not until the F_{15} to F_{20} generations that the bulk consisted, rather uniformly, of types similar to those grown commercially in California and became about equivalent to Atlas in yields. He suggested that there should be a minimum of 15 generations of natural selection.

Composite Cross V that was developed by Harlan, was a bulk of F_1 plants derived from crossing 31 varieties, and then crossing the resulting F_1 plants in increasing numbers through four successive pairings to give a complete recombination. Analysis of this composite in terms of changes in genotypic frequencies occurring over 18 generations was done by Jain and Allard (1960). The results showed that the frequency of the dominant phenotype increased sharply for rough-awned, blue aleurone color, and remained much the same for long-haired rachillas in later generations. It also indicated that reduction in heterozygosity was slower at several marker loci than expected for the observed amount of outcrossing. It was explained on the basis of heterozygote advantage associated with segments of chromosomes.

Both directional and stabilizing selection, involving a number of quantitative characters in C.C.V., have been reported by Allard and Jain (1962). Six generations (F_3, F_5, F_6, F_{13}, F_{15} and F_{18}) were spaced-seeded, and observations on heading time, plant height, spike length, spike density and seed size were made on a single plant basis. No change in average spike density was observed from F_3 to F_{18}. The constancy of the means of spike density showed that for this character stabilizing selection was involved. Directional selection was observed for plant height, spike length, heading time and seed size. The generation means for these characters shifted slowly toward shorter stature, shorter spikes, earlier heading and larger seeds. Linear increase in the average population fitness was found with advance in generation.

Finlay (1970) reported that the overall mean yield of each population of 100 lines derived from C.C.V. increased with advancing generations from F_5 to F_{24}. This further supported the results of Suneson (1956). This overall mean yield improvement resulted not only from the loss of low-yielding lines, but also from the selection of increasingly higher-yielding lines with progression from F_5 to F_{24}.

Rasmusson et al. (1967) grew a barley composite population, obtained by mixing seed of 6000 entries from the barley world collection, under severe stress conditions in Minnesota for five years. They found that yield of the population increased significantly. The improvement amounted to 57 per cent during the six years or an average of 9.5 per cent for each year of natural selection.

Thus, this evolutionary plant breeding method not only provides a source population in breeding programs, but also continuously improves its performance through natural selection.

3. Changes in single hybrid populations

As pointed out by Allard (1960), varietal mixtures differ from hybrid populations in at least two particulars: (1) segregation will occur in the hybrid bulks with the result that the competing genotypes are not expected to be constant from generation to generation, and (2) even when a hybrid population has reached a degree of homozygosity comparable with that of a varietal mixture, it will differ from the mixture in that a vastly larger number of genotypes will be competing against each other. On the other hand, most of the composite populations are derived from several to many crosses, and intercross competition may or may not occur. It is, therefore, a question whether the results from varietal mixtures, or composite populations can be applied to single hybrid populations.

It is probable that the easily synthesized property of varietal mixtures and the attractive population structure of composite populations has resulted in more studies on the effect of natural selection having been carried out in varietal mixtures and composite populations than in single hybrid populations.

Palmer (1952), comparing grain yield and its components in F_2 and F_8 from a wheat cross, found that natural selection, acting between these generations, had raised the population mean in F_8 for average number of grains, but had reduced it for the weight of individual grains. However, grain yield was the same in both the F_2 and F_8.

In a lima bean population which contained two simply inherited characters: indeterminant (D-) vs. determinant growth habit (dd) and white (W-) vs. green seed coat (ww), Tucker and Harding (1965) found that gene frequency of d was initially 0.50 but after eleven generations of selection it was reduced to less than 0.03. Strong selection against dd genotypes was predictable because of extreme morphological differences between bush and vine phenotypes. Logically, the bushes would compete unfavorably for light, soil moisture, and nutrients. Selection intensity against W was of the same magnitude as that for d. Starting with a gene frequency of 0.50, after eleven generations the frequency of W was 0.06. There were no obvious morphological differences between the phenotypes which could be associated with competitive ability.

The F_3 and F_7 generations of 58 populations of oats were evaluated by Marshall (1972) for freezing resistance and winter survival. He found that initially nonhardy populations become more resistant to freezing in response to natural selection, whereas initially hardy populations were not responsive. He suggested that the ineffectiveness of natural selection in the hardy populations appeared to be the result of inadequate selection pressure rather than narrow variability for winter hardiness. In another study, Marshall (1973) reported that after growing them for five years under natural selection for winter survival, ten out of twelve populations of oats were more decumbent in juvenile growth habit, five were taller and all were significantly later in maturity in the F_8 than in the F_3. No apparent relationship between these changes and the amount of increase in winter hardiness was detected.

4. Changes in population variance

Very little information is available on changes in population variance under natural selection pressures. Palmer (1952) reported that the variances of yield and its components, except number of grains per plant, decreased between F_2 and F_8 in a wheat cross. These changes were the result of natural selection.

Allard and Jain (1962) found that changes in variances for heading time, plant height, spike length, spike density, and seed size were as striking, or more so, than changes in means. The change was always in the direction of decreased variance. Frequency distributions showed that these decreases in variance were associated with steady elimination of extreme individuals from the tails of the curves.

5. Changes in stability

A regression method was proposed by Eberhart and Russell (1966) for describing the performance of a variety over a series of environments. Their model was given as

$$Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$$

in which Y_{ij} is the mean yield of the i^{th} variety in the j^{th}

environment; μ_i is the i^{th} variety mean over all environments; β_i is the regression coefficient for the i^{th} variety; I_j is the index for the j^{th} environment, it is the mean yield of all varieties in that particular environment; and δ_{ij} is the deviation from regression of the i^{th} variety in the j^{th} environment.

The effect of the environment was partitioned into a linear and a nonlinear component, and a stability parameter was associated with each of these components. The regression coefficient β_i was associated with the linear component, and σ^2_{ei} (a function of the δ_{ij}'s) with the nonlinear component. The best estimates of β_i and δ^2_{ei} were respectively b_i and S^2_{ei} , where

$$S^2_{ei} = \sum_j d_{ij}/(n-2)$$

in which n is the number of environments; and

$$d_{ij} = \hat{\delta}_{ij} = Y_{ij} - (a_i - b_i I_j)$$

in which Y_{ij} and I_j are as above, and $a_i = \hat{\alpha}_i$.

Finlay and Wilkinson (1963) defined average stability as regression coefficients approximating to 1.0. When average stability was associated with high mean yield, varieties had general adaptability; when associated with low mean yield, varieties were poorly adapted to all environments. Regression values increasing above 1.0 described varieties with increasing sensitivity to environmental change (below average stability) and greater specificity of adaptability to high-yielding environments.

Regression decreasing below 1.0 provided a measure of greater resistance to environmental change (above average stability) and therefore increasing specificity of adaptability to low-yielding environments. With respect to the second statistic, a variety with $S^2_{ei} = 0$ will display little variation in performance over environments that have similar indices. The desirable variety was the one with a high mean ($\overline{X}_i$), unit regression coefficient ($b_i = 1.0$) and the deviations from regression as small as possible ($S^2_{di} = 0$). It would perform above average in all environments.

The approximate analysis of variance is given in Table 1. The F-test is used for tests of significance. Eberhart and Russell (1966) and Freeman and Perkins (1971) considered the significance levels obtained for mean squares for heterogeneity of regression to be approximate with the F-test; but with homogeneous errors, levels of significance with the F-test were exact (Mandel 1961; Shukla 1972). The significance of the differences among variety means could be tested approximately by the F-test with a pooled error mean square.

Several workers have suggested that mixtures, on the average, are more stable than their components (Simmonds 1962; Allard 1961; Pfahler 1965a, 1965b; Jensen 1965). Populations derived from hybrids which were considerably more heterogeneous than mixtures have been found to be both higher yielding and more stable than pure line varieties (Allard 1961, 1967; Finlay 1963; Rasmusson 1968). Thus, it would be worthwhile to study the role that natural selection plays in population stability.

TABLE 1. Analysis of variance when stability parameters are estimated*

Source	d.f.	SS
Total	nv-1	$\sum_{i}\sum_{j} Y_{ij}^2$ - C.F.
Variety (V)	v-1	$\frac{1}{n} \sum_{i} Y_i^2$ - C.F.
Environments (Env) V x Env	n-1 (v-1)(n-1) } v(n-1)	$\sum_{i}\sum_{j} Y_{ij}^2 - \sum Y_i^2/n$
Env (linear)	1	$\frac{1}{v}(\sum_{j} Y_{ij} I_j)^2/\sum_{j} I_j^2$
V x Env (linear)	v-1	$\sum_{i} [(\sum_{j} Y_{ij} I_j)^2/\sum_{j} I_j^2]$ - Env (linear)S.S.
Pooled deviations	v(n-2)	$\sum_{i}\sum_{j} \delta_{ij}^2$
Variety 1	n-2	$[\sum_{j} Y_{ij}^2 - \frac{(Y_i)^2}{n}] - (\sum_{j} Y_{ij} I_j)^2/_{j} I_j^2$
:	:	:
Variety p	n-2	$[\sum_{j} Y_{vj}^2 - \frac{Y_v^2}{n}] - (\sum_{j} Y_{vj} I_j)^2/\sum_{j} I_j^2 = \sum_{j} \delta_{vj}$
Pooled error	n(r-1)(v-1)	

*Adapted from Eberhart and Russell (1966).

Finlay (1970) reported that the regression stability index changed with generations in Composite Cross V. The dominant feature was the reduction or loss of the very stable and very unstable lines, and an increase in lines with roughly average stability (i.e., regression coefficient near 1.0).

Population evolution toward average stability was also reported by Fatunla and Frey (1974) in a study of stability indexes of radiated and nonradiated oat genotypes propagated in bulk populations. Mean regression stability indexes for grain yield decreased from 1.17 to 1.02 in the nonradiated line, and increased from 0.82 to 1.04 in the radiated line of descent over generations. The changes in mean regression stability indexes for plant weight paralleled those for grain yield, but no trends in this statistic occurred for other traits.

The above papers both indicated that populations would gradually tend to show average stability under the pressure of natural selection. It would be interesting to study the stability of bulk populations under different locations.

B. Effect of location on natural selection

1. Varietal mixtures

A textbook example of the effect of natural selection at different locations was given by Harlan and Martini (1938). A mixture of equal amounts of eleven barley varieties was grown at ten experiment stations in the northern and western United States for four to 12 years. Each year the plots were threshed and sufficient seed saved to plant two plots the following year. One plot was again harvested in bulk and the other used to take a census of the number of plants of each of the 11 varieties remaining in the population. The dominant variety at each station was soon evident. Varieties that were dominant at one or more stations were eliminated at others. In general, there was good agreement between the success of a variety in the mixture and its status as a commercial variety except at two locations. Surveying the results of their research as a whole, they concluded that the success of a variety in a mixture could be regarded as a measure of adaptation and yielding ability under commercial conditions. A striking feature of the experiment was the rapidity with which one or two varieties became dominant at certain locations. At some stations, one variety dominated in as few as four years of natural selection. At other stations, changes occurred much more slowly.

Sandfaer (1970) provided another extensive and systematic study on barley mixtures grown at different locations. Three variety mixtures were produced, Maja + Freja, Carlsberg II + Freja, and T. Prentice + Freja. Each mixture consisted of the same number of kernels of the two varieties in the first year. These mixtures were grown every year from 1956 to 1966 at five different locations in Denmark. The results showed that the mixtures of Maja and Freja were rather stable at all five locations, and the percentage of Freja in the mixture involving Carlsberg II and Freja declined at four of the five locations. There was a slight increase in the relative amount of Freja at the other location. In the third mixture, the percentage of Freja was reduced at the end of the experimental period at all five locations. Barley stripe mosaic virus was the cause of elimination of Freja in the mixture of Freja and T. Prentice.

2. Composite populations

Composite Cross I was a mixture of equal quantities of F_3 seeds from 32 crosses involving 11 varieties of barley. These varieties were the same as those used in a survival study of mixtures at 10 stations by Harlan and Martini (1938). Suneson and Stevens (1953) grew this composite at 10 stations for various periods. They found that genetic characters, like varieties, did not survive equally in mixtures, nor similarly at different stations. Smooth-awned segregates persisted at original frequencies, or increased at six stations, but decreased at two other stations. They suggested that the basis of the difference might not lie in the character itself but might be caused by adaptation factors linked with it.

Three bulk hybrid populations of rice were grown by Adair and Jones (1946) for eight generations at locations in Arkansas, Texas, and California. Each population was a composite of seed in the F_2 of three to eleven crosses, the original composition of the composites being somewhat different for the three locations. A study of the types that survived in the bulk populations showed that selection for date of heading and for height had differed with location. The proportions of different grain types and of awnless plants that survived also were quite different.

Bulk populations of 20 barley crosses were grown from F_2 to F_4 generations at four locations in Iowa (Taylor and Atkins 1954). The authors found that the location at which the segregating generations had been grown had a highly significant effect upon subsequent bulk population yields, date of maturity, and average heading date, but not on plant height. Neither rough- nor smooth-awned types showed a tendency to be favored in survival. However, differences were found among crosses and among locations for the degree of selection for this character. It was concluded that the effectiveness of the bulk method of breeding in securing desired types was dependent in part upon the location at which the bulk populations were grown.

A composite of 105 crosses involving 15 barley varieties was grown for five years at nine locations in widely different latitudes. Considerable differences were observed among the samples from different locations regarding heading date, maturity date, and yield. Very little difference was observed for plant height and 1000-kernel weight. Differential selection was observed for spike and awn types. The proportions of two-rowed spikes and rough awns increased at some locations and decreased at others. Natural selection had very little effect upon the collar type, neck shape, and leaf width. Shape of basal rachis internode and neck length were not influenced by the locations at which seed was grown (Singh and Johnson 1969).

3. Single hybrid populations

An extensive study of the bulk population method was done by Akemine and Kikuchi (1958). One of the crosses was between Zuiho and Noren 20, which were, respectively, the earliest and latest rice varieties grown in Japan. Bulk populations were grown from F_2 to F_5 generations at 20 experiment stations scattered throughout Japan. The results showed that the effect of natural selection differed considerably for the various locations. The plants from seed grown in northern locations were generally early, whereas those from southern locations showed the reverse tendency. The amount of variation also differed with location. It was very large for centrally located stations and, although smaller for southern and northern stations, it remained much larger than for the parents.

Miu (1965) and Miu _et al_. (1967) mixed thoroughly seeds from two single hybrid populations of rice separately, and each single hybrid population was divided into four equal portions for planting at four different locations, representing northern, central, southern and extreme southern Taiwan. These materials were harvested at each location and were grown continuously at that location from F_2 to F_6 generations. They found that selected lines differed in yield among and within populations from the four different locations.

Takahashi and Yasuda (1970) grew barley crosses in bulk from F_2 up to F_6 generations in successive years at four stations, located in northern, central, and southern Honshu and the southernmost part of the Kyushu district in Japan. They found that the populations from two crosses definitely tended to head out earlier on the average when going from north to south. The population means of days to flag leaf emergence under 12-hour daylength in the northern station became larger and larger with the advance of hybrid generations. In contrast, plants insensitive to short days increased gradually in the southern locations, and population means decreased. There was almost the same tendency under 24-hour daylength. The effect of natural selection on growth habit was very strong. Abrupt elimination of spring-type plants from the populations occurred at the northern station. On the contrary, the frequency of spring plants tended to increase, though slightly, at the three other stations, and this tendency became marked moving from north to south.

Tucker and Harding (1974) developed two bulk populations of lima beans from two different biparental crosses of varieties. Each bulk population was grown in two different sites in the same commercial growing area in California for nine generations. A yield test was conducted in one of the two sites, designated the test location. The populations grown in the test location had higher yields than the population grown in the non-test location and showed significant divergence in yield from the F_6 to F_{11} generations, especially in the last three years.

C. Competitive ability and yield

Factors of natural selection should be numerous, such as maturity, seed size, habit of growth (erect vs. prostrate), heading habit (spring or winter type), vigor of growth, extent and depth of root system, disease and insect resistance, the capacity for nutrient uptake, allelopathic reaction and so on. However, only two factors pertinent to this study, grain yield and plant height, are reviewed.

Several studies indicated that there was a high correlation between competitive ability and yielding ability. Suneson (1949), based on his findings, stated that the relative yield of a variety was not necessarily a criterion of its ability to competition with other varieties. However, there seems to have been an unrecognized bias, as he pointed out later (Suneson and Ramage 1962). Vaughn could be sown and managed to yield either strikingly more or less than Atlas. Furthermore, the reported seven per cent yield advantage for Vaughn, based on 114 California tests, had since, with a total of 319 tests, been turned into a two per cent deficit. Although both varieties were losing favor, the 1960 acreage ratio in California was 10 to 1 in favor of Atlas. Using the same four varieties for studying intergenotypic interaction, Allard and Adams (1969a, 1969b) found that Atlas was better yielding than Vaughn. They believed that the interpretation of Suneson's experiment did not appear to be justified. In a study of competition between near-isogenic genotypes, Suneson and Ramage (1962) concluded that yield and survival relations for alleles, hybrids and varieties were generally, but not universally, in accord.

Laude and Swanson (1942) speculated that the predominance of Kanred after nine years of natural selection was partly because of the production of more seeds per plant by this variety.

Roy (1960) reported that when two varieties of rice were planted together, either fully mixed, in alternate rows, or in separate halves of the same small plot surrounded by a dam, each might influence the yield of the other. The effect was as often unfavorable as favorable. High yielding varieties were also good competitors.

Jensen and Federer (1965) noted that strain yielding ability was highly correlated with competition ability. In other words, the strain with the highest mean yield imposed the greatest mean yield depression when it was a neighbor.

Though no differences between observed yields of the mixtures and midcomponent means were found, corn hybrids that yielded highest in pure stand did contribute more to a mixture than would be expected based on the pure stand yield, and the lower yielding hybrids less than expected (Kannenberg and Hunter 1972). In a recent study, Kannenberg (1974) reported that the high yielding hybrids yielded more when in low proportions in a mixture; as their frequency increased, and thus the competition was increasingly among like genotypes, their relative yield decreased with the least yield being in pure stand. Conversely, low yielding hybrids yielded their highest in pure stand.

Studying competitive interactions in an eight-barley-variety mixture, Blijenburg and Sneep (1975) concluded that yield in pure stand of seven out of eight varieties appeared to be in agreement with their competitive ability in mixtures.

The results of composite population studies showed that yielding ability was steadily improved by natural selection (Suneson 1956; Singh and Johnson 1969; Rasmusson 1968; Finlay 1970). These further confirm that competitive ability indeed is associated with yielding ability.

There is, however, a growing body of opinion that yield of any cereal genotype in a mixture will be negatively related to its yield in pure stand. The earliest example in the literature was probably given by Montgomery (1912). When two varieties were planted in competition, one variety was very apt to have an advantage which, if continued, would in time cause it to practically replace the other. It appeared that the one yielding best alone would not always be the one surviving under competition.

This viewpoint was also supported by Wiebe et al. (1963) based on simulated generations of barley. Three genotypes, VV, Vv, and vv, from an advanced isogenic line of barley contrasting the six-row vs. two-row head character, were grown in pure stands and in F_2, $F_=$, F_3, F_4 and F_∞ populations. Significant reversals in relative yield were found to exist in comparisons between the same genotype, VV or vv, when grown in pure stands and in an advanced generation. Significant shifts due to competition were also found for heads per unit area, and number of kernels per head, whereas kernel weight was unaffected. The same general results were obtained where blue vs. white aleurone was used as the distinguishing character.

Donald (1963) stated, in his review of competition among crop and pasture plants, that productivity and competitive ability should be distinguished. He felt that a notable deficiency in our understanding of competition was the substantial independence of competitive ability and yield.

Schutz and Brim (1967) evaluated the effect of intergenotypic competition on yield and other attributes in both hill and row plots utilizing four diverse adapted varieties of soybean. Jackson was the best competitor, in terms of yield response, of the four genotypes tested. It was also the tallest and latest maturing variety. The best competitor, however, was not the highest yielding variety in pure stand.

Hamblin and Donald (1974) reported in their study that weakly competitive plants were likely to be higher yielding as monocultural crops. Other studies showed that competitive ability was associated with plant height rather than with yielding ability.

Other workers considered that there was no consistent relationship between the yield of a variety or genotype in a mixture and its yield in pure stand. Sakai (1955) found that competitive ability was not associated with grain yield or other characters. Tucker and Webster (1970) reported that there was no relationship between yielding ability in a pure stand and survival ability in a bulk population.

D. Competitive ability and plant height

The importance of height as a factor in competition was emphasized by Clements *et al*. (1929). They stated, "The plants may be so nearly the same height that the difference is only a millimetre, yet this may be decisive since one leaf overlaps the other."

Montgomery (1912) found that when black oats were sown alone they outyielded white oats, but when sown in competition the white oats returned the greatest yield. The possible explanation given was that the white oats grew more rapidly in height at an earlier stage.

Pendleton and Seif (1962) studied competition between rows, between hills, and within hills of corn of different heights. They found that a single row of dwarf corn bordered by normal corn yielded 30 per cent less than when bordered by dwarf corn. Conversely, a single row of normal bordered by dwarf yielded only six per cent more than when bordered by tall corn. Competition effects noted on the yields were primarily due to light.

Jensen and Federer (1964) found competitive effects associated with height in wheat nurseries. Yields increased by an average 5.0 bushels per acre in taller wheats and decreased by an average 2.3 bushels per acre in shorter wheats.

Jennings and de Jesus (1968) reported that a tall, leafy rice variety nearly replaced four other varieties in mixtures after four generations of natural selection, even though the short, sturdy varieties in the mixtures were far superior in yielding ability when grown in pure stands. Growth analysis of mixed populations showed that competition for light by mutual shading was the principle environmental component causing competition in rice (Jennings and Aquino 1968). Jennings and Herrera (1968) carried out the same kind of study but with tall and dwarf segregates from a rice hybrid. They found that in each generation following the F_2 the proportion of dwarf plants was less than would be expected in the absence of competition. In the F_6 only 23.7 per cent were observed, compared with 48 per cent expected.

Marshall (1973) reported that five of the oat populations were taller in the F_8 than in the F_3, no artificial selection had been applied.

Khalifa and Qualset (1974), working with a mixture of tall and short-statured wheat varieties, found that the dwarf variety decreased in frequency over time with a concurrent decrease in the population yield level.

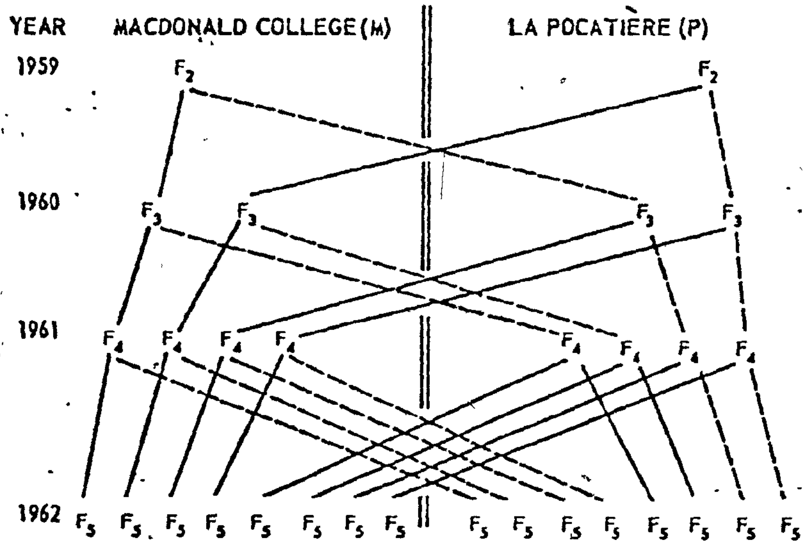
Kawana et al. (1974), based on the results of their study on a rice mixture, suggested that vegetative vigor, large leaf area, a high rate of nitrogen adsorption in early growth stages, and plant height were the most significant characters related to competitive ability.

From the above studies, it appears that short-statured plants are always in a position of selection disadvantage. They finally would be eliminated from the mixture or hybrid population.

E. Genotype-environment interaction

The mathematical aspects of genotype-environment interaction were given by Comstock and Moll (1963). Allard and Brashaw (1964) discussed in detail the implications of genotype-environment interactions in applied plant breeding. Work has also been done on whether selection should be made under stress or non-stress environmental conditions in programs for the development of new varieties (Falconer 1952; Frey 1964; Yen 1969; Roy and Murty 1970). However, research on using genotype-environment interaction in practical breeding programs is still inadequate.

St-Pierre et al. (1967) carried out a pedigree selection from F_2 to F_5 from a segregating population of barley under the environmental conditions of Macdonald College and La Pocatière. In each generation, seed from selected plants was divided into two parts and subsequently seeded at the two locations (see Figure 1). The



GENERATION	SELECTION PATHWAYS															
F_2	M	P	M	P	M	P	M	P	M	P	M	P	M	P	M	P
F_3	M	M	P	P	M	M	P	P	M	M	P	P	M	M	P	P
F_4	M	M	M	M	P	P	P	P	M	M	M	M	P	P	P	P
F_5	M	M	M	M	M	M	M	M	P	P	P	P	P	P	P	P

Figure 1. The 16 selection pathways to the F_5 generation (adapted from St-Pierre *et al.*, 1967).

adaptability of the selected strains was estimated from yield trials conducted at the two locations during F_7 and F_8. They found that strains selected at alternate locations in successive years, starting at La Pocatière in F_2, possessed the widest adaptation.

In the CIMMYT wheat breeding programs, segregating populations were grown near Ciudad Obregon, Sonora, at about 28° latitude on the coastal strip only a few feet above sea level during the winter. During mid-May, a second generation was planted at 8500 feet and 18° latitude near Toluca. Borlaug (1968) claimed that this process of moving the wheat plants back and forth, and up and down, twice a year, not only reduced by half the time required to develop a new variety, but also simultaneously permitted the identification of lines and the development of varieties with wide adaptation. He further pointed out that this, at least to a large extent, was the result of the selection of lines that are insensitive to changes in daylength and date of planting, and hence are broadly adapted. Other selection pressures also were undoubtedly acting under the very diverse conditions that prevailed at these two nursery sites.

III. MATERIALS AND METHODS

A. Source and propagation of plant materials

The project was initiated by Dr. H. R. Klinck to study the effect of alternating segregating generations between two locations on pedigree selection and bulk population method. The results of a study carrying individual plant selections through a pedigree program were published by St-Pierre et al. (1967). The results of the study involving bulk population method are reported in this thesis.

A cross between the barley cultivar, Star, and selection M.C.2950 was made in 1958. Star is a short-strawed cultivar which originates from Sweden. It has a dense spike, rough awns, yellow aleurone and a short-haired rachilla. M.C.2950 is a selection from the cross Montcalm x Fort. It has a lax spike, smooth awns, blue aleurone and a long-haired rachilla. For purposes of simplicity, M.C.2950 is referred to in the text as a parental cultivar.

The F_1 hybrids were grown in the greenhouse. Seeds from F_1 plants were bulked and divided equally into two parts. One part was grown at Macdonald College in F_2, and the other at La Pocatière. In each subsequent generation, these materials were again divided, one portion being retained for seeding in loco and the other portion sent for seeding at the other location (Figure 1). In each location/year each lot of material was seeded at 50 seeds per meter in rows 20 cm apart. Each plot was of sufficient dimension to contain approximately 10,000 plants. At least 1500 mature plants were harvested at random from each plot, excluding the border rows. Standard cultural and fertilizer practices were employed. By 1966, the number of propagated plots for each population had exceeded the available land and labour resources. It was decided, therefore, to reduce the number of plots to eight or nine at each location. A list of the F_6 populations is given in Table 3, and of both F_{10} and F_{15} populations in Table 4. Populations were alternated either annually or after two to eight years at one location. Also, one population was grown continuously at each location.

These materials from F_1 to F_{14} were handled by Dr. H. R. Klinck. Seeds of F_6 and F_{10} populations were stored at the location where harvested.

B. Experimental sites

Macdonald College is situated at the extreme west end of Montreal island, while La Pocatière is 250 miles to the northeast. The exact geographical location of these two locations is: Macdonald College, 45°25'N and 73°56'W; La Pocatière, 47°21'N and 70°02'W. Both are at an altitude of about 100 feet, with a continental climate.

Soil texture at La Pocatière is heavy clay. It is more compact and has a higher water-retention capacity than the loam to

TABLE 2. Average monthly rainfall, average monthly maximum and minimum temperature from May to August at Macdonald College and La Pocatière

Year	Macdonald College			La Pocatière		
	Temperature (°C)		Rainfall (cm)	Temperature (°C)		Rainfall (cm)
	Maximum	Minimum		Maximum	Minimum	
1959	23.75	12.64	4.60	21.53	10.14	9.73
1960	24.03	13.10	5.66	21.66	10.47	7.52
1961	22.13	12.47	9.12	20.50	9.99	8.13
1962	22.22	12.50	7.80	20.00	10.14	8.61
1963	22.92	12.50	8.94	20.69	10.00	7.80
1964	23.61	12.92	8.10	20.28	9.58	8.61
1965	23.19	12.08	7.80	20.00	9.31	6.99
1966	22.92	12.50	6.71	20.83	9.86	6.86
1967	22.64	12.08	5.94	20.42	10.56	11.99
1968	22.64	11.94	7.16	20.14	9.03	5.46
1969	23.33	13.19	9.12	20.56	10.14	6.10
1970	24.03	13.06	5.36	21.67	10.97	8.81
1971	23.33	12.36	6.07	20.97	9.86	10.52
1972	22.22	12.22	11.20	19.44	9.31	9.09
Mean	23.07	12.54	7.40	20.62	9.95	8.37

Source: Bulletin Météorologique. Ministère des Richesses Naturelles, Québec.

sandy loam soil at Macdonald College. Average monthly rainfall and average monthly maximum and minimum temperature from May to August at both locations are given in Table 2. In general, the temperature at Macdonald College is approximately 3°C higher than at La Pocatière during early growing season, but only 2°C higher during late growing season. Differences in the amount of rainfall at these two locations varies with years. On the average, monthly rainfall at Macdonald College is slightly lower than at La Pocatière. Average total monthly bright sunshine at both locations is approximately 200 hours.

The date of maturity at Macdonald College is about one to two weeks earlier than at La Pocatière.

C. The alternated patterns

According to the system of alternation, the F_6 populations have been grouped into 12 different patterns, and the F_{10} and F_{15} populations are each grouped into eight (Tables 2 and 3). Among these, pattern 0 represents those grown continuously at one location, no alternation having taken place. Each of the alternated patterns consists of two populations which have the same system of alternation but differ in their starting location. A few populations do not have their counterparts; thus, each one is included with the nearest similar pattern. The patterns range from the one with the highest alternated frequency at the top of the table, to the pattern having no alternation at the bottom.

TABLE 3. Barley bulk populations in F_6 generation, each differing in previous history

Pattern	Population	Pattern	Population
I	PMPMP †*	VII	PMPPP
	MPMPM		MPMMM
			MPMMP
II	PMPMM	VIII	PMMMP
	MPMPP		MPPPM
III	PMMPM	IX	PMMMM
	MPPMP		MPPPP
IV	PPMPM	X	PPPMM *
	PPMPP		PPPMP
	MMPMP		MMMPP
V	PPMMP *	XI	PPPPM *
	MMPPM		MMMMP
VI	PMMPP	0	PPPPP *
	MPPMM		MMMMM

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

* These patterns were continuously propagated to F_{10} and F_{15} generations.

TABLE 4. Barley bulk populations in F_{10} and F_{15} generations, each differing in previous history

F_{10}		F_{15}	
Pattern	Population	Pattern	Population
I	PMPMPMPMP †	I	PMPMPMPMPMPMPM
	MPMPMPMPM		MPMPMPMPMPMPMP
II	2P2M2P2M1P*	II	2P2M2P2M2P2M2P
	2M2P2M2P1M		2M2P2M2P2M2P2M
III	3P3M3P	III	3P3M3P3M2P
	3M3P3M		3M3P3M3P2M
IV	4P4M1P	IV	4P4M4P2M
	4M4P1M		4M4P4M2P
V	5P4M	V	5P5M4P
	5M4P		5M5P4M
VI	6P3M	VI	6P6M2P
	6M3P		6M6P2M
VII	7P2M	VII	7P7M
	8P1M		8P6M
	8M1P		8M6P
0	9P	0	14P
	9M		14M

† The first letter represents the location in which the F_2 was grown. P = La Pocatière and M = Macdonald College.

* The number represents the years grown continuously at a location.

Such grouping enables the population sum of squares to be partitioned into between patterns and within patterns sum of squares in the analysis of variance. Since these patterns vary with alternated frequency, a non-significant between alternated patterns mean square for any character clearly indicates that there is no major effect of alternation on natural selection for this character. On the other hand, the effect of using a different alternating frequency may be revealed by a significant between alternated patterns mean square. A significant within alternated patterns mean square would mean that there is a significant difference between two populations (or three in some cases) having the same alternating system. This difference may be caused by the following factors and their interactions: (a) difference in number of times grown at each location; (b) yearly climatic fluctuations at each location; (c) yearly variation in cultural practices such as seeding date or harvesting date at each location; (d) soil variation among propagated plots at each location in each year; (e) generation-location-year interaction; (f) cumulative effect of these factors; and (g) other factors having an effect during propagation periods.

D. Segregation studies

In the summer of 1972 there were eight propagated plots of F_{15} at Macdonald College and nine at La Pocatière. Plot size and seeding rate were as indicated in section B, above. Several hundred heads were taken from each plot. Each head was examined and the following characters recorded: awn type, aleurone color, length of rachilla hairs, length of five rachis internodes, hairiness of the rachis edges, hairiness of the glume, rachilla hair type, collar type and shape of basal rachis internode. These characters were chosen for this study because of their distinguishable features and their usefulness for varietal identification. Studies also extended to the two parental cultivars, of which heads were obtained from test plots in 1973.

Barley is a predominantly self-pollinated species. Jain and Allard (1960) found that the amount of outcrossing ranged from one to two per cent. Thus, if outcrossing was neglected, the proportion of homozygotes in the population increased from F_2 onwards according to the well-known formula $[\frac{2r-1}{2r}]^n$, where r = the number of generations after F_1 and n = the number of independently segregating genes. In the one gene case, expected phenotypic ratios would be 33:31 in the F_6, 513:511 in the F_{10}, and approximately one to one in the F_{15}. In the case of two complementary and non-linked genes, expected phenotypic ratios in F_{15} would be about three to one. The observed ratio was compared with the expected phenotypic ratio by the chi-square test for some of the characters in this study.

An analysis of variance was carried out for testing the differences among the alternated patterns. It was done by using the percentage of a particular type for the character in question. The between patterns mean square was tested against the within patterns mean square. However, it was not possible to test the significance of the within patterns mean square because only one replication was used in this study.

E. Yield trials

Yield trials were conducted at Macdonald College and La Pocatière in 1973 and 1974. Seeds from the F_6 populations were grown in a 5 x 6 simple rectangular lattice layout with the three standard cultivars (Loyola, Champlain and Conquest) included. These cultivars were also included in the F_{10} population trials, but only Loyola and the two parental cultivars were included in F_{15} population trials. Seeds from both F_{10} and F_{15} populations were grown in 4 x 5 triple rectangular lattice design. These were the same at both locations in both years.

Plot size was about 1.0 x 3.2 m (5 links x 16 links). Seeding rate was 50 seeds per meter of row length. Only the central three rows of the five-row plot were harvested for yield determinations. In order to eliminate border effect, plants for a length of 20 cm at each end of the plot were discarded.

The following characters were measured in the yield trials: grain yield, yield components, awn length, head length, flag leaf width, flag leaf length and plant height. The number of heads per plot was calculated from an average of two samples of the number of heads per meter. The number of kernels per head was an average value of 10 heads counted in each plot. The 1000-kernel weight was estimated from three samples of 100-kernel weights. Awn length was measured from the top of spike to the awn tip. Plant height was measured from ground level to the base of the spike. Flag leaf area was estimated by flag leaf width x flag leaf length x 0.67, as suggested by Fowler and Rasmusson (1969).

Although adequate germination had been indicated in a test carried out before seeding, poor emergence percentage occurred in F_6 populations in 1973. Thus, these data were not included in any analyses in this study. Seeds in 1974 trials were obtained from the test plots at Macdonald College of 1973. No populations x years interaction, or populations x environmental interaction was observed in most of the characters studied. Thus, populations of 1974 were considered as previous generations (F_6, F_{10} and F_{15}) instead of their actual generation (F_7, F_{11} and F_{16}) in the combined analysis.

In the statistical analysis, these tests were analyzed as a randomized complete block design, excluding the standard cultivars and the parental cultivars. The population sum of squares in the analysis of variance was partitioned into between patterns and within patterns sum of squares. Both between patterns and within patterns mean squares were tested against the pooled error mean square, but the between patterns mean square was tested against the within patterns mean square if the latter was heterogeneous. Generation means were compared by a t-test.

The data were also analyzed by multivariate analysis of variance and stepwise regression.

F. Selection trial

Selection for desirable head type had been made in the F_{16} propagated plots at La Pocatière at two different dates of maturity in 1973. These two dates differed by one week. Selected heads were sent to California for multiplication in the winter of 1973-74.

As a result, 345 lines were obtained and were tested at Macdonald College. Because of the limited amount of seed available, only two replicates were used, with a randomized complete block design. Each line was grown in a single-row plot alternated with a single row of spring wheat. Plot size was about 0.2 x 3.2 m. Seeding rate was 50 seeds per meter of row length. At harvest, 20 cm at each end of the plot was discarded. Heading date was recorded as 50 per cent of the heads emerged from the boot. About 50 per cent of the heads with yellow awns in the plot was taken as the date of maturity.

In the analysis of variance, the lines sum of squares was partitioned to the following sum of squares: populations, selection dates, populations x selection dates, and lines within population x selection dates. The tests of significance for populations, selection dates and their interaction mean square were made against the lines within populations x selection dates mean square, if the latter was significant. Otherwise, as with the lines within populations x selection dates mean square, they were tested by the experimental error mean square.

IV. RESULTS AND DISCUSSION

A. Segregation studies

1. Awn type

Most investigators have reported that the difference between rough and smooth awns in barley is determined by a single gene, with rough awns dominant. This gene, located on chromosome V, has been designated Rr by Robertson et al. (1947). Table 5 gives the observed values and chi-square values for segregation of this character in the F_{15} populations. All of these populations deviate significantly from the expected phenotypic ratio, with the rough-awned type predominating.

Remnant heads were obtained in some populations of F_6 and F_{10} generations. Also, four F_{10} populations were reseeded at Macdonald College. As indicated in Appendix Table 1, only three out of 16 F_6 populations were significantly different from the expected phenotypic ratio. The reason for these three populations showing significant deviation is not known; it may be due to randomness or due to their being subject to greater pressures of natural selection in their growing environments. Appendix Tables 2 and 3 show that deviations from the expected phenotypic ratio appear in all the F_{10} populations. When the chi-square values in F_6, F_{10} and F_{15} generations are compared, they become larger in the

TABLE 5. Observed values and chi-square values for segregation of rough- and smooth-awned types in F_{15} barley populations

Pattern	Population	Rough	Smooth	X^2-value
I	PMPMPMPMPMPMPM †	560	438	14.6703**
III	3M3P3M3P2M *	602	398	41.2090**
II	2M2P2M2P2M2P2M	603	396	42.4784**
VIII	8M6P	293	191	21.0764**
V	5P5M4P	412	230	51.0295**
0	14P	340	177	50.7620**
VI	6P6M2P	407	197	72.3195**
IV	4P4M4P2M	684	314	136.4338**
VI	6M6P2M	694	302	153.4949**
II	2P2M2P2M2P2M2P	381	150	99.6233**
III	3P3M3P3M2P	420	164	111.3441**
V	5M5P4M	720	280	192.7210**
0	14M	735	265	219.9610**
VIII	8P6M	766	231	286.0140**
I	MPMPMPMPMPMPMP	450	130	175.4500**
IV	4M4P4M2P	425	118	172.4419**
VII	7P7M	791	209	337.5610**
	Total	9283	4190	1924.4759**
	Expected phenotypic ratio	1	1	

**Significant deviation from the expected phenotypic ratio at the 0.01 level.

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

* The number represents the years grown continuously at a location.

later generations. This indicates that populations increasingly shifted away from the expected phenotypic ratio in advancing generations.

The results suggest that natural selection selects in favor of the rough-awned type. This was also reported by several workers (Middleton and Chapman 1941; Suneson and Stevens 1953; Jain and Allard 1960; Suneson and Ramage 1962). However, the factors that provide competitive advantage for the rough-awned type are not clearly known. Harlan _et_ _al_. (1940) and Middleton and Chapman (1941) reported that the rough-awned type was associated with higher yield. Suneson and Ramage (1962) found that smooth-awned types tended to produce heavier but fewer grains. Studies on correlations between awn type and number of kernels per head as well as kernel size were carried out. The results indicate that the rough-awned type produces more kernels per head and its kernel size is at least equal to if not heavier than that of the smooth-awned type (Appendix Tables 4 and 5).

Harlan _et_ _al_. (1940) gave an explanation for the association between the rough-awned type and more kernels per head. They pointed out that floret sterility was much more common in the smooth-awned type. They further speculated that low temperature seemed to affect the smooth-awned type more than it did the rough ones. The lemmas and paletas of smooth-awned barley usually were not as firmly cemented to the caryopsis as in the case of the rough-awned ones. Almost without exception stigma hairs disappeared about in the same proportion to the disappearance of teeth from the awns. This doubtless was a factor in sterility.

The analysis of variance for the percentage of smooth-awned types in the F_{15} populations indicates that there is no significant variation among the alternated patterns (Table 6). This suggests that the alternating segregating population procedure has no major effect on awn type.

TABLE 6. The analysis of variance for the percentage of smooth-awned types in F_{15} barley populations

Source	d.f.	Mean square
Between patterns	7	16.4775 NS
Within patterns	9	75.5030
I	1	230.4804
II	1	64.8660
III	1	68.6792
IV	1	47.3364
V	1	30.5762
VI	1	2.6220
VII	2	102.5452
O	1	29.8764

NS - non-significant at the 0.05 level

2. Aleurone color

Aleurone color in barley is useful to distinguish one cultivar from another and may serve as a hallmark of quality, viz., Canadian malting barley is commonly blue. Myler and Stanford (1942) found that complementary genes conditioned the development of blue color. The blue aleurone condition occurs when complementary dominant genes Bl and Bl2 are present in the genotype. Yellow aleurone occurs when either gene is homozygous recessive. Bl and Bl2 are located on chromosomes IV and I, respectively.

The genotype of the yellow aleurone parent, Star, is not known. If there is only one homozygous recessive gene in Star, the results show that all these populations differ from the expected phenotypic ratio, and they all shifted toward the yellow aleurone color (Table 7). On the other hand, if both genes were homozygous recessive, the population grown continuously at Macdonald College includes more blue aleurone than expected. Yellow aleurone was favored in the one grown continuously at La Pocatière, however, and most of the alternated populations shifted toward the yellow aleurone color. In general, the blue aleurone type was eliminated from most of the populations. Thus, since Canadian malting cultivars are desired to have a blue aleurone, if segregating populations in a malting barley breeding program are carried in bulk, attention should be paid to this phenomenon.

TABLE 7. Observed values and chi-square values for segregation of blue and yellow aleurone color in F_{15} barley populations

Pattern	Population	Blue	Yellow	X^2-value[a]	X^2-value[b]
O	14M ††	465	536	4.8951 *	244.5717**
V	5M5P4M	428	564	18.4090**	173.2271**
VI	6M6P2M	362	631	72.3303**	68.8851**
I	PMPMPMPMPMPMPM †	293	690	15.5279**	11.8579**
O	14P	114	457	204.8406**	7.4541**
V	5P5M4P	118	607	328.4744**	28.9659**
IV	4P4M4P2M	140	859	516.0400**	63.7200**
II	2P2M2P2M2P2M2P	71	525	344.3104**	53.7472**
VII	8P6M	89	905	668.2344**	135.6458**
VI	6P6M2P	56	570	420.3977**	85.1970**
III	3P3M3P3M2P	56	582	432.0141**	88.6854**
VII	7P7M	87	921	688.3819**	143.1759**
II	2M2P2M2P2M2P2M	70	928	735.9208**	171.2277**
I	MPMPMPMPMPMPMP	40	583	471.5313**	113.7084**
VII	8M6P	27	562	457.7142**	129.8477**
III	3M3P3M3P2M	46	952	820.6663**	220.2217**
IV	4M4P4M2P	21	587	525.0411**	115.5049**
	Total	2483	11459	5777.5516**	384.0688**
	Expected phenotypic ratio			1:1	1:3

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

a Chi-square value comparing the observed values with the expected ratio, 1:1.

b Chi-square value comparing the observed values with the expected ratio, 1:3.

* Significant deviation from the expected ratio at the 0.05 level.

** Significant deviation from the expected ratio at the 0.01 level.

It should be noted here that the classification of aleurone character was done visually; no chemical tests were made. Thus, errors in classification could have occurred. Even so, the discrepancy of these two sorts was so wide (in some cases the blue aleurone was almost eliminated) that even if chemical tests had been used, results would have been very similar.

Studies on composite populations have revealed that blue increased in some populations whereas yellow increased in others (Bal et al. 1959; Jain and Allard 1960; Jain and Suneson 1964). Inconclusive results were obtained by Dubbs (1958) from bulk hybrids and mixtures of isogenic lines. Harlan et al. (1940) and Qualset and Schaller (1966) showed that only small differences exist between blue and yellow types in terms of yield and its components. Aleurone color appears to have no association with awn type (see Appendix Table 6). Thus, it is likely that the differences observed in these studies are due to other genes affecting fitness and other quantitative traits linked with the aleurone color loci.

Since the percentage of blue aleurone types ranged from 3.45 to 46.45, arcsin transformed data were used in the analysis of variance (Snedecor and Cochran 1967). Table 8 shows that there were no differences among the alternated patterns. This indicates that the alternating procedure has little influence on the survival of plants having a particular aleurone color, as far as these two locations are concerned.

TABLE 8. The analysis of variance for the arcsin transformed percentages of blue aleurone types in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	131.6405 NS
Within patterns	9	83.2225
I	1	170.0168
II	1	9.2020
III	1	11.8584
IV	1	62.6080
V	1	128.2642
VI	1	196.2180
VII	2	7.9314
O	1	134.9724

NS - non-significant at the 0.05 level

3. Rachilla hairs

Long-haired rachilla is dominant over short-haired rachilla, and a number of investigators have found the difference to be determined by a single gene pair located on chromosome V (Smith 1951). Deviations from the expected phenotypic ratio were found to be significant in all populations except two (Table 9). The values of chi-square are relatively small when compared with those values for awn type and aleurone color. Thus, it appears that the pressure of natural selection on this character was not as strong as it was on awn type and aleurone color. Hence, changes in genotypic composition were rather slow.

In most populations, natural selection seemed to favor short-haired rachilla types. Population shifts toward short rachilla hairs were also reported by Bal _et al_. (1959). However, it is hard to believe that short-haired rachilla has more adaptive value than its other allele unless it is linked with other loci. It was not unexpected that rachilla hairs would be associated with awn type (Appendix Table 7). These two loci are separated by about 30 crossover units in chromosome V (Bal _et al_. 1959). Rachilla hairs probably are not related to aleurone color (Appendix Table 8).

Table 10 gives the results of analysis of variance for the percentage of short-haired rachillas in the F_{15} populations. There is no significant variation among alternated patterns. This suggests that the segregation of this character did not differ under the environmental conditions of this study.

TABLE 9. Observed values and chi-square values for segregation of long and short rachilla hairs in F_{15} barley populations

Pattern	Population	Long	Short	X^2-value
II	2M2P2M2P2M2P2M ††	518	480	1.3717
VII	8M6P	275	314	2.4516
V	5P5M4P	331	394	5.3020 *
I	MPMPMPMPMPMPMP †	281	342	5.7784 *
III	3P3M3P3M2P	277	361	10.7978**
II	2P2M2P2M2P2M2P	257	339	11.0083**
III	3M3P3M3P2M	427	569	19.9608**
I	PMPMPMPMPMPMPM	399	578	32.4298**
VI	6P6M2P	254	377	23.5879**
IV	4M4P4M2P	249	386	29.1275**
V	5M5P4M-	387	605	47.4687**
IV	4P4M4P2M	388	611	49.6814**
VII	7P7M	386	622	54.7867**
O	14P	211	360	38.3607**
VI	6M6P2M	353	641	82.8661**
O	14M	340	661	102.2977**
VII	8P6M	332	658	106.6919**
	Total	5665	8298	496.1271**
	Expected phenotypic ratio	1	1	

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected phenotypic ratio at the 0.05 level.

** Significant deviation from the expected phenotypic ratio at the 0.01 level.

TABLE 10. The analysis of variance for the percentage of short-haired rachilla types in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	28.6458 NS
Within patterns	9	19.3649
I	1	9.1164
II	1	38.5442
III	1	19.2623
IV	1	0.0722
V	1	22.0448
VI	1	11.2338
VII	2	44.3287
O	1	4.4700

NS Non-significant at the 0.05 level.

4. Spike density

Spike density was determined by measuring five rachis internodes in the middle of each spike. There was no significant variation in the means of spike density among the alternated patterns (Table 11). However, when the appropriate populations were pooled to obtain the variances of alternated patterns, the variance of pattern 0 was found to be smaller than that of the other patterns, except for pattern VII which had the same size of variance (Table 12). A very large variance was observed in pattern II. This is due to the relative contrast in the frequency distributions for spike density of the two populations (Figure 2). All of these frequency distributions are apparently bimodal. The frequency distribution of the population grown continuously at La Pocatière (pattern 0) shows that the lax spike type has been almost eliminated. This indicates that natural selection at this location selected against the lax spike type. However, two peaks occur in the population grown continuously at Macdonald College, and the frequency of the dense spike type is slightly less than that of the lax spike type. Thus, it appears that natural selection at Macdonald College does not favor either spike type. Figure 2 also indicates that the frequency distribution of the populations covers a wider range than that of either parental varieties.

TABLE 11. The analysis of variance for spike density in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	0.0556 NS
Within patterns	9	0.8969
I	1	0.8050
II	1	2.1121
III	1	1.3751
IV	1	1.6311
V	1	0.4227
VI	1	0.6287
VII	2	0.4467
O	1	0.2044

NS Non-significant at the 0.05 level.

TABLE 12. Variances for spike density of the alternated patterns in F_{15} barley populations

Pattern	Sample size	Variance
I	1602	6.1292
II	1593	13.5533
III	1634	5.4369
IV	1627	6.4316
V	1711	6.3003
VI	1626	5.6663
VII	2582	4.9430
O	1572	4.9546

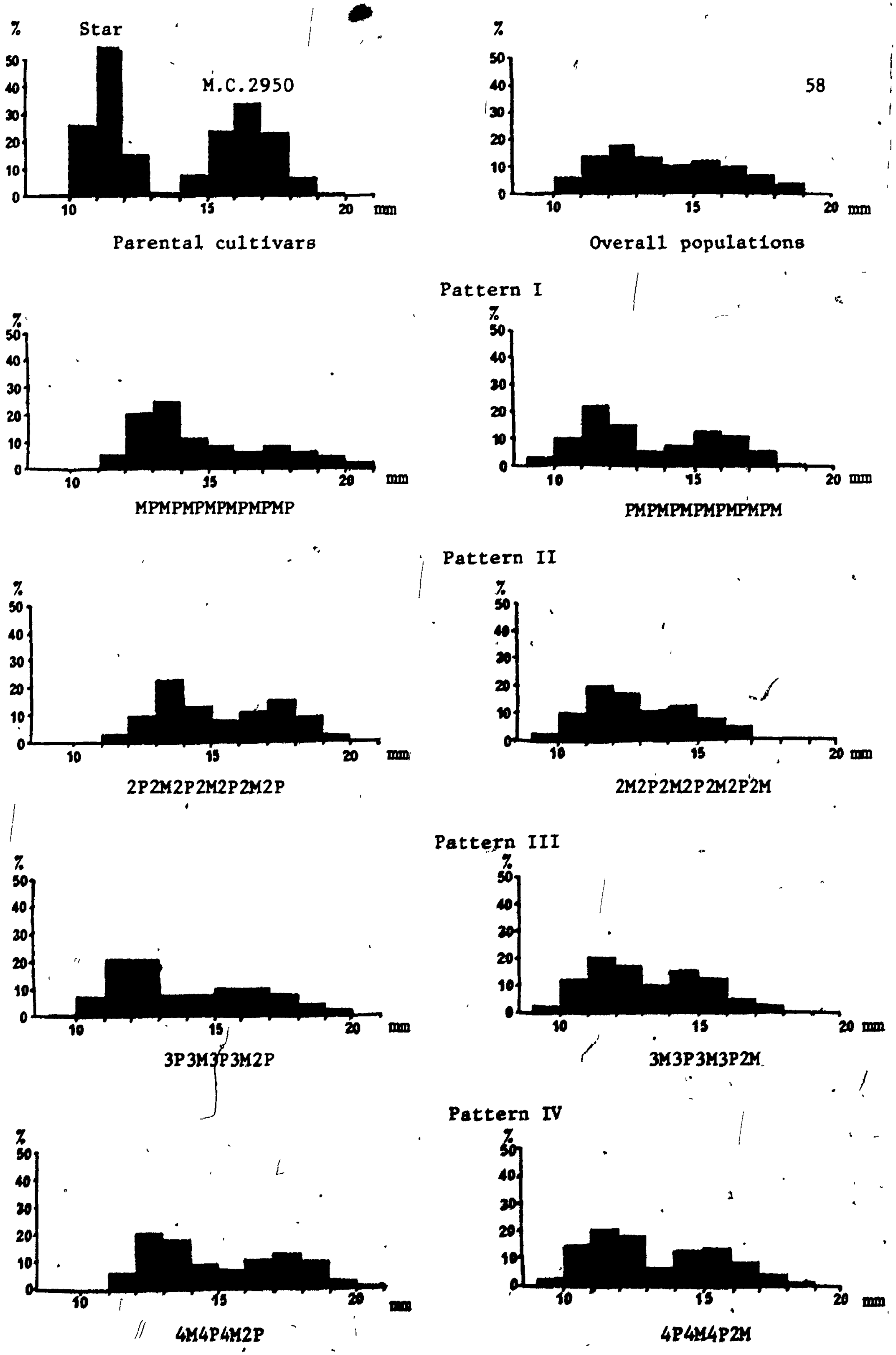
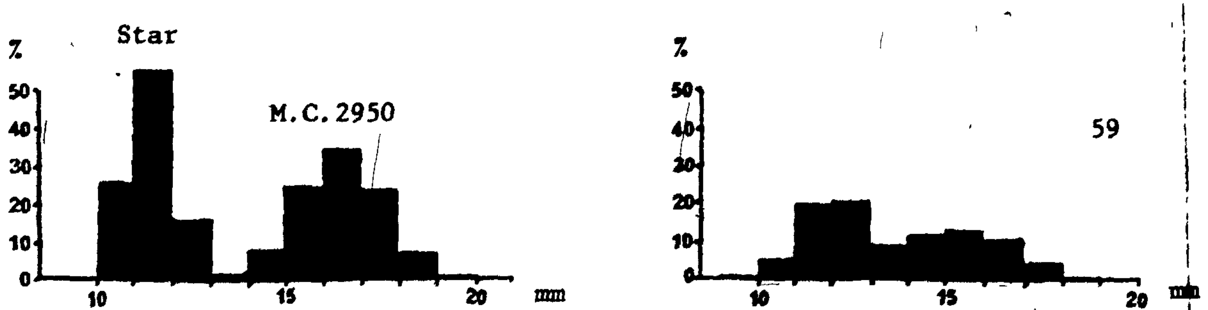


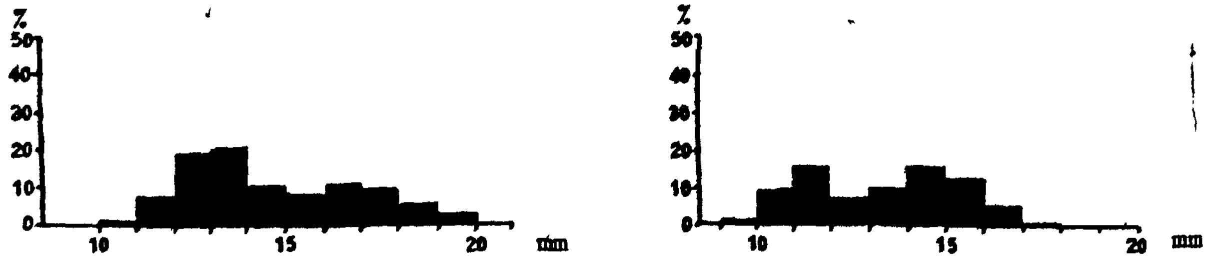
Figure 2. The frequency distributions of spike density in F_{15} barley populations.



Parental cultivars

7P7M

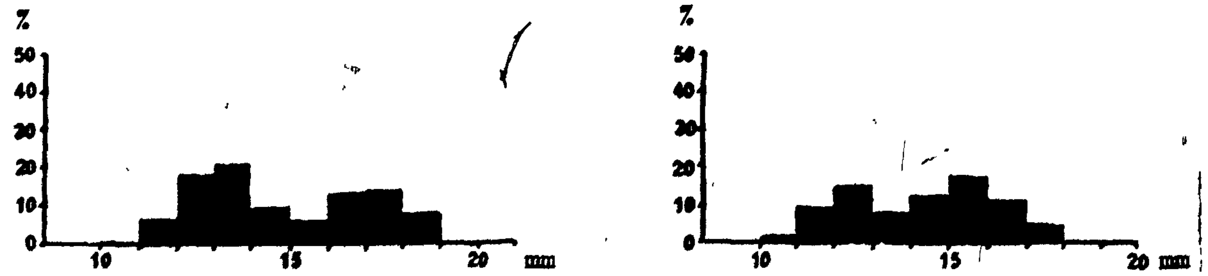
Pattern V



5P5M4P

5M5P4M

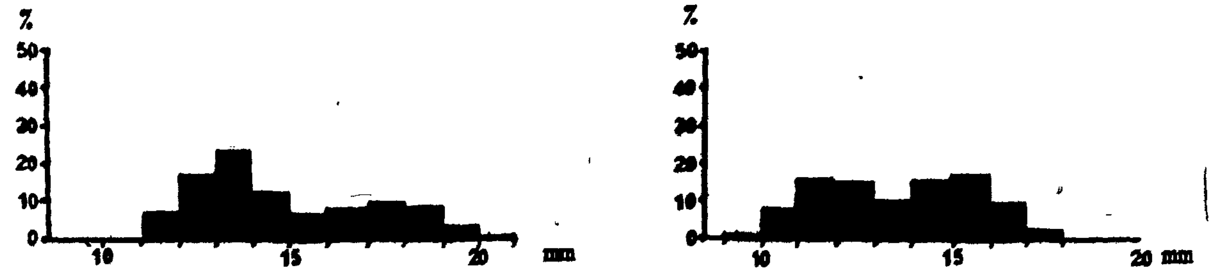
Pattern VI



6P6M2P

6M6P2M

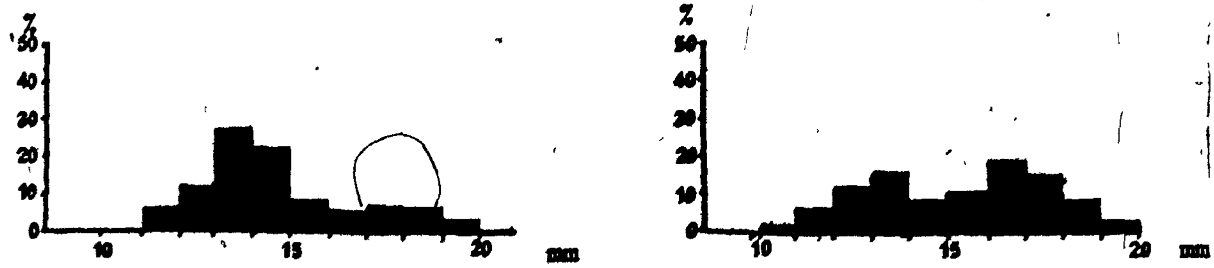
Pattern VII



8M6P

8P6M

Pattern O



14P

14M

Figure 2 (continued)

5. Hairy rachis

Inheritance studies on this character are very limited. Fung (1947) reported complete linkage between a factor for rachis pubescence and the main gene for rough awns. A strong correlation between this character and awn type was also observed in this study. Thus, a single gene hypothesis is assumed for this character.

Populations apparently shifted toward hairy rachis types (Table 13). It is believed that this shift is associated with the rough-awned type. Table 14 shows no significant variation among the alternated patterns.

It was noted that those spikes with short hairs on the glume also had short-haired rachillas and short-haired rachis edges. On the other hand, all those with long hairs on the glume had long-haired rachillas and long-haired rachis edges, with only a very few exceptions.

6. Collar type

Since the number of genes involved in this character is not known, the observed numbers of different collar types for the F_{15} populations only are listed in Table 15 and no chi-square test was carried out. A lower proportion of open-collar types appeared in most of these populations. There is an interesting feature: the nine populations grown at Macdonald College in the F_{15} generation contained more open-collar types than those grown at La Pocatière.

TABLE 13. Observed values and chi-square values for segregation of hairy and non-hairy rachis edges in F_{15} barley populations

Pattern	Population	Hairy	Non-hairy	X^2-value
I	PMPMPMPMPMPMPM †	551	428	15.2032**
III	3M3P3M3P2M ††	603	353	64.8546**
II	2M2P2M2P2M2P2M	604	388	46.5977**
VII	8M6P	283	194	16.2348**
V	5P5M4P	412	215	61.2695**
0	14P	336	144	76.0020**
VI	6P6M2P	380	191	61.8984**
IV	4P4M4P2M	680	311	136.6538**
VI	6M6P2M	698	292	165.6818**
II	2P2M2P2M2P2M2P	359	141	94.1780**
III	3P3M3P3M2P	413	153	118.5176**
V	5M5P4M	730	262	219.8477**
0	14M	761	241	268.8233**
VII	8P6M	768	216	308.5376**
I	MPMPMPMPMPMPMP	440	117	186.1472**
IV	4M4P4M2P	396	109	161.9722**
VII	7P7M	792	210	336.8872**
	Total	9206	3965	2084.7012**
	Expected phenotypic ratio	1	1	

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

** Significant deviation from the expected phenotypic ratio at the 0.01 level.

TABLE 14. The analysis of variance for the percentage of non-hairy rachis types in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	15.0781 NS
Within patterns	9	79.4224
I	1	257.8720
II	1	59.5140
III	1	48.9060
IV	1	48.0200
V	1	31.0472
VI	1	7.8408
VII	2	121.9504
0	1	17.7012

NS Non-significant at the 0.05 level.

TABLE 15. The observed number of collar types (open vs. V-shaped) in F_{15} barley populations

Pattern	Population	Open	V-shaped
VII	7P7M ††	452	552
I	PMPMPMPMPMPMPM †	435	539
III	3M3P3M3P2M	431	559
IV	4P4M4P2M	414	579
II	2M2P2M2P2M2P2M	412	585
V	5M5P4M	403	582
0	14M	399	592
VII	8P6M	394	588
VI	6M6P2M	384	603
II	2P2M2P2M2P2M2P	200	332
VII	8M6P	196	349
IV	4M4P4M2P	193	399
V	5P5M4P	219	461
I	MPMPMPMPMPMPMP	158	376
III	3P3M3P3M2P	150	439
0	14P	122	416
VI	6P6M2P	121	414

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

TABLE 16. The analysis of variance for the percentage of open collar types in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	26.6950 NS
Within patterns	9	76.8437
I	1	113.7032
II	1	6.9564
III	1	163.2624
IV	1	41.3140
V	1	37.9320
VI	1	132.6820
VII	2	20.5200
O	1	154.7040

NS Non-significant at the 0.05 level.

It seems that this character is highly influenced by growing conditions. Singh and Johnson (1969) reported that differences in collar types were observed among tillers of the same plant. Thus, it appears that this character is not reliable for cultivar identification. Variation among alternated patterns was not significant (Table 16).

7. Shape of basal rachis internode

Table 17 lists the observed number of spikes showing different shapes of basal rachis internode. No chi-square test was carried out because the inheritance of this character is not known. Straight internode predominated in most of the populations. No significant variation in rachis internode shapes occurred in the patterns (Table 18).

The mean squares of the alternated patterns were compared in their magnitudes and their order among the plant types described in the foregoing sections. However, no relationship for these mean squares between any two plant types was found, except between the percentage of smooth-awned and non-hairy rachis types. This suggests that the latter two plant characters are closely linked.

TABLE 17. The observed number of spikes showing different shapes of basal rachis internodes (closed vs. straight) in F_{15} barley populations

Pattern	Population	Closed	Straight
I	PMPMPMPMPMPMPM †	486	485
VI	6M6P2M ††	486	501
0	14M	437	512
V	5M5P4M	417	567
IV	4P4M4P2M	402	590
III	3M3P3M3P2M	368	621
II	2M2P2M2P2M2P2M	347	650
VII	7P7M	288	715
V	5P5M4P	192	500
II	2P2M2P2M2P2M2P	146	387
VII	8P6M	251	730
III	3P3M3P3M2P	141	453
I	MPMPMPMPMPMPMP	129	416
0	14P	121	429
IV	4M4P4M2P	131	480
VII	8M6P	118	437
VI	6P6M2P	115	428

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† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

TABLE 18. The analysis of variance for the percentage of closed basal rachis internodes in F_{15} barley populations

Source of variation	d.f.	Mean square
Between patterns	7	34.6105 NS
Within patterns	9	162.9269
I	1	348.2160
II	1	27.4540
III	1	90.7204
IV	1	182.0232
V	1	107.0184
VI	1	393.9624
VII	2	13.9936
O	1	288.9608

NS - non-significant at the 0.05 level.

B. Yield trials

1. Trait means

The results for all the characters studied in these trials in F_6, F_{10} and F_{15} populations are simplified in Tables 19, 20 and 21, respectively. Details are provided in the following section and in the appendix.

i. Grain yield

Results of grain yield for the F_6, F_{10} and F_{15} populations are shown in Tables 22, 23 and 24, respectively. The populations were not significantly different in grain yield in any of the generations. When the population sum of square was partitioned to between (alternated) patterns and within (alternated) patterns sum of square, the mean squares for the latter two were not significant, with the exception of pattern IV in the F_6. Therefore, grain yield was not affected by alternating segregating populations between the two locations. This is partly because of no differential selection for grain yield at these locations, as indicated by a non-significant variation between the unalternated populations in pattern 0. It may also be due to the fact that natural selection cannot bring about any significant changes in grain yield in a single hybrid population. This is demonstrated by the similarity of the three generation means.

Though the magnitude of coefficient of variation was reduced by the F_{15} generation, nevertheless it was still high. Since 20 or more

TABLE 19. A simplified table showing results for several agronomic characters of F_6 barley populations

Source of variation	Mean squares									
	Grain yield	No. of beads per plot	No. of kernels per head	1000-kernel weight	Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area	Plant-height
Populations	-	-	-	-	-	-	-	-	-	-
Between patterns	-	-	-	**	-	-	-	-	-	-
Within patterns	-	-	-	-	-	-	-	-	-	-
I	-	-	-	-	-	-	-	-	-	-
II	-	-	-	-	-	-	**	-	-	-
III	-	-	-	*	-	-	-	-	-	-
IV	*	-	-	-	*	-	-	-	-	-
V	-	-	-	-	-	-	-	-	-	-
VI	-	-	-	-	-	-	-	-	-	-
VII	-	-	-	-	-	-	-	-	-	-
VIII	-	-	-	-	-	-	-	-	-	-
IX	-	-	-	-	-	-	-	-	-	-
X	-	-	-	-	-	-	-	-	-	-
XI	-	-	-	-	-	-	-	-	-	-
0	-	-	-	-	-	-	*	-	-	-

* Significant at the 0.05 level when tested against pooled error mean square

** Significant at the 0.01 level when tested against pooled error mean square

\- Non-significant at the 0.05 level

TABLE 20. A simplified table showing results for several agronomic characters of F_{10} barley populations

Source of variation	Mean squares									
	Grain yield	No. of heads per plot	No. of kernels per head	1000-kernel weight	Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area	Plant height
Population	–	–	–	–	–	–	–	–	–	–
Between patterns	–	–	–	–	–	–	–	–	–	–
Within patterns	–	–	–	–	–	–	–	–	–	–
I	–	–	–	–	–	–	–	–	–	–
II	–	–	–	–	–	–	–	–	–	–
III	–	–	–	–	–	–	–	–	–	–
IV	–	*	–	–	–	–	–	–	–	–
V	–	–	–	–	–	–	–	–	–	–
VI	–	–	–	–	–	–	–	–	–	–
VII	–	–	–	–	–	–	–	–	–	–
O	–	–	*	–	–	–	–	–	–	–

* Significant at the 0.05 level when tested against pooled error mean square

– Non-significant at the 0.05 level

TABLE 21. A simplified table showing results for several agronomic characters of F_{15} barley populations

Source of variation	Mean squares									
	Grain yield	No. of heads per plot	No. of kernels per head	1000-kernel weight	Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area	Plant height
Populations	-	-	**	-	**	**	**	*	*	-
Between patterns	-	-	-	-	-	-	-	-	-	-
Within patterns	-	-	*	-	**	**	*	*	*	-
I	-	-	-	-	**	-	-	*	-	-
II	-	-	-	-	-	-	-	-	-	-
III	-	-	**	-	-	*	-	*	-	-
IV	-	-	-	-	**	*	-	-	-	-
V	-	-	-	-	-	-	-	-	-	-
VI	-	-	-	-	-	*	*	*	*	-
VII	-	-	-	-	-	*	**	-	*	-
O	-	*	-	-	*	**	**	-	*	-

* Significant at the 0.05 level when tested against pooled error mean square

** Significant at the 0.01 level when tested against pooled error mean square

\- Non-significant at the 0.05 level

TABLE 22. The results of partitioning the populations sum of squares for grain yield and its components in F_6 barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Populations	26	6714.26	5711.49	14.7252	1.6634
Between patterns	11	8737.99	5215.50	22.0962	2.6262**
Within patterns	15	5230.26	6075.22	9.3197	0.9550
I	1	760.50	12736.08	0.0800	1.4450
II	1	10296.13	79.38	23.8050	0.2112
III	1	3403.13	13073.45	5.6112	6.3012*
IV	2	16742.25*	2585.73	6.4658	0.6458
V	1	10.13	1607.45	16.8200	0.5000
VI	1	8320.50	16689.65	0.0612	0.1512
VII	2	1944.33	3220.77	7.1175	0.1408
VIII	1	2850.13	9604.98	0.4512	0.4050
IX	1	18.00	10195.92	0.0800	1.7112
X	2	6715.08	5509.56	19.2325	0.0625
XI	1	338.00	3018.65	19.8450	0.0012
O	1	1653.13	1490.58	7.4112	1.9012
Pooled error	52	5503.72	7991.50	21.2328	1.1513
Generation mean		438.81	453.33	47.0833	32.2583
C.V.		16.91%	19.71%	9.78%	3.32%

* Significant at the 0.05 level

** Significant at the 0.01 level

TABLE 23. The results of partitioning the populations sum of squares for grain yield and its components in F_{10} barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Populations	16	2036.82	4966.96	11.9752	1.6379
Between patterns	7	1330.90	5858.78	9.2387	1.7841
Within patterns	9	2582.08	4273.32	14.1040	1.5239
I	1	2709.37	0.00	2.7337	2.2450
II	1	165.37	1422.96	0.2204	0.8623
III	1	2321.45	73.50	18.2011	0.0352
IV	1	3015.05	25977.84*	21.6600	0.0210
V	1	1162.05	2143.26	0.0104	4.1493
VI	1	35.04	1693.44	11.3437	0.1649
VII	2	3378.86	3441.76	2.7240	2.9312
O	1	7072.69	265.34	70.0430*	0.3750
Pooled error	128	5091.73	5177.68	14.9914	1.5532
Generation mean		444.97	498.26	45.1471	30.1636
C.V.		16.04%	14.44%	8.57%	4.13%

* Significant at the 0.05 level

TABLE 24. The results of partitioning the populations sum of squares for grain yield and its components in F_{15} barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Populations	16	4939.09	6610.00	31.0519**	1.6232
Between patterns	7	5912.08	5106.02	21.2612	0.9981
Within patterns	9	4182.32	7779.76	38.6671*	2.1177
I	1	5828.14	3398.64	30.3744	8.7121
II	1	8362.70	36.02	51.0428	2.2201
III	1	8251.03	11119.82	132.0722**	1.3344
IV	1	737.04	800.42	55.2090	4.0679
V	1	18.37	3888.38	29.9057	0.1717
VI	1	1162.05	1176.00	12.4709	1.0837
VII	2	6288.69	1294.09	11.8539	0.7296
O	1	704.16	20010.38*	13.2028	0.0104
Pooled error	128	3123.18	4942.06	16.6045	1.5167
Generation mean		442.16	465.05	44.4608	30.9692
C.V.		12.16%	15.11%	9.16%	3.97%

* Significant at the 0.05 level

** Significant at the 0.01 level

populations were entered in the trials, significant amount of variation within replicates might be present. The coefficient of variation value might be further reduced if the data were analyzed as a rectangular lattice design. On the other hand, each plot was seeded with a sample of bulk seeds. Thus, genotype-to-genotype or sample variation might also be one of the factors of obtaining high coefficient of variation. Variation might be minimized if several genotypes were used instead of bulk plots in the trials.

ii. Number of heads per plot

Assuming uniform germination and seedling survival among populations, changes in the number of heads per plot are dependent upon tillering, which in turn is influenced by weather conditions. There was no significant variation among populations in number of heads per plot in F_6. Neither were differences observed among alternated patterns nor within alternated patterns. The two pattern IV populations in F_{10}, however, did differ in number of heads per plot (Table 23). Even though these two populations originated from the pattern XI populations of F_6, no difference was found between the two original (F_6) populations. No difference was found in their advanced (F_{15}) generation either (Table 24). Thus, it appears that the difference between these two populations in F_{10} arose from random or other unexplainable factors. In F_{15}, the two populations grown continuously at each location (pattern O) differed in this character due to more tillers in population 14M (Table 24).

However, no trend was evident for these populations in the earlier generations. These results indicate that a population grown continuously for as long as nine generations at Macdonald College did not differ in number of tillers from that grown continuously at the other location. Whether or not propagated five more years at Macdonald College could significantly increase production of more tillers was not known. The reason why population 14M had more tillers is not known. However, the alternating procedure seems to have had no significant effect on this yield component.

The generation mean for this character increased from F_6 to F_{10}, but decreased again by the F_{15} generation. This up and down pattern in generation mean also occurred in head length, flag leaf width, length or area. The reason for this is not known. It is probably due to one or a few of the F_{15} populations being highly affected by previous environmental conditions for these characters. Coefficients of variation were high in this character. This is probably because of the fact that this character was highly influenced by the soil variation. Or it may be due to the fact that seeding was not uniform within each row, and two samples taken for this character within each plot were not precisely estimated.

iii. Number of kernels per head

Populations differed in the F_{15} generation but not in F_6 or F_{10} (Tables 22, 23 and 24). Variation among the F_{15} populations was not caused by the alternating procedure because there is no difference among patterns. It was caused by a significant difference between the two populations within pattern III. In the F_{10} generation, population 9M had significantly fewer kernels per head than the population grown continuously at La Pocatière. However, no such differences between the two unalternated populations were found in the F_6 or F_{15} generations. Thus, this difference was probably caused by chance. No changes were observed in the generation means. This suggests that continuing in bulk with the hope of improving this character would be unlikely to succeed in a single hybrid population.

iv. 1000-kernel weight

There was no significant variation among the F_6 populations, but differences appeared among alternated patterns (Table 22). A comparison of the means of the alternated patterns in F_6 is given in Table 25. Most of the patterns did not differ in their kernel weight, including the two patterns with the highest alternating frequency and the one with no alternation at all. Thus, it appears that variation among alternated patterns is not associated with the effect of alternation but with other factors. Though differences among alternated patterns for grain yield in the F_6 populations do not reach the 0.05 significance level, a response similar to that for 1000-kernel weight does exist among these patterns in grain yield. No variation was found among populations, between patterns or within patterns for this character in either the F_{10} or F_{15} generations (Tables 23 and 24). This is probably due to the fact

TABLE 25. Means of 1000-kernel weight for the alternated patterns in F_6 barley populations

Pattern	Population	Mean (grams)
V	PPMMP MMPPM †	33.33 a ϕ
VI	PMMPP MPPMM	32.99 a
X	PPPMM PPPMP MMMPP	32.68 ab
O	PPPPP MMMMM	32.34 b
I	PMPMP MPMPM	32.30 b
VII	PMPPP MPMMM MPMMP	32.28 b
IV	PPMPM PPMPP MMPMP	32.21 b
XI	PPPPM MMMMP	32.19 b
IX	PMMMM MPPPP	32.16 b
VIII	PMMMP MPPPM	32.03 b
III*	PMMPM MPPMP	31.51 bc
II	PMPMM MPMPP	31.14 c

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

ϕ Means followed by the same letters are not significantly different at the 0.05 level when tested by least significant difference.

* The populations in this pattern are significantly different at the 0.05 level.

that some of the patterns in F_6 were not included in the advanced generations. This may also be due to natural selection having selected in favor of lighter kernels. Thus, the magnitude of these differences among patterns became smaller and could not be detected. Natural selection favoring lighter kernels is indicated in their generation means. The means of F_6 was higher than that of either F_{10} or F_{15}; however, the latter two were not statistically different. The trend of populations moving toward lighter kernels was also reported by Palmer (1952). Singh and Johnson (1969) observed this trend, but they interpreted it as the result of selecting against two-rowed spikes in their materials.

v. Awn length

Populations differed in awn length only in the F_{15} generation (Tables 26, 27 and 28). However, there was a significant population x environment interaction for this character in the F_{15} generation (Appendix Table 15). Thus, individual analysis for each location in each year was carried out. Populations were not different at each location in 1974, but they were different at each location in 1973. The individual analyses of 1973 data are given in Table 29. There was no variation among alternated patterns at either location. This suggests that the alternating procedure could not bring about any significant changes in awn length at these locations. The generation mean for awn length increased with advancing generation.

TABLE 26. The results of partitioning the populations sum of squares for other agronomic characters in F_6 barley populations

Source of variation	df	Mean square				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Populations	26	0.4817	0.3074	0.0186	0.8620	2.2623
Between patterns	11	0.6417	0.0657	0.0213	0.3321	1.5262
Within patterns	15	0.3642	0.4845	0.0165	1.2503	2.8021
I	1	1.0804	0.1653	0.0012	0.0039	0.1012
II	1	0.0392	0.0210	0.0946**	1.7672	5.1681
III	1	0.1081	0.0741	0.0040	0.2556	1.9800
IV	2	2.4024*	0.3459	0.0300	0.2975	3.0888
V	1	0.0066	0.1922	0.0098	1.1476	3.8781
VI	1	0.1922	0.0450	0.0003	1.7955	1.6471
VII	2	0.3612	1.3426	0.0009	0.6496	0.4047
VIII	1	0.0084	0.0120	0.0040	4.2340	4.6208
IX	1	0.2244	1.0731	0.0050	2.2578	3.6046
X	2	0.1008	0.7549	0.0047	1.9523	2.9680
XI	1	0.0220	0.0666	0.0003	0.1984	0.4656
0	1	0.4560	0.7330	0.0578*	1.2960	7.6440
Pooled error	52	0.3387	0.5003	0.0135	1.0503	2.8054
Generation mean		12.10	6.38	1.24	11.46	9.81
C.V.		4.80%	11.09%	9.37%	8.94%	17.06%

* Significant at the 0.05 level

** Significant at the 0.01 level

TABLE 21. The results of partitioning the populations sum of squares for other agronomic characters in F_{10} barley populations

Source of variation	df	Mean square				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Populations	16	0.2348	0.3040	0.0073	0.6030	1.8118
Between patterns	7	0.1104	0.3773	0.0108	0.9183	3.2112
Within patterns	9	0.4306	0.2468	0.0045	0.3577	0.7234
I	1	0.3198	0.0198	0.0032	0.0693	0.0360
II	1	0.3901	0.2166	0.0121	0.3432	2.5741
III	1	0.0002	0.0246	0.0099	0.3877	1.2133
IV	1	0.0088	0.0259	0.0054	0.3358	1.0690
V	1	0.0681	0.6302	0.0000	0.0705	0.3720
VI	1	0.9720	0.4620	0.0000	0.4348	0.3127
VII	2	0.6084	0.4183	0.0029	0.7657	0.4533
O	1	0.0384	0.0059	0.0048	0.0467	0.0274
Pooled error	128	0.3192	0.1812	0.0121	1.4191	3.7504
Generation mean		12.72	6.68	1.36	13.11	12.33
C.V.		4.44%	6.37%	8.09%	9.09%	15.71%

TABLE 28. The results of partitioning the populations sum of squares for other agronomic characters in F_{15} barley populations

Source of variation	df	Mean square				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Populations	16	0.7598**	0.8769**	0.0230**	1.8720*	5.7263*
Between patterns	7	0.7681	0.9584	0.0180	1.0695	1.4427
Within patterns	9	0.7499**	0.8099**	0.0269*	2.4964*	2.4143*
I	1	2.1600**	0.1768	0.0025	4.6559*	4.5132
II	1	0.0804	0.0025	0.0020	0.0273	0.0010
III	1	0.7455	0.5371*	0.0034	4.2084*	4.6823
IV	1	2.0184**	0.7141*	0.0080	2.7744	5.5966
V	1	0.1218	0.1617	0.0001	0.3953	0.5154
VI	1	0.0028	0.8893*	0.0467*	4.5247*	14.7178*
VII	2	0.2704	0.6523*	0.0667**	2.3165	19.0610*
0	1	1.0796*	3.5030**	0.0459*	3.5657	13.4622*
Pooled error	128	0.1994	0.1331	0.0105	1.0255	2.8786
Generation mean		12.85	6.50	1.33	12.65	11.53
C.V.		3.47%	5.61%	7.69%	8.00%	14.71%

* Significant at the 0.05 level

** Significant at the 0.01 level

TABLE 29. The analysis of variance for awn length in F_{15} barley populations in 1973

Source of variation	d.f.	Mean square	
		Macdonald College	La Pocatière
Replicates	2	0.0560	0.4731
Populations	16	0.3048**	0.6923**
Between patterns	7	1.2497	0.5861
Within patterns	9	0.2747**	0.7740
I	1	0.6209**	2.2693
II	1	0.0352	0.3313
III	1	0.7141**	0.2646
IV	1	0.2521	1.1618*
V	1	0.0037	0.3456
VI	1	0.2128	0.1633
VII	2	0.0194	0.8819*
O	1	0.5953**	0.6667
Experimental error	32	0.0648	0.2191
Overall mean		13.67	12.89
C.V.		1.86%	3.63%

* Significant at the 0.05 level.

** Significant at the 0.01 level.

vi. Head length

There were no differences for head length among populations in either F_6 or F_{10} generations, but considerable variation existed among the F_{15} populations (Tables 26, 27 and 28). This variation was caused by differences between the populations within alternated patterns. It has nothing to do with the alternating frequency between the two locations. No relationship could be established with the five alternated patterns having significant variation in their populations. The generation mean of head length increased from F_6 to F_{10}, but heads of F_{15} were significantly shorter than those of the F_{10} generation.

vii. Flag leaf width

Variation among populations was not observed until the F_{15} generation (Tables 26, 27 and 28). It was not affected by the alternating procedure. The means of flag leaf width for the F_{15} populations of the three patterns having significant variation in this character are presented in Table 30. It appears that natural selection at Macdonald College favors wider flag leaves, or that narrower flag leaves are favored at La Pocatière. This is also true in the two unalternated populations in the F_6 generation, but no difference was found between these two in F_{10}. For the generation mean of this character, it increased from F_6 to F_{10} then decreased in the F_{15} generation.

TABLE 30. Means of flag leaf width (cm) for the F_{15} barley populations in the three alternated patterns having significant variation

Pattern	Population	Mean
VI	6P6M2P ††	1.3100
	6M6P2M	1.3517
VII	7P7M	1.3342
	8P6M	1.4275
	8M6P	1.2800
0	14P	1.3025
	14M	1.3900

†† The number represents the years grown continuously at a location.

viii. Flag leaf length

Tables 26, 27 and 28 show that populations differed in this character only in the F_{15} generation. This, again, was not affected by the alternating procedure. There was a significant variation within the alternated patterns. The generation means indicate that the longest flag leaves occurred in the F_{10}; length decreased by the F_{15} generation.

ix. Flag leaf area

There was a significant variation among populations in F_{15}. This variation was not due to the various kinds of alternated patterns (Tables 26, 27 and 28). The direction of variation in the F_{15} populations of the three patterns having significant variation in flag leaf area was similar to that for flag leaf width. Just like its components, the generation mean of flag leaf area moved up in F_{10} and down in the F_{15} generation.

x. Plant height

Plant height was recorded only in 1974. The results are presented in Table 31. Populations did not differ in the three generations, or in the alternated patterns. However, the generation mean increased and the coefficient of variation decreased with advancing generation. This indicates that short-statured plants were eliminated from these populations and that changes in plant height were independent of location. Elimination of short-statured

TABLE 31. The results of partitioning the populations sum of squares for plant height

Source of variation	F_6		F_{10}		F_{15}	
	d.f.	M.S.	d.f.	M.S.	d.f.	M.S.
Populations	26	23.2130	16	11.5889	16	6.6218
Between patterns	11	18.6988	7	10.1178	7	8.2051
Within patterns	15	26.5234	9	12.7572	9	5.3902
I	1	61.0512	1	3.3599	1	0.7500
II	1	7.8012	1	0.0018	1	0.5635
III	1	33.0078	1	24.7968	1	15.5268
IV	2	18.2189	1	28.3668	1	0.7751
V	1	16.8200	1	1.7634	1	1.1409
VI	1	21.2878	1	5.7405	1	12.1010
VII	2	27.8958	2	4.0172	2	3.3461
VIII	1	88.5115				
IX	1	27.1953				
X	2	24.6414				
XI	1	00.1128				
O	1	0.5512	1	42.7518	1	10.9626
Pooled error	52	33.4567	64	20.4421	64	12.8149
Generation mean		85.5431		91.7848		92.2929
C.V.		6.76%		4.92%		3.87%

plants has also been reported by other workers (Jennings and de Jesus 1968; Jennings and Herrera 1968; Khalifa and Qualset 1974, 1975).

2. Multivariate analysis of variance

The above analyses show that significant variations among populations for several characters occurred in the F_{15} generation. An attempt was made to generalize these differences among populations by canonical analysis. With this multivariate technique, several independent variables can be condensed into a single judgement. It can assist in the grouping of material into broadly similar or dissimilar units (Whitehouse 1970).

Data from two locations in two years were used in this study. The results of multivariate analysis of variance show that there was no significant variation among populations. This is probably due to the fact that a very large error mean square is present. Thus, it appears that the use of canonical analysis in material of this kind is unlikely to succeed unless the number of replicates is increased or there are homogeneous environments.

3. Stepwise regression analysis

Results of yield trials indicate that even though the F_{15} populations differed in number of kernels per head and other characters, no significant variation among populations occurred in grain yield. Thus, the relationship of grain yield to all other characters was examined.

Data obtained in the three generations were pooled and regression techniques were used. Five current procedures: forward selection, backward elimination, stepwise regression, maximum R^2 improvement and minimum R^2 improvement, were applied, but each procedure gave the same kind of conclusion. This suggests that any one of these procedures is as effective as any other. Among these procedures, stepwise regression has been highly recommended for selecting the "best" regression equation, because it can re-examine at every stage of the regression the variables incorporated into the model in previous stages (Draper and Smith 1966). Thus, results of stepwise regression analyses are reported here.

Table [illegible]2 gives the models with R^2 values. Since flag leaf width and flag leaf area are correlated with flag leaf length, they were not entered in the models. The results indicate that 1000-kernel weight was the plant component most closely related to grain yield; then flag leaf length was the next. Including awn length and head length in the model improved only slightly the R^2 value. The results suggest that flag leaf length, perhaps area, should be considered as one of the major plant components contributing to grain yield.

TABLE 32. Models entered with different variables and their R^2 values

Model number	R^2	Variables in model
1	0.1120	Y, X_3 †
2	0.2359	Y, X_3, X_6
3	0.2752	Y, X_3, X_6, X_2
4	0.3236	Y, X_3, X_6, X_2, X_1
5	0.3341	Y, X_3, X_6, X_2, X_1, X_5
6	0.3396	Y, X_3, X_6, X_2, X_1, X_5, X_4

† Y is grain yield

X_1 is the number of heads per plot

X_2 is the number of kernels per head

X_3 is 1000-kernel weight

X_4 is awn length

X_5 is head length

X_6 is flag leaf length

4. Stability

Stability of the F_{10} and F_{15} populations was evaluated according to the method proposed by Eberhart and Russell (1966). Data obtained in the yield trials at two locations in two years are considered as representing four different environments.

A significant Env (linear) x Pop interaction indicates that there is at least one regression coefficient of a population differing from the others. However, the results show that none of the Env (linear) x Pop interactions for any of the characters examined in any population was significant when tested against the pooled mean square. Pooled deviations were significant only for awn length in the F_{15} population (Table 33).

For pooled deviations in awn length in the F_{15} populations, only two of them deviated significantly from zero. They are populations MPMPMPMPMPMPMP and 5P5M4P. No relationship could be found when comparing these two populations. Thus, it appears that the significant pooled deviations of these two populations arose from chance or other unexplainable factors.

Freeman and Perkins (1971) reported that the environment had often been assessed by the mean of the genotypes grown in it, but found that this method led to statistically invalid regressions in which the sum of squares for the joint regression was the same as the total sum of squares between environments, and not part of it. Two solutions were suggested. One of these was to use one or more

TABLE 33. Mean squares of environments (env) (linear) x populations (pop) interaction and pooled deviations in F_{10} and F_{15} generations of barley

Character	Mean square			
	F_{10}		F_{15}	
	Env x pop	Pooled deviation	Env x pop	Pooled deviation
Grain yield †	2140.55	1205.25	1585.55	1150.83
No. of heads/plot	1238.25	1519.94	1236.51	1256.86
No. of kernels/head	4.3498	5.2909	2.2754	5.3837
1000-kernel weight	0.2253	0.5620	0.3526	0.5904
Awn length	0.0909	0.0708	0.0646	0.1078*
Head length	0.0384	0.0554	0.0475	0.0554
Flag leaf width	0.0017	0.0030	0.0020	0.0042
Flag leaf length	0.4402	0.4494	0.1577	0.2500
Flag leaf area	0.7304	0.9306	0.6178	0.9378

† Degrees of freedom for environments (linear) x pop interaction is 16.

Degrees of freedom for pooled deviations is 34.

* Significant at the 0.05 level.

genotypes that could be regarded as standards to assess the environment. Therefore, the data were further evaluated by using three standard (or parental) cultivars to determine both the environmental effects and the genotype-environment interaction. The results of grain yield in both F_{10} and F_{15} populations are given in Table 34. The same conclusions were reached as before. Thus, it appears that either method of assessing the environment would describe adequately the performance of a population at different locations.

Both Finlay (1970) and Fatunla and Frey (1974) reported that populations shifted toward average stability as far as grain yield was concerned. Results comparing the mean regression coefficients of grain yield in the F_{10} and F_{15} populations show that mean regression coefficients were not different in these two generations. Neither are they significantly different from 1.0. Since the data for earlier generations were not available, it was not possible to confirm any change in stability.

There were no differences in stability parameters for most of the characters in the two populations. This clearly indicates the lack of population x environmental interaction in these populations. It suggests that alternating the segregating populations of a single hybrid between these two locations would not bring about any significant changes in stability.

TABLE 34. Analysis of variance for grain yield in F_{10} and F_{15} barley populations (the environment was assessed by other cultivars)

Source of variation	d.f.	Mean square	
		F_{10}	F_{15}
Populations (P)	16	681.44	1649.06
Environments (env) x P	51	2896.98**	4251.14**
Env (linear)	1	33148.76**	141739.20**
P x env (linear)	16	2286.04	1621.80
Pooled deviations	34	2294.68	1444.61
Pooled error	128	1697.24	1041.06

**Significant at the 0.01 level.

C. Selection trial

1. Grain yield

The analysis for grain yield of lines selected from the F_{16} populations at two different dates of maturity is summarized in Table 35. Significant variations among these lines were mainly due to selection dates and the population x selection date interaction. However, no variation in grain yield is shown among the nine populations. These populations are listed in Table 36. Data from the same nine populations in yield trials were grouped and tested against the pooled error mean square. No significance was found. Thus, it appears that there is a high degree of association between yields in bulks and yields of selections made from them.

High significance in selection dates reveals that the later the date of maturity, the higher the grain yield. This was expected because much more photosynthate is available to fill the kernels of later maturing plants. Not all populations showed the same pattern, however, because a significant interaction was also found. In some of the populations, genotypes selected at the later date did not yield any better than those selected at the early date (Table 36). Thus, it seems that early maturing genotypes could be selected in some of these populations without reducing their yielding ability.

The overall mean yield of this trial was about 260 grams per row. When this is compared with the overall mean of the F_{15}

TABLE 35. Analysis of variance for lines selected from F_{16} barley populations at La Pocatière in 1973 and tested at Macdonald College in 1974

Source of variation	d.f.	Mean squares		
		Grain yield	Heading date	Maturity date
Replicates	1	446889.28**	77.3348**	1.3043
Lines	344	2592.48*	5.7046**	17.4117**
Populations (pop)	8	3568.49	10.4979**	36.7998**
Selection dates (S.D.)	1	45412.09**	623.3258**	2372.9539**
Pop x S.D.	8	5783.35*	4.1482	16.4876
Lines within pop x S.D.	327	2359.58	3.7366**	9.7599**
Experimental error	344	2134.56	0.6604	1.9613
Overall means		259.82	49.09	68.69
C.V.		17.78%	3.69%	4.52%

*Significant at the 0.05 level.

**Significant at the 0.01 level.

TABLE 36. Mean yields of barley lines selected from different F_{16} populations at two different dates

Populations	Selection dates	
	Early	Late
7P7M1P^7††	269.05	256.80
PMPMPMPMPMPMPM †	253.29 a ϕ	270.35 b
2M2P2M2P2M2P2M2P	261.59	263.16
3P3M3P3M3P	267.03	268.45
5P5M5P	245.64 a	263.68 b
8M7P	222.90 a	267.20 b
6P6M3P	247.95 a	274.68 B
4M4P4M3P	258.46	272.75
15P	243.31 a	273.39 b

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College

†† The number represents the years grown continuously at a location.

ϕ Means followed by a different letter in same population are significantly different at 0.05 level when tested by least significant difference.

populations in yield trials, i.e., about 144 grams per row, approximately an 80 per cent increase occurred in the selections of the F_{16} generation. This increase may have been due to the efficiency of selection, but more likely to the competitive advantage of the barley over the adjacent spring wheat rows, the wheat being rather short throughout the growing period. A higher coefficient of variation was inevitable because only two replicates and many entities were included in this trial.

2. Heading ~~date~~

Populations differed significantly in heading date as shown in Table 35. However, the magnitude of the populations mean square is relatively small when compared with the selection dates mean square. The means of heading dates for these populations are presented in Table 37.

There was also a significant variation within populations. The frequency distributions, as given in Table 38, indicate that the range of heading dates was large enough to permit selection of desirable, heading date types. It is quite interesting to note that even though these populations had been subjected to fifteen years of natural selection, significant genetic variability for this character was still present. Allard and Jain (1961), working on C.C.V., also found a vast number of different genotypes for heading date after 18 generations of exposure to natural selection. They

TABLE 37. Means of days from seeding to heading and to maturity for lines selected from F_{16} barley populations at La Pocatière in 1973 and tested at Macdonald College in 1974

Population	Days from seeding to heading	Days from seeding to maturity
7P7M1P ††	48.49 a ϕ	67.35 a
PMPMPMPMPMPMPMP†	48.67 ab	68.31 ab
2M2P2M2P2M2P2M1P	48.79 ab	68.53 b
3P3M3P3M3P	49.14 abc	69.95 b
5P5M5P	49.18 abc	68.92 b
8M7P	49.24 bc	68.89 b
6P6M3P	49.32 bc	68.40 b
15P	49.55 cd	69.06 bc
4M4P4M3P	50.12 d	69.88 c

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

ϕ Means in the same column followed by the same letter are not significantly different at the 0.05 level when tested by least significant difference.

TABLE 38. Frequency distributions for means of days from seeding to heading for lines selected from F_{16} barley populations

Populations	Class means of days from seeding to heading									
	46	47	48	49	50	51	52	53	54	Total
7P7M1P ††	8	11	6	7	1	5	0	1	1	40
PMPMPMPMPMPMPMP †	3	9	8	11	4	2	2			39
2M2P2M2P2M2P2M1P	4	5	7	8	9	2				35
3P3M3P3M3P	1	5	8	11	7	5				37
5P5M5P	4	7	3	12	6	2	2	2		38
8M7P	5	7	6	6	5	4	5	2		40
6P6M3P	2	3	11	9	4	9	1			39
4M4P4M3P	1	3	7	16	5	2	2	2		38
15P	1	8	3	6	14	3	4			39
Total	29	58	59	86	55	34	16	7	1	345

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

suggested that genetic variance did not depend exclusively on differences among multiple coexisting homozygous lines in the population, but also arose from segregation within families. Thus, heterozygote advantage may have important adaptive implications in the maintenance of population variability. Differences in heading date after a period of natural selection under various locations was also reported in a single hybrid population by Akemine and Kikuchi (1958) in rice and Takahashi and Yasuda (1970) in barley.

3. Maturity date

The results of the maturity date analysis are presented in Table 35. A non-significant replicates mean square indicates that this character is not affected by soil variation. Such was not the case for heading date. Populations, as in the case of heading date were significantly different, but the magnitude of the mean square is relatively small compared with that of selection dates. The populations-selection dates interaction is not significant. This indicates that heads selected at the later date always tended to mature later in each population. Variation occurred not only among populations, but also within each population, as indicated by a significant lines within Pop x S.D. mean square. This is also indicated in their frequency distributions (Table 39).

Maturity date means for these populations are given in Table 37. It appears that the differences among populations is not associated with alternating frequency. This is indicated by

TABLE 39. Frequency distributions for means of days from seeding to maturity for lines selected from F_{16} barley populations

Populations	Class means of days from seeding to maturity								
	62	64	66	68	70	72	74	76	Total
7P7M1P ††	1	8	11	9	4	6	0	1	40
PMPMPMPMPMPMPMP †	1	3	10	6	11	6	1	1	39
2M2P2M2P2M2P2M1P	0	2	7	8	13	3	2		35
3P3M3P3M3P	0	1	7	12	5	10	2		37
5P5M5P	0	5	6	7	8	6	5	1	38
8M7P	0	8	7	4	3	9	7	2	40
6P6M3P			14	8	10	6	1		39
4M4P4M3P	0	1	3	8	11	10	4	1	38
15P		2	8	7	10	11	1		39
Total	2	30	73	69	75	67	23	6	345

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

no difference between population with high alternating frequency and the one with no alternation.

It was found that populations differed in their maturity dates. However, they did not differ in grain yield. On the other hand, heads selected at later dates yielded higher. Thus, there seems to be some contradiction. It should be noted that selection was done during a one-week interval. However, the maturity dates of these populations differed by only one or two days. Thus, a significant change in grain yield is unlikely to appear.

V. GENERAL DISCUSSION

Changes in genotypic frequency can result from different factors. These factors can be classified broadly into: (1) directed processes, including mutation, migration and selection; (2) random processes, including sampling errors associated with population size and random fluctuations of the viabilities (selective or adaptive values) primarily due to season-to-season fluctuations in environmental conditions. It is doubtful that mutation had much effect over the 15-generation period involved in the present study. Since these populations were closed, migration seems unlikely to have appeared. Baker and Christy (1964), using the data obtained by Suneson (1949), demonstrated that for populations and censuses of the size ranging from 500 to 1500 plants, the sampling errors were small compared with the fluctuations introduced by the randomness of the relative viability. Allard and Honsche (1964) showed that with a population size of 500, few if any favorable alleles had been lost due to drift. Furthermore, Jain (1968) pointed out that as population size increased, drift effects diminished relative to the effects of selection and mating system until, for populations of size N = 1000, the distribution of gene frequencies approached those for deterministic cases. In the present experiment, the size of each population was approximately 1500 plants per generation. Thus, random drift appears to have had only a minor effect on changes in genotypic frequencies. Besides selection, another factor that may affect genotypic frequency is seasonal fluctuation, as reported by Allard and Workman (1963). This may not have been the case in this study, because the same trend of shifting was shown in most of the populations, or the results were obtained from data at two locations in two years. Hence, the most likely factor to have produced significant directional changes in genotypic frequencies in these populations appears to have been natural selection.

Nine of the F_{15} populations were grown at La Pocatière and the other eight at Macdonald College. The census data were compared as in the analysis of variance in the segregation studies. The results appear to be biased because comparisons were made among populations which were not grown at the same location. Jain and Marshall (1967) studied the changes over a period of six generations of a bulk population in the components of selection at several life cycle stages at three loci. They found that fertility and fecundity appeared to account for a larger portion of the total selective differential than the pre-adult stages (germination and seedling establishment). Therefore, though these populations were grown separately at two locations, owing to less selective differential in the pre-adult stages, there is unlikely to have been a major effect on the phenotypic ratios of most of these loci in these populations in that single year.

The lack of differences among generation means for grain yield indicates that stabilizing selection occurred in these populations.

This, at least, does not support the view of a negative relationship between yielding ability and competitive ability. Negative relationships may exist in cultivar mixtures, under certain circumstances. In mixtures, competition occurs only among a few of the stable genotypes; there is a clear-cut choice for natural selection to make. However, the situation in a hybrid population may be different. Since segregation is taking place in the population, competition occurs among numerous segregates. If the major yielding genes are not linked with other genes of adaptive character, such as plant height, disease susceptibility and the like, the recombinants of both high yield and adaptiveness would survive in the population. Then a positive relationship would likely be observed. This has been well demonstrated by the steady improvement of yield in composite cross populations (Suneson 1956; Allard and Jain 1962; Finlay 1970).

The results for grain yield in the selection trial support the conclusion of the yield trials in that no significant variation in grain yield was observed in the F_{15} populations. This suggests that bulk population yield appears to be able to predict the yield of selfed line selections, at least at the F_{15} or later generations. Harrington (1940) tested F_3 bulks of six wheat crosses and determined their predictive ability by growing F_6 through F_8 selected lines. The results indicated that replicated bulk F_3 tests could be used to predict the yield potential of selfed lines from the crosses. Busch et al. (1974) found that the average cross performance of lines and the average of the highest five lines were correlated with the mean of the F_4 and F_5 bulks, $r = 0.90$ and $r = 0.88$, respectively. Thus, they claimed that selection of crosses with high yielding lines and a higher frequency of desirable lines was possible by yield testing the advanced bulk generations. If bulks continue to provide reasonably accurate measures of derived line performance, greater numbers of crosses could be made and evaluated with the same amount of financial support and facilities used in a more conventional selection program.

It has been shown by Jennings and Aquino (1968) that the competition for light by mutual shading was the principle environmental component causing competition between tall and dwarf genotypes. Elimination of the short strawed genotypes from these populations suggests that when two contrasting plant types are involved in a hybridization program, precautions should be taken if the progenies are maintained in bulk and where particular plant type, such as dwarfness, is a desirable one. Precautions should also be given to other desirable characters which are eliminated by natural selection such as blue aleurone color. For plant height, several measures of preserving dwarf genotypes have been suggested. A modified bulk method is practised successfully at the International Rice Research Institute. The F_2 and subsequent bulk populations of wide crosses of rice are hand-rogued shortly before flowering and again when nearly all plants have flowered. All tall, leafy and spreading plants are cut at water level with small sickles (Jennings and Aquino 1968). Another modification is the use of wider spacing among the plants in a bulk population since the effect of competition usually decreases as the distance between plants increases.

Perhaps another effective method is subdividing the early (F_2) population into separate groups based on characters known to be important in competition (Khalifa and Qualset 1975). The latter method may also be used to prevent loss of blue aleurone genotypes in the populations. Other alternatives to preserve a sufficiently high proportion of blue aleurone genotypes would be to use single seed descent method, pedigree selection, or other location in which blue aleurone is favored by natural selection.

The results obtained in this study differ from those carried out by St-Pierre _et al_. (1967) with pedigree selection involving the same cross and using the same alternating pattern. In their study they found that strains selected at La Pocatière in F_4 possessed better adaptation than those selected at Macdonald College. Strains selected at alternate locations in successive years, starting at La Pocatière in F_2, possessed the widest adaptation. They thought that the station with stress limitations, La Pocatière, seemed to show higher heritability of quantitatively inherited characters and may permit more efficient selection for wide adaptation. However, in the material there were no significant changes in mean yield and adaptability under the pressures of natural selection in the same environmental conditions.

Stability analysis of bulks, as in the case of this study, may or may not be able to predict the performance of selected lines derived from the bulk. As pointed out by Allard and Bradshaw (1964), there are two obvious general ways in which a cultivar can achieve stability. First, the cultivar can be made up of a number of genotypes, each adapted to a somewhat different range of environments. Second, the individuals themselves may be well buffered so that each member of the population is well adapted to a range of environments. Genetically homogeneous populations, such as pure line cultivars or single crosses, obviously depend heavily on individual buffering to stabilize productivity, whereas both paths are open to genetically heterogeneous populations, such as mixture and bulk populations. So far, to the best of my knowledge, there is no information on the relationship between bulk stability and stability of selected lines derived from it.

Differences in grain yield among bulk populations from various locations have been reported by Taylor and Atkins (1954) in barley composites, by Miu (1965) and Miu et al. (1967) in rice single hybrid populations. It should be mentioned that the results of Tucker and Harding might be confounded with the effect of seed source, as shown by McFadden (1963). Also, Borlaug (1968) claimed that the process of moving segregating populations back and forth and up and down twice a year permitted the development of new cultivars with wide adaptation. However, the results of the present study show that alternating populations between these two locations did not affect the ratios of several plant types, mean yield or its components, adaptability or other characters. Certainly, this is due to no differential selection between these two locations. This is indicated by the lack of differences between the two populations grown continuously at each location for most of the characters studied in this experiment.

If there are to be any significant changes due to the effect of alternating material between locations on natural selection in bulk populations, two criteria must be met. These criteria are genetic diversity in the bulk material and environmental diversity in the locations. Shifts with advancing generation have been shown for several characters in this study. This indicates that there was considerable genetic variability in the material. Thus, it appears that genetic diversity was not a limiting factor. Environmental diversity, however, appears to have been limited.

The environmental components that induce pressures of natural selection can be broadly classified into four categories: (1) climatic factors, such as photoperiod, temperature, rainfall, and light intensity; (2) edaphic factors, such as soil type, soil fertility, water supply, soil temperature, and soil pH; (3) cultural factors, such as sowing date, planting density, harvesting date, irrigation and drainage; and (4) biological factors, such as disease and insect infestation, allelopathic effects, and the competitive effects of like and unlike genotypes. The effect of natural selection at any location is not only the result of individual environmental factors at the location, but of their interaction as well. Since there is no literature reporting studies of the effect of natural selection under the pressure of any single environmental factor, it is hard to predict what kind of locations should be used in order to bring about significant changes in certain characters in a bulk population, or to evaluate the most important environmental factor in natural selection. Besides, the results will vary with crops and genotypes in the population. To deal with such problems, examining the influence of environmental factors on vegetative growth and reproductive capacity should disclose some clues.

Barley is a long-day crop, but cultivars differ in their response to photoperiod. Some barley cultivars are virtually day-neutral, while others show a marked response to photoperiod (Takahashi and Yasuda 1960). Aspinall (1966) grew ten barley cultivars under 8, 12, 14, 16 and 24 hours daylength, and compared apical growth, floral development, stem elongation, tillering and dry weight at ear emergence. He found that there was a wide range of response to photoperiod. On the other hand, Kirby and Eisenberg (1966) reported that the effect of lengthening photoperiod (from 12 or 15 to 18 hours light per day) was to hasten flowering, reduce the leaf number before flowering, increase the rate of leaf emergence, and change the pattern of leaf size up the stem, but the 14 barley cultivars differed in the magnitude of their responses. Guitard (1960) found that the eight-hour photoperiod approached the minimum for leaf development and subsequent spikelet differentiation of the first culm of the barley cultivar, Vantage, but was adequate for normal growth of the other cultivar, Olli. Downs _et al_. (1959) concluded that, in general, barley in photoperiods of 16 hours produced a greater number of grains per spike and heavier grains than did plants in shorter photoperiods of 12 hours. Tillering of barley was not inhibited by either of the photoperiods, but the response of one cultivar, Trebi, to daylength was not consistently like that of the other cultivars tested. Therefore, it appears that considerable difference between two locations in daylength might induce significant variation between alternated and unalternated populations. Borlaug (1968) believed alternating segregating populations between two locations with different daylengths was one of the reasons for success in selecting widely adapted lines. The daylength at the two locations in the present study is only half an hour different. It appears that this difference could not have induced any significant pressure of natural selection on these populations.

Tingle _et_ _al_. (1970) reported that percentage fertility was higher at 18°C than at either 12°C or 24°C, and eight out of 17 barley cultivars tested exhibited a pronounced reduction in florets per tiller head at 24°C. Guitard (1960) also found a reduction in floret numbers per head in barley with increasing temperatures from 13° to 24°C. Faris and Guitard (1969) showed that growth at 24°C decreased days to maturity by 40 per cent and grain yield by 85 per cent, compared with growth at 13°C. It appears that photoperiod and temperature always influence each other. Aspinall (1969) found that flower formation at 30°C was considerably delayed in short photoperiods when compared with low temperature (20°C). Ray and Bretschneider Herrmann (1969) observed that cultivars differed in development under photoperiods of 14.9 or 13 hours, and temperatures of 22-23.5°/ 18-19.5°C or 17.5°/12°C. However, the more light-insensitive cultivars were scarcely affected by temperature (Takahashi and Yasuda 1960). On the average, the temperature at Macdonald College was only 2°C higher than that at La Pocatière in this study. These temperatures seem unable to induce differential selection on barley bulk populations at these two locations.

There is little information on the effect of light intensity on growth of barley. Edwards and Allard (1963) studied the influence of light intensity on competitive ability of two barley cultivars, Atlas and Vaughn. They found that the relative competitive abilities of the two cultivars remained constant over the entire range of shading treatments. Thus, it was concluded that the competition of these two cultivars was not associated with a struggle for limited supplies of light. There were no data on light intensity in the two locations of this experiment.

The relative performance of four spring barley cultivars was found to vary with the time of rainfall (Prikryl 1971). There is no doubt that dwarf genotypes should be favored in a heavy rainfall region because of their lodging resistance. Rainfall at these two locations differed only one cm on the average. The magnitude of difference varies yearly, but this yearly fluctuation in rainfall would be unlikely to be exploited in this alternating procedure.

Hartmann and Allard (1964) grew Atlas and Vaughn barley, alone and mixed, at four levels of fertility and four of soil moisture. At intermediate levels of fertility and soil moisture, Atlas performed better in mixtures with Vaughn than when grown alone. This difference disappeared at higher soil moisture levels but not at higher levels of fertility. Wells and Dubetz (1970) observed that at all levels of fertilizer application the reduction in yield of Compana was proportionately less than that of Betzes, and the difference between cultivars was greatest when no fertilizer was applied. The influence of soil fertility on the effect of competition was also reported by Sakai (1961). Seven cultivars of barley were tested for their competitive ability against a test cultivar at various fertility levels. It was found that the effect of interaction between fertilizer levels and competition was statistically significant for plant weight and number of ears per plant. In a study on the effect of fertilizer, plant number per hill and duration of the nursery-bed period on competition between two rice cultivars, it was found that the number of plants per hill did not cause much difference in competitive ability but a long period of growth in the nursery-bed made it lower. Application of a high dosage of fertilizer produced high competitive ability. Another similar experiment was conducted with upland rice cultivars. The workers found that when four times as much fertilizer as the standard dose was applied, red rice was no longer a strong competitor against the commercial cultivar, but its competitive ability increased with the decrease in the amount of fertilizer applied. Marked cultivar differences were also observed by Shpogis and Vevers (1975) in their reaction to the content of humus, clay, phosphorus and potassium in the soil, and to soil pH. The effect of these edaphic factors should be rather significant in competition involving genotypes with different root systems or differences in efficiency of root functions. Both locations in this study are experimental stations. In addition to their good basic fertility, supplemental fertilizers were added each year. Therefore, the soil fertility of the two locations should be similar. However, soil texture in the two locations is different. There are times when stresses from the lack of moisture at Macdonald College are severe, due to the sporadic rainfall pattern. Such stresses are less likely to occur at La Pocatière, partly because the heavier soil is more moisture retentive and partly because its rainfall distribution is more uniform.

One of the most influential environmental factors on natural selection is plant density. With increasing density, plants not only compete for nutrients and water supply underground, but also for light. Sakai (1955) grew two barley cultivars, one being a strong competitor against the other, in rows 70 cm apart, with interplant spacings at 2, 4, 8, 16, 32, and 64 cm. It was found that the smaller the interplant spacings, the larger was the increment due to competition in per cent of the quantities found in pure stands. Finlay et al. (1971) reported that high-yielding cultivars displayed a greater response (increased yield) to narrow rows than low-yielding cultivars. On the other hand, Angus et al. (1972) reported that the erect-leaf cultivar, Lenta, responded to increased planting density by increasing dry-matter production and yield, while the cultivar Research, with long, lax leaves, responded by decreased productivity. Undoubtedly, increasing plant density would tend to eliminate the dwarf genotypes. In our experiment, the same row width and seeding rate were applied at both locations.

Probably, because of this no differences among populations in plant height were observed.

A study was made by Harrington (1946) of the reaction of 53 barley cultivars when sown at two dates at two locations, for five or seven years at each, in Saskatchewan. The data revealed cases where some cultivars yielded well at one date but poorly at the other, whereas other cultivars behaved in the opposite manner. Eighty-two per cent of the barley tests at Saskatoon and 62 per cent of the tests at Tisdale showed significant cultivar-date interactions for yield at the five per cent level. The effect of seeding date was probably associated with the response of cultivars to photoperiod and temperature. A record of the seeding dates at La Pocatière for the present investigation was not available. At Macdonald College the seeding dates were generally in line with normal seeding dates for other barley materials at that location, and they are unlikely to have influenced the results.

Andrushchenko (1972) classified 40 barley cultivars into three groups: (1) drought-resistant and also highly responsive to irrigation; (2) drought-susceptible and responsive to irrigation; and (3) drought-resistant with little response to irrigation. Kirby (1968) also reported that response to irrigation differed among cultivars.

Disease or insect infestation apparently affects the outcome of natural selection. For example, Sandfaer (1970) found that in a mixture of two barley cultivars, T. Prentice and Freja, the percentage of Freja was reduced at the end of the experimental period at all five locations. It was later found out barley stripe mosaic virus was the cause of the elimination of Freja.

Growth of some higher plants can be influenced by the production of allelopathic substances in neighbouring plants (Grummer 1961). However, whether allelopathic effects occurred within these or other barley populations is not known.

Sakai (1955) found that the increment of plants with stronger competitive ability seemed to be proportional to the number of weaker plants surrounding the former when interplant spacing remains constant. But, as pointed out by Schutz _et_ _al_. (1968), certain types of frequency-dependent competitive effects can lead to feedback systems with stable equilibria. Thus, the final outcome of a population under natural selection would be determined not only by the frequency of like and unlike genotypes but also by the types of inter-genotypic competitive effects involved.

In short, under normal growing conditions, photoperiod, temperature, plant density, and disease infestation appear to be the most influential environmental factors on natural selection. It may be possible to evaluate the effect of alternating segregating populations between two locations involving more divergence in these environmental factors.

VI. SUMMARY AND CONCLUSIONS

A barley cross was made in 1958. One of the parents, Star, is a short-strawed cultivar which comes from Sweden. The other parent, M.C.2950, is a selection from a cross between Montcalm and Fort, made at Macdonald College. It is taller and yields better than Star under the environments used in this study.

Bulked F_1 materials were equally divided and one part grown at Macdonald College in F_2. The other part was grown at La Pocatière. In each subsequent generation each bulk was again divided, and a portion grown at each location. Thus, from F_2 to F_{15}, materials were alternated either annually, or after two to eight years at one location. No selection had been made from these materials.

In general, bulk populations grown at these two locations shifted toward rough-awned, yellow aleurone, short rachilla and hairy rachis types. V-shaped collars and straight basal rachis internodes predominated in these populations. Alternating segregating populations between the two locations appears to have had only a minor effect on the segregation of these characters.

The rough-awned type seemed to be associated with more kernels per head. An association between rough-awned types and heavier kernel size was also found in some populations. This may explain, at least in part, the reasons for the rough-awned type predominating in these populations.

The short rachilla and the hairy rachis are linked with the rough-awn locus. It was also observed that all the heads with short hairs on the glumes had short-haired rachillas and short-haired rachis edges, and all those with long hairs on the glumes had long-haired rachillas and long-haired rachis edges, with only a few exceptions. These three loci are probably closely linked.

The results obtained from the yield trials show that there was no significant effect of alternating segregating populations between the two locations on natural selection for grain yield, number of heads per plot, number of kernels per head, 1000-kernel weight, awn length, head length, flag leaf width, flag leaf length, flag leaf area, or plant height. Studies on stability using regression techniques indicate that there was no variation in stability indexes for most of the characters among these populations in the F_{10} and F_{15} generations.

Stabilized selection occurred in grain yield. This is probably due to the narrow genetic variability in these populations, and natural selection was unable to bring about any significant changes in grain yield. This result does not support the theory that competitive ability is negatively correlated with yielding ability.

Elimination of short-statured genotypes was indicated. This suggests that precautions should be taken when hybridization involves two contrasting plant types as regards straw length, and the progenies are maintained in bulk.

Similar conclusions are drawn from bulk yields and the mean yield of selected lines derived from these bulks. Thus, it is possible to use the bulk yield to predict derived line performance. Differences in heading date and maturity date were observed among the F_{16} populations. Significant variation in these two characters among genotypes selected within each of the F_{16} populations was also shown.

The environmental factors that induce pressures of natural selection have been discussed. An increased environmental diversity is apparently needed in order to evaluate the effect of a procedure involving the alternation of segregating populations on natural selection. Moreover, if greater genetic diversity was available the effects of natural selection may appear sooner and be more prominent for evaluation.

It appears, from this limited study, that little would be gained in the barley breeding programs by adopting a procedure involving the exchange of bulk populations, during segregating generations, between Macdonald College and La Pocatière.

VII. CONTRIBUTIONS TO ORIGINAL KNOWLEDGE

Studies on the effect of natural selection at different locations has been reported by several investigators. To the best of this author's knowledge, however, there have been no reports in the literature on attempts to study or to use a procedure involving alternation of segregating populations to utilize the effect of natural selection. Such an attempt is the uniqueness of the present study. Wider environmental and genetic diversity are apparently needed to make this procedure effective in bulk population breeding.

There are few and inadequate reports on the effect of natural selection on a single hybrid population. This study has fully examined the changes in single hybrid populations. These include changes in genotypic composition for several characters, in means of several traits, and in their stabilities. The results of yields of bulk populations and the mean yield of selected lines derived from them were also compared. No other study in any crop has provided as thorough and adequate information on changes in a single hybrid population under pressures of natural selection.

Steady improvement in productivity has been reported in several composite populations of barley. However, no reports on single hybrid barley populations were found in the literature. It is believed that this is the first report on productivity of single hybrid barley populations over a long period of natural selection.

The information resulting from this study will provide useful guidelines for practical barley breeding programs, particularly where the bulk population method is to be used.

VIII. SUGGESTIONS FOR FURTHER RESEARCH

The two locations used in this study differ by only about two degrees of latitude, and broadly speaking, they are within the same agricultural production region. Thus, discrepancy in photoperiod, rainfall, temperature, pathogen races, cultural practices, soil conditions and so forth, is comparatively small. It would be better to grow segregating populations alternating between two or more locations with a greater degree of variation in certain known environmental factors. Using composite cross populations may further provide evidence of significant changes under the pressure of natural selection over a shorter period of time.

Not only trait means should be studied, but examining their genetic variance would give us an indication about the degree of the pressure of natural selection under different environmental conditions. It would also indicate the genetic variability in each population, such that expected progress in head selection could be predicted.

It is believed that one of the possible advantages of the procedure of alternating segregating populations is that it could increase the adaptability of bulks. But whether or not widely adapted lines could be selected from the widely adapted bulks remains an unanswered question.

Natural selection was not able to bring about any significant changes in grain yield in these single hybrid populations. Kernel size was found to be the character most related to grain yield. What would happen in such populations if mass selection were applied to kernel size?

There is little information on the effect of competitive ability under different environmental factors. It seems that more research is needed on this aspect. If the relationship between competitive ability and environmental factors were identified, environmental factors could be fully exploited in a bulk population breeding program.

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APPENDIX TABLES

APPENDIX TABLE 1. Observed values and Chi-square values for segregation of rough- and smooth-awned types in F_6 barley populations

Populations	Rough	Smooth	X^2-value
PMPMP †	152	175	3.1775
PPPMP	297	306	1.1961
PMMMP	298	299	0.5835
MMPMP	310	303	0.2032
MMMMP	335	316	0.0001
MPPMP	210	197	0.0012
MPPPP	182	162	0.1980
PPMMP	249	218	0.5087
MMPPP	278	240	0.8370
PMMPP	278	232	1.6577
MPMMP	385	319	2.6289
PPMPP	260	207	2.9991
MPMPP	201	155	3.2265
PMPPP	368	284	6.0210*
5P ††	329	248	6.6618**
MMMPP	367	272	8.5852**
Total	4499	3933	10.791 **
Expected phenotypic ratio	33	31	

† The first letter represents the location in which the F_2 was grown. P = La Pocatiere; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected phenotypic ratio at the 0.05 level.

** Significant deviation from the expected phenotypic ratio at the 0.01 level.

APPENDIX TABLE 2. Observed values and chi-square values for segregation of rough- and smooth-awned types in F_{10} barley populations (these data were obtained from remnant heads)

Populations	Rough	Smooth	X^2-value
3P3M3P ††	230	188	3.8629*
4P4M1P	304	233	8.8534**
PMPMPMPMP †	235	158	14.4018**
8M1P	222	137	19.3279**
5M4P	330	200	30.8963**
2P2M2P2M1P	238	136	26.8823**
9P	258	134	38.1155**
6M3P	335	156	63.8363**
Total	2152	1342	183.8098**
Expected phenotypic ratio	513	511	

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected phenotypic ratio at the 0.05 level.

** Significant deviation from the expected phenotypic ratio at the 0.01 level.

APPENDIX TABLE 3. Observed values and chi-square values for segregation of rough- and smooth-awned types in F_{10} barley populations (these data were obtained from reseeding at Macdonald College in 1972)

Populations	Rough	Smooth	X^2-value
3M3P3M ††	601	399	39.6198**
7P2M	644	356	81.2520**
5P4M	676	324	121.8341**
9M	689	311	140.6606**
Total	2610	1390	366.7451**
Expected phenotypic ratio	513	511	

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected phenotypic ratio at the 0.05 level.

** Significant deviation from the expected phenotypic ratio at the 0.01 level.

APPENDIX TABLE 4. The relationship of awn type to number of kernels per head in F_{15} barley populations

Populations	Rough-awned			Smooth-awned			t-value
	n_1[a]	$\overline{X}_1$	S_1^2	n_2	$\overline{X}_2$	S_2^2	
PMPMPMPMPMPMPM †	199	38.9397	105.7741	135	39.0370	90.4538	-0.0887
8M6P ††	97	48.1753	123.0210	190	41.7316	127.5096	4.6270**
3M3P3M3P2M	142	38.6549	69.0219	112	35.4643	80.5753	2.9059**
2M2P2M2P2M2P2M	100	44.6700	97.5363	119	38.9328	85.0971	4.4126**
14P	106	48.2736	110.4673	100	44.6500	162.2702	2.2197*
5P5M4P	200	44.4300	174.9599	119	40.3025	129.3992	2.9465**
6P6M2P	123	47.1220	140.8129	105	42.1143	108.9099	3.3900**
2P2M2P2M2P2M2P	100	44.9300	153.3991	111	38.6216	137.7283	3.7870**
3P3M3P3M2P	120	40.5083	208.8066	123	37.4146	155.8840	1.7839
4P4M4P2M	166	39.5241	96.1782	108	39.6852	91.9748	-0.1346
6M6P2M	182	40.2857	93.3433	114	38.7807	109.1285	1.2412
4M4P4M2P	180	46.0667	127.6380	118	45.6780	173.4851	0.2633
MPMPMPMPMPMPMP	100	46.9600	124.8065	123	37.9268	159.0028	5.6670**
5M5P4M	201	36.6517	191.9581	236	36.9153	137.5077	-0.2125
14M	283	40.4028	109.1069	265	37.6528	110.4548	3.0700**
8P6M	131	42.2748	104.1855	124	37.1694	122.2231	3.8231**
7P7M	130	41.0615	90.6319	127	37.0709	82.3838	3.4398**
Total	2560	42.2121	137.3027	2329	39.1348	127.2163	9.3528**

[a] n_1 and n_2 are the sample size of rough- and smooth-awned types, respectively. $\overline{X}_1$ and S_1^2 are the mean and the variance, respectively.

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant differences between the two means at the 0.05 level.

** Significant differences between the two means at the 0.01 level.

APPENDIX TABLE 5. The relationship of awn type to kernel size in F_{15} barley populations

Populations	Rough-awned			Smooth-awned			t-value
	$n_1{}^a$	$\overline{X}_1$	$S_1^2 X10^{-5}$	n_2	$\overline{X}_2$	$S_2^2 X10^{-5}$	
PMPMPMPMPMPMPM †	200	0.0270	1.626	135	0.0276	1.614	-1.3387
8M6P ††	96	0.0315	2.861	191	0.0308	3.228	1.0243
3M3P3M3P2M	141	0.0293	1.846	113	0.0263	1.121	6.2537**
2M2P2M2P2M2P2M	105	0.0291	1.371	113	0.0284	1.659	1.3291
14P	106	0.0359	1.562	98	0.0346	1.646	2.3151
5P5M4P	199	0.0284	6.068	118	0.0279	2.836	0.6771
6P6M2P	124	0.0284	3.142	105	0.0286	4.385	-0.2442
2P2M2P2M2P2M2P	100	0.0333	1.538	111	0.0328	2.570	0.8055
3P3M3P3M2P	120	0.0313	3.698	127	0.0308	7.340	0.5312
4P4M4P2M	168	0.0273	1.982	108	0.0259	1.437	2.7942**
6M6P2M	185	0.0277	9.468	113	0.0276	1.913	0.1212
4M4P4M2P	179	0.0312	5.422	116	0.0299	3.255	1.7018
MPMPMPMPMPMPMP	99	0.0304	3.684	121	0.0305	5.129	-0.1121
5M5P4M	205	0.0280	4.321	129	0.0274	1.919	1.0006
14M	245	0.0281	2.634	223	0.0284	1.762	-0.0654
8P6M	130	0.0303	1.202	123	0.0274	1.976	5.7642**
7P7M	128	0.0291	1.695	127	0.0264	1.310	5.5629**
Total	2530	0.0294	3.859	2171	0.0289	3.043	2.9225*

a n_1 and n_2 are the sample size of rough- and smooth-awned types, respectively.
$\overline{X}_1$ and $S_1{}^2$ are the mean and the variance, respectively.

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant differences between the two means at the 0.05 level.

** Significant differences between the two means at the 0.01 level.

APPENDIX TABLE 6. The association of aleurone colour with awn type in barley populations

Populations	Rough-awned		Smooth-awned		X^2-value
	Yellow	Blue	Yellow	Blue	
14M ††	425	313	112	152	17.3725**
5M5P4M	402	309	162	119	0.0611
6M6P2M	455	241	175	119	2.8089
PMPMPMPMPMPMPM †	379	170	291	139	0.1480
14P	268	65	114	33	0.3734
5P5M4P	319	77	214	17	15.7846**
4P4M4P2M	607	73	245	66	18.6006**
2P2M2P2M2P2M2P	303	52	132	13	2.4582
8P6M	690	68	206	20	0.0058
6P6M2P	333	45	185	8	8.2379**
3P3M3P3M2P	363	46	152	5	8.0378**
7P7M	711	78	204	9	6.0829*
2M2P2M2P2M2P2M	541	59	389	3	31.7440**
MPMPMPMPMPMPMP	407	25	117	8	0.0016
8M6P	263	20	189	5	3.8115
3M3P3M3P2M	553	49	351	3	21.6496**
4M4P4M2P	382	15	103	5	0.0153
Total	7401	1705	3341	724	1.4985

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation at the 0.05 level.

** Significant deviation at the 0.01 level.

APPENDIX TABLE 7. The association of rachilla hairs with awn type in barley populations

Populations	Rough-awned		Smooth-awned		X^2-value
	Long	Short	Long	Short	
2M2P2M2P2M2P2M ††	254	346	274	118	67.2240**
8M6P	86	197	123	71	49.6249**
5P5M4P	157	239	142	89	26.9902**
MPMPMPMPMPMPMP †	197	235	56	69	0.0032
3P3M3P3M2P	157	252	96	61	23.7753**
2P2M2P2M2P2M2P	140	215	63	82	0.5307
3M3P3M3P2M	169	433	226	128	116.1556**
PMPMPMPMPMPMPM	174	375	226	204	42.5030**
6P6M2P	140	238	95	98	7.3389**
4M4P4M2P	138	259	61	47	15.8784**
5M5P4M	250	461	137	144	15.0737**
4P4M4P2M	223	457	162	149	32.6384**
7P7M	261	528	133	80	59.3766**
14P	96	237	92	55	47.3653**
6M6P2M	207	489	143	151	31.4766**
14M	196	542	145	119	68.4317**
8P6M	237	521	101	125	13.3225**
Total	3082	6024	2275	1790	568.9487**

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected frequencies at the 0.05 level.

** Significant deviation from the expected frequencies at the 0.01 level.

APPENDIX TABLE 8. The association of rachilla hairs with aleurone colour in barley populations

Populations	Long		Short		X^2-value
	Yellow	Blue	Yellow	Blue	
2M2P2M2P2M2P2M ††	502	26	428	36	2.9196
8M6P	203	6	249	19	3.8115
5P5M4P	253	46	280	48	0.0227
MPMPMPMPMPMPMP †	245	8	279	25	0.0098
3P3M3P3M2P	229	24	286	27	0.0431
2P2M2P2M2P2M2P	187	16	248	49	7.1721**
3M3P3M3P2M	390	5	514	47	21.4331**
PMPMPMPMPMPMPM	237	163	433	146	25.7135**
6P6M2P	207	28	311	25	2.7779
4M4P4M2P	188	11	297	9	1.4953
5M5P4M	225	162	339	266	0.3453
4P4M4P2M	338	47	514	92	1.4886
7P7M	364	30	551	57	0.7259
14P	151	37	231	61	0.0419
6M6P2M	240	110	390	250	5.3730*
14M	178	163	359	302	0.3230
8P6M	313	25	583	63	1.2369
Total	4450	907	6292	1522	13.5359**

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

* Significant deviation from the expected frequencies at the 0.05 level.

** Significant deviation from the expected frequencies at the 0.01 level.

APPENDIX TABLE 9. Means and variances of spike density in F_{15} barley populations

Pattern	Population	Sample size	Mean	Variance
I	PMPMPMPMPMPMPM †	980	13.1541	5.6933
	MPMPMPMPMPMPMP	623	14.4230	6.1291
II	2P2M2P2M2P2M2P ††	594	15.1279	5.2011
	2M2P2M2P2M2P2M	999	13.0726	7.6082
III	3P3M3P3M2P	637	14.4733	6.1715
	3M3P3M3P2M	997	12.8149	3.9002
IV	4P4M4P2M	992	12.9725	4.9592
	4M4P4M2P	635	14.7787	6.7510
V	5P5M4P	725	14.3739	7.0890
	5M5P4M	986	13.4544	5.3685
VI	6P6M2P	632	14.6305	5.9469
	6M6P2M	994	13.5091	5.0045
VII	7P7M	1006	13.3136	4.5043
	8P6M	992	13.3372	4.1014
	8M6P	584	14.4829	6.1078
O	14P	573	13.4677	4.2966
	14M	999	14.1071	5.1877

† The first letter represents the location in which the F_2 was grown. P = La Pocatière; M = Macdonald College.

†† The number represents the years grown continuously at a location.

APPENDIX TABLE 10. Pooled analysis of variance for grain yield and its components in F_6 barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Locations	1	148,889.82**	9,964.80	2,031.4682**	506.5668**
Error A	2	1,730.24	14,251.32	1.1380	2.2182
Populations	26	6,714.26	5,711.49	14.7252	1.6634
Locations x Populations	26	4,356.14	7,092.54	17.2864	0.8985
Error B	52	5,503.72	7,991.50	21.2328	1.1513

** Significant at the 0.01 level

APPENDIX TABLE 11. Pooled analysis of variance for grain yield and its components in F_{10} barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Years (Y)	1	86,141.49	11,520.04	2,443.3137**	99.9880**
Locations (L)	1	130,821.35*	8,256.30	1,794.2402**	876.8541**
Y x L	1	501.96	4,614.16	506.3626*	311.4424*
Replicates in Y and L	8	19,628.22	11,063.74	54.8475	8.6358
Populations (P)	16	2,036.82	4,966.96	11.9752	1.6379
P x Y	16	5,057.37	5,768.67	14.5307	1.7165
P x L	16	4,803.06	4,237.32	14.5266	1.1429
P x L x Y	16	4,250.02	3,408.76	17.7512	1.4300
Pooled error	128	5,091.73	5,177.68	14.9914	1.5532

* Significant at the 0.05 level

** Significant at the 0.01 level

APPENDIX TABLE 12. Pooled analysis of variance for grain yield and its components in F_{15} barley populations

Source of variation	df	Mean squares			
		Grain yield	No.of heads/plot	No.of kernels/head	1000-kernel weight
Years (Y)	1	312,863.34*	18,939.13	3,472.0126**	160.7529**
Locations (L)	1	97.46	18,939.13	2,095.3649**	470.8049**
Y x L	1	143,842.59	3,741.06	781.9626**	80.9298**
Replicates in Y and L	8	46,880.46	18,829.06	4.9343	2.0860
Populations (P)	16	4,939.09	6,610.00	31.0519**	1.6232
P x Y	16	4,140.44	6,785.73	8.0423	1.7751
P x L	16	2,696.08	5,031.65	18.4295	1.0096
P x L x Y	16	5,264.24	4,671.39	14.7021	2.1367
Pooled error	128	3,123.18	4,942.06	16.6045	1.5167

* Significant at the 0.05 level

** Significant at the 0.01 level

APPENDIX TABLE 13. Pooled analysis of variance for other agronomic characters in F_6 barley populations

Source of variation	df	Mean squares				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Locations	1	0.6533	6.6504**	0.1121	206.1447**	212.9419**
Error A	2	0.0529	0.1109	0.0813	0.5765	6.5008
Populations	26	0.4817	0.3074	0.0186	0.8620	2.2623
Locations x Populations	26	0.3091	0.3358	0.0196	1.4332	3.5167
Error B	52	0.3387	0.5003	0.0135	1.0503	2.8054

** Significant at the 0.01 level

APPENDIX TABLE 14. Pooled analysis of variance for other agronomic characters in F_{10} barley populations

Source of variation	df	Mean squares				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Years (Y)	1	32.0428**	4.4975**	0.0712	0.1884	0.1701
Locations (L)	1	10.6952**	12.6951**	0.0000	25.2849	24.9017
Y x L	1	0.6791	2.5999	2.7233**	770.8815**	1585.0913**
Replicates in Y and L	8	0.2647	0.6444	0.0620	6.6979	17.1673
Populations (P)	16	0.2348	0.3040	0.0073	0.6030	1.8118
P x Y	16	0.2979	0.2214	0.0141	1.5517	4.2844
P x L	16	0.2746	0.1272	0.0047	1.5792	1.8077
P x L x Y	16	0.1778	0.1289	0.0063	1.0852	2.0565
Pooled error	128	0.3192	0.1812	0.0121	1.4191	3.7504

** Significant at the 0.01 level

APPENDIX TABLE 15. Pooled analysis of variance for other agronomic characters in F_{15} barley populations

Source of variation	df	Mean squares				
		Awn length	Head length	Flag leaf width	Flag leaf length	Flag leaf area
Years (Y)	1	38.0644**	0.1529	0.1970**	12.9155	26.7708
Locations (L)	1	21.0050**	13.0113**	0.0246	78.5789**	39.8568
Y x L	1	0.9174	8.6471**	1.8373**	406.6729**	856.6914**
Replicates in Y and L	8	0.2039	0.1401	0.0164	4.5997	10.0736
Populations (P)	16	0.7598**	0.8769**	0.0230**	1.8720*	5.7263*
P x Y	16	0.3536*	0.1379	0.0120	0.7831	2.6865
P x L	16	0.2047	0.1585	0.0116	0.9684	3.2254
P x L x Y	16	0.3489*	0.2080	0.0100	0.3397	1.9421
Pooled error	128	0.1994	0.1331	0.0105	1.0255	2.8786

* Significant at the 0.05 level

** Significant at the 0.01 level

APPENDIX TABLE 16. Pooled analysis of variance for plant height

Source of variation	F_6		F_{10}		F_{15}	
	df	M.S.	df	M.S.	df	M.S.
Locations	1	474.0147	1	1997.2238**	1	2599.4373**
Error A	2	138.7941	4	35.8714	4	46.3172
Populations	26	23.2130	16	11.5889	16	6.6218
Locations x Populations	26	13.6140	16	23.2767	16	24.4981*
Error B	52	33.4567	34	20.4421	64	12.8149

* Significant at the 0.05 level

** Significant at the 0.01 level