EFFECT OF VARIATION IN PLANT SPACING, SEED SIZE AND GENOTYPE ON PLANT-TO-PLANT VARIABILITY IN WHEAT

By

Farouk Saleh Chebib, B. Sc., M. Sc.

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
AND RESEARCH IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF MANITOBA

March, 1970

ACKNOWLEDGEMENT

This study was carried out under the supervision of Professor S. B. Helgason of the Department of Plant Science, the University of Manitoba, whose continual guidance and encouragement is sincerely appreciated. Grateful acknowledgement is offered to Associate Professor A. K. Storgaard of the same department for her constructive criticism and assistance in the preparation of this manuscript.

Statistical consultations with Assistant Professor S. K. Sinha, of the Department of Statistics, Dr. R. N. Sinha of the Canada Department of Agriculture and Dr. P. J. Lee of the Fisheries Research Board of Canada were also valuable.

Dr. I. Kleinberg, of the Faculty of Dentistry merits special recognition. His persistent prodding and frequent solicitations forced the author to find time to complete this manuscript. Mr. D. Summerfield of the Dental College is to be thanked for his help in the preparation of the photographic plates.

ABSTRACT

Factors affecting single-plant selection procedures were investigated in a field experiment involving small, large and unsorted seed of a genetically segregating and a pure population of wheat sown at three plant spacings. Harvest data on eleven agronomic characteristics were recorded on individual plant basis and subjected to a principal component analysis. Five principal components, accounting for over 99% of the variability in the eleven characteristics were isolated and interpreted. The two major components were termed yielding ability and physiologic homeostasis.

The intraplot variances for each of the eleven agronomic characteristics and five principal components were independently analyzed by two methods. Results of the analyses of the principal components were in accord with the results of the analyses of the agronomic characteristics. It was demonstrated that the major factor contributing to intraplot variability is wide plant spacing followed by differences in initial seed size and competition due to differences in seed size. Competition due to genetic differences was found to be much less important than wide plant spacing as a source of error in the selection nursery.

The results obtained strongly favor the adoption of close plant spacing in selection nurseries and the advisability of sowing seed of approximately the same size in a nursery.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
LITERATURE REVIEW	4
I. Single plant selection	4
II. Yield components	5
III. Plant spacing	7
IV. Seed size	12
V. Competition in plants	15
A. Definitions and concepts	15
B. Competition among equal genotypes	22
C. Competition among associated species	22
D. Survival in mixed populations	23
E. Intraplot competition	26
F. Interplot competition	30
G. Genotypic blends	31
H. Implications of competition in plant breeding	37
MATERIALS AND METHODS	39
Statistical analysis	40
I. Principal component analysis	42
II. Analysis of variance	45
III. Multiple regression	47
A. Additive model	47
B. Multiplicative model	51

Page

EXPERIMENTAL RESULTS 54

I. Principal component analysis 54

II. Analysis of variance 61

III. Multiple regression analysis 68

A. Additive model 71

B. Multiplicative model 76

DISCUSSION AND CONCLUSIONS 85

I. The principal components 86

II. Analysis of variance 90

III. Multiple regression 100

A. Methodology 102

B. Results 109

IV. General conclusions 118

SUMMARY 122

LITERATURE CITED 124

APPENDIX 1 148

APPENDIX 2 151

APPENDIX 3 153

APPENDIX 4 154

APPENDIX 5 155

APPENDIX 6 156

LIST OF TABLES

Table		Page
1.	Values of the independent variables (x_0 - x_5) assigned to each treatment combination in the multiple regression analyses	49
2.	Pearson product moment correlation coefficients among pairs of eleven agronomic characteristics	55
3.	Principal component matrix for eleven agronomic characteristics	56
4.	Distances between all possible pairs of characteristics in 3-dimensional space	60
5.	Analyses of variance of the logarithm intraplot variance for eleven agronomic characteristics	62
6.	Analyses of variance of the logarithm intraplot variance for five principal components	63
7.	Means and standard errors of intraplot variances for plots sown at three plant spacings for eleven agronomic characteristics and five principal components	65
8.	Means and standard errors of intraplot variances for pure and segregating genotypes for each of eleven agronomic characteristics and five principal components	66
9.	Means and standard errors of intraplot variances of three seed sizes for eleven agronomic characteristics and five principal components	67

Table		Page
10.	Effect of competition due to differences in genotype on eleven agronomic characteristics and five principal components	69
11.	Effect of competition due to differences in seed size on eleven agronomic characteristics and five principal components	70
12.	Results of the multiple regression analyses for eleven agronomic characteristics according to the additive model	72
13.	Per cent variance due to the variance components for eleven agronomic characteristics (additive model)	74
14.	Results of the multiple regression analyses for five principal components according to the additive model	75
15.	Per cent variance due to the variance components for five principal components (additive model)	77
16.	Results of the multiple regression analyses for eleven agronomic characteristics according to the multiplicative model	78
17.	Per cent variance due to the variance components for eleven agronomic characteristics (multiplicative model)	80
18.	Results of the multiple regression analyses for five principal components according to the multiplicative model	82
19.	Per cent variance due to the variance components for five principal components (multiplicative model)	83

Table | Page

20. Comparison of significance of results obtained from the analyses of variance for eleven agronomic characteristics and five principal components 101

21. Per cent of the total variance in eleven agronomic characteristics due to each of the variance components for two models 112

22. Number of cases where the standardized partial regression coefficients for the multiplicative model exceeded that for the additive model for each of five effects 114

23. Significant effects revealed by the multiple regression analyses for eleven agronomic characteristics and five principal components for two models 115

24. Comparison of significant results obtained by the two methods of statistical analysis for eleven agronomic characteristics and five principal components 117

25. Calculation of heritability estimates under four sowing conditions based on the total variability in eleven agronomic characteristics (additive model) 121

LIST OF FIGURES

Figure		Page
1.	Arrangement of the main plots within a replication	41
2.	Relative positions of eleven agronomic characteristics in 3-principal component space	59
3.	Major interrelationships of eleven agronomic characteristics and five principal components	87
4.	Effect of plant spacing on the intraplot variance of six agronomic characteristics	92
5.	Effect of plant spacing on the intraplot variance of five agronomic characteristics	93
6.	Effect of plant spacing on the intraplot variance of the scores of five principal components	94
7.	Effect of plant spacing on intraplot variance of mono- and mixed-cultures for hypothetical competition cases	97
8.	Regression of intraplot variance on genotype, a nominal-type variable	103
9.	Regression of intraplot variance on plant spacing, an interval-type variable	104
10.	Proportions of the total variance in the eleven agronomic characteristics due to each of the variance components for two models	113

INTRODUCTION

Breeding for quantitative characters in cereal crops involves crossing and subsequent selection for superior genotypes from segregating populations. In a conventional plant breeding program, the opportunity for selection is limited not only by the parental genotype and the size of the population grown in early generations but also by the ability of the plants to express their genotype to a degree distinguishable by the plant breeder. The necessity for identifying high yielding genotypes in the earliest possible generation is obvious, for once they are lost, they can not be recovered in subsequent generations (198).

The major objective of most plant breeders is to breed for higher yield and good quality and most breeders use the pedigree method of selection (252). The ineffectiveness of single plant selection for yield and yield components has been long recognized (13, 14, 17, 76, 101, 219, 278). This view is held by most plant breeders (198) and is stressed in most of today's text books in plant breeding (5, 112) with recent experimental evidence (198, 252) to support it. Plant breeders have, therefore, diverted their attention to selection among families of segregating crosses (26) where genotype is presumably better expressed in the phenotype.

The ineffectiveness of single plant selection has been attributed to low heritability resulting from the inability of a genotype to express itself sufficiently in the phenotype of one plant due to the confounding effect of various macro- and micro-environmental factors. (5, 14, 29, 89, 132, 146, 185, 234). Of these factors, interplant competition has been recognized (37, 68, 120, 138, 206, 238, 262, 293, 296) and wide plant spacing has been adopted to reduce its effect. Wide plant spacing enables the breeder to differentiate more efficiently among phenotypes; but, on the other hand, involves a deviation from normal planting procedures and may introduce a new source of non-genetic variation into the selection nursery due to the larger nursery size and local micro-environmental differences. Increased variability due to wider spacing has been noted in the results of several workers (2, 103, 108, 117, 166). The performance of a genotype under wide spacing does not give a reliable prediction of its performance under close spacing (72, 120, 147, 171, 175, 223, 228, 258, 268). It has been suggested (97) that selection efficiency for yield might be increased by increasing plant density in the selection nursery. The effect of seed size differences (2, 33, 153, 154, 151, 284) and its indirect effect as a source of interplant competition (19, 33, 37, 117, 152) were also demonstrated to contribute to non-genetic variability. These may be corrected by sorting the seed according to size or weight, and planting only seed of approximately the same size in each nursery (33, 37, 150, 152).

Very little is known about the distribution of yield and yield components of single plants of cereal crops under space planted conditions. The observed variability in a selection nursery is the combined effect of the genotypic differences, the environmental differences and their interaction. Genetic-environmental interactions which result in subtle but nevertheless important variations in micro-environment have received increasing attention in recent years, both experimentally and analytically (40, 43, 53, 117, 148, 177, 191, 215). The environmental differences may include: variation due to competition of unlike genotypes, variation due to differences in seed size, variation due to competition of unequal seeds and variation due to micro-environment resulting from wide plant spacing.

Accurate measurement of the relative magnitude of the effect of each of these sources of variation will give plant breeders a better understanding of these relationships and will lead to a better design of the selection nursery.

LITERATURE REVIEW

I. Single Plant Selection

The efficiency of single plant selection for quantitative characters in early generations has been examined by several workers. Hayes and Immer (112) stated: "Selection for yield on the individual plant basis seems of little value, since environmental conditions seem the major cause of variation. This is shown by the extreme variation in yield per plant within parental varieties". Allard (5) indicated that the magnitude of the environmental effect on a single plant is so large that selection for inherent ability is virtually impossible. Atkins (13) and Atkins and Murphy (14) found, in barley and oats, that selection in early generations was not effective in isolating appreciably higher yielding lines. Immer (132) concluded from a study on the distribution of yields of single plants of barley varieties and F_2 crosses under space-planted conditions, that the variation is almost completely environmental. Bubar (29) postulated that the lack of response of timothy to conventional selection techniques as far as yield is concerned is due to the fact that the genotype x environment variance exceeded the additive genetic variance. Estimates of genotype x environment interaction were reported by Johnson et al (148) to be higher for yield in soybeans than for other important characters. Hamilton (101) postulated in 1959 that either wheat breeders have reached the limit potential or that the methods used were inadequate to detect small increments which would represent an advance.

In more recent studies, Shebeski (252) tested 440 single F_2 wheat selections for yield in F_3 against controls of unselected plants. Half the lines yielded more and half less than the controls. In a further study McGinnis and Shebeski (198) reported no difference between yields of F_3 lines selected for high yield and those taken at random in F_2. Further, the correlations between F_2 plants and F_3 plot yields were in all cases not significant.

Low heritability estimates and low inter-generation correlations for yield in self pollinated plants were reported by Fowler and Heyne (76), Lupton (182) and Sikka et al (254) in wheat; Grafius et al (89), Peterson (219) and Taylor and Atkins (278) in barley; Degras (51) in oats; and by Johnson (146), Mahmud and Kramer (185), Weber and Moorthy (289) and Weiss et al (290) in soybeans.

Rutgar et al (234) obtained a higher heritability estimate for barley malting qualities than for fourteen agronomic traits.

II. Yield Components

The relationships between yield and other agronomic characteristics have been the subject of many early investigations. Reviews of early literature were given by Fore and Woodworth (75) and Aastveit (2). Some investigators divided the characters into so called "morphological yield components". According to this principle, grain yield per unit area is made up of the number of plants per unit area and the weight of grains per plant. The weight of grains per plant is again made up of the number of heads or panicles and the grain weight per ear or panicle. The latter is a function of the number and size of seeds. This principle is perhaps best presented by Engledow (72). He describes the total yield as "peng" where _p_, _e_, _n_, _g_ are the number of plants per unit area, the number of ears per plant, the number of grains per ear and the weight of a single grain respectively. A number of other papers reported the results of analyses of lines and varieties with regard to these components. The papers of Bonnet and Woodworth (22), Bridgeford and Hayes (25), Engledow and Wadham (73), Huttunen (130), Rudorf (233) and Vidme (282) may serve as examples of this type of investigation. These papers contain the results of correlations calculated between the various components and grain yield. Some others, Goulden and Elders (85), Hayes _et al_ (113), Immer and Stevenson (134), Immer and Ausemus (133), Bridgeford and Hayes (25), David (49), Leasure _et al_ (172) and Strand (265) have tried to relate yield to characters other than the "morphological yield components" such as earliness, length of straw and disease resistance. Some results seem to be rather conflicting. Immer and Stevenson (134) for example reported a correlation coefficient of -.56 between days from sowing to heading and grain yield in oats whereas Strand (265) reported a correlation coefficient of +.72 for the same characters in barley.

Grafius (86) presented the grain yield of oat plants geometrically as the volume of a rectangular parallelopiped with the three edges representing the number of panicles per unit area, the number of kernels per panicle and the average kernel weight, respectively. He applied this theory to data on corn (87) and on ten oat varieties (88) and concluded that, in theory, no yield component is more important than the other.

Stoskopf and Reinbergs (264) observed in barley and oats negative correlations between the number of tillers per plant and the number of grains per head and found that the latter was the most reliable component to use in estimating yield. Lupton (182) estimated the yield of a single wheat plant by the product of the number of ears per plant, grams per ear and the 1000-grain weight.

Goodall (83) postulated that the relationship between yield and plant population has been obscured by the common practice of expressing yield in terms of unit area. This introduces the independent variable again in the expression of the dependent variable, which can be avoided if yields are expressed per plant.

III. Plant Spacing

Changes in planting density have been shown to influence the yield of most crops through their effect on yield components. In wheat, barley and oats, higher densities were shown by Guitard et al (97) to decrease the number of fertile heads per plant, the number of kernels per head and the 1000-kernel weight. In corn, Davies (50) found that increasing crop density increased the number of sterile stocks, but increased vegetative yield per unit area. In barley, Sakai and Iyama (243) found that higher plant densities caused a decrease in vegetative growth per plant. Higher plant density was shown by Cutcliffe (48) to decrease yield of snap beans but had no effect on seed size. In soybeans, Harris _et al_ (109) reported an increase in yield by narrower plant spacing; Giesbrecht (82) found that closer plant spacing did not increase yield per unit area while the closer row spacing reduced plant height and increased yield. Similar yield results were reported by Mader (184) in the same crop. The increase in yield due to narrower row widths increased with delayed planting date.

Differential responses of genotypes to spacing have been reported by Engledow (72) in wheat; Sakai and Iyama (243) in barley: Raqual and Jackobs (228) in maize; Åkerberg (4) in timothy and by Hartwig _et al_ (110), Johnson and Harris (147), Lehman and Lambert (175), Probst (223), Smith (258) and Weiss _et al_ (290) in soybeans. In most of these studies significant lines x spacing interactions were observed. Engledow (72) published an investigation concerning the wheat varieties, Hybrid and Red Fife. Under close spacing Red Fife was superior while under medium spacing yield was similar and under wide spacing Hybrid was superior.

Hinson and Hanson (120), from results of competition studies on soybeans, concluded: "A genetic analysis of individual plant variability for yield can be extremely misleading when differential response to spacing is a factor". They obtained different heritability estimates for different spacial arrangements.

The effect of plant spacing on the efficiency of selection has been referred to by several workers. Aastveit (2) suggested that, in the absence of line x spacing interactions, there seems to be no importance which planting distance is chosen. Edwards (68) reported that selection for high grass yields under very close spacing failed to produce any regular improvement in yield. Lazenby and Rogers (171) have shown that the performance of a genotype under wide spacing does not give a reliable prediction of its performance under close spacing. Gotoh and Osanai (84) have demonstrated that selection from a wheat cross for high yield under the standard density was fairly effective compared with denser conditions. They pointed out that wider space planting increased the phenotypic variation and magnified genotypic potentialities. Comstock and Moll (44) postulated that when plants are grown in spacing that is abnormal relative to culture of the same plant for production purposes, genetic effects other than those of interest are being investigated. Harper (108) concluded from his competition studies in barley: "It is unfortunate that, because isolated plants are the more convenient tool for the geneticists to work with, the effect of interference tends to be regarded as the unfortunate distortion of the real thing. It is very important that the plant breeder bear constantly in mind that it is the behavior of the isolated or spaced individuals which represent the distortion".

Guitard et al (97) suggested that the inadequacy of the present methods of individual plant selection from space planted early generation hybrid material of wheat, oats and barley is due to the interactions of the yield components and the number of plants per acre. They inferred that there is little value in using tillering as a selection index unless spacing and fertility are uniform and that selection efficiency for yield might be increased by seeding hybrid material sufficiently heavy to eliminate tillering and by selecting individual heads on the basis of the number of kernels per head and the 1000-kernel weight. Hinson and Hanson (120) concluded that in soybeans, selection at close spacing is possible only for those secondary characteristics which are not influenced by competition.

Theoretic and analytic studies on the effect of plant density on yield were presented by several workers. Hinson and Hanson (120) found that the grain yield response to spacing of soybean plants followed a logarithmic curve. Mitscherlich, as reported by Harper (107) suggested the relationship $W = (1-e^{-cx})$ where W = plant weight in absence of interference from neighbors, x = space available for each plant and c is a constant. Shinozaki and Kira (253) plotted the inverse of the yield per plant against plant density. The scatter diagram approximated a straight line. The studies of Kira et al (161) were based on the formula $Wd^a = k$ where W is the plant weight, d the crop density, a a competition index, showing intensity of competition and k a constant. This relationship yields a straight line when the logarithm of the individual plant weight is plotted against the logarithm of the reciprocal of plant density. When applied to data on the development of swards of subterranean clover supplied by Donald (58), the slope of the straight line increased with time. Warne (288), independently of the studies of Kira et al (161), found a similar relation between plant weight and spacing distance in vegetables and root crops. de Wit (54, 55 and 56) considered spacing experiments a special form of competition experiments. He calculated a straight line formula to describe the inverse of yield by the inverse of seeding rate.

Koyama and Kira (166) studied the distribution of plant weights at various planting densities. They showed that a population which at low density may show a normal distribution, will at higher densities, move progressively towards a skew distribution. Aastveit (2) performed an analysis of variance on the intraplot variances of barley plots sown at different plant spacings. The variances for four characters studied were shown to increase linearly with increased plant spacing. The variances based on individual plant variability reported by Hanson (103) for soybean yields progressed from 52.5 for the two inch plant spacing to 1250.9 for the thirty-two inch spacing. Helgason and Chebib (117) found in a greenhouse experiment in barley, that wider plant spacing increased the variability unaccounted for by the treatments. Stern (263) presented results of individual plant weights in swards of three densities of subterranean clover which showed that variation in growth rate is greatest at higher densities.

Competition intensity was shown to be affected by plant density. Sakai (238) found that the increments due to competition in several characteristics of barley including plant weight were inversely proportional to the logarithm of the logarithm of the distance between plants. In barley, Helgason and Chebib (117) detected significant competition effects at closer plant spacings only. Harper (108) reported many examples where the more important contributor to seed production in mixtures at low density becomes less important at higher densities. Tysdal and Kiesselbach (281) in their experiments on alfalfa found that interplot competition for yield could be prevented by wider row spacing. Competition effects between small grain plots were reported by Hulbert and Remsberg (127) to increase noticeably when adjacent plots were seeded at different rates. Puckridge and Donald (226) found that maximum dry weight per tiller in wheat occurred at medium plant density. They contributed this to an interaction between the effect of strong interplant competition on plant and tiller size at high densities, and acute inter-tiller competition within the abundantly tillered plants at very low densities, an effect discussed by Donald (61). Sakai and Iyama (243) found that competitive ability of barley and density response were not closely correlated.

IV. Seed Size

The influence of initial seed size on plant development has been demonstrated in many crops and pasture species.

In cereal crops, the early work of Kiesselbach (159), Kiesselbach and Helm (160), Krosby (167), Love (179), Waldron (283) and Zavitz (299, 300 and 301); and later studies of Aastveit (2), Chebib (33), Christian and Gray (37), Kaufmann (150), Kaufmann and McFadden (152, 153 and 154), Kaufmann and Guitard (151), McFadden (195) and Waldron (284 and 285) emphasize the importance of seed size. The general conclusions derived from these studies indicate that plants grown from large seeds are more vigorous and higher yielding than otherwise comparable ones grown from smaller seeds; that this effect starts at an early stage of development (2, 37, 151) and affects yield mainly through the number of tillers (33, 37, 153, 195). Furthermore, large seeds have been demonstrated to have a competitive advantage over small seeds (33, 37, 152) as expressed by the differences in the number of tillers and yield of mono- versus mixed-culture plots.

Taylor (276) and Taylor and Harland (277) reported that small kernels of wheat and barley, respectively, carry a larger proportion of loose smut infection than large kernels. Suneson and Ramage (271) argued that the increase in yield of awned wheat over the awnless types was due to difference in seed size. McMillan (199) concluded that twenty-four per cent of the variance among closely spaced plants of a pure line of wheat were influenced by factors associated with seed weight and early growth. Christian and Gray (37) estimated that six to eight per cent of the variance in yield was accounted for by seed size.

Initial seed size may bias genetic effects (2, 33, 150, 151). It has also been shown (154) that yield ranking of varieties in field tests may depend upon the seed size used.

These studies led to the recommendation that, in selection work, seeds of segregating populations should be separated into size or weight groups prior to seeding in order to eliminate non-genetic variation due to seed size, and selection could then be made from within each size group (33, 150, 152). McFadden et al (196) have also suggested that seed stocks to be used in breeding and testing procedures should each have the same proportion of small seeds removed to guard against misleading results due to the higher incidence of loose smut in smaller seeds.

Some investigators found little effect of initial seed size *per se* on plant development. In the studies of Christian and Gray (37) differences between wheat mono-culture plots of small and large seeds were not significant. McNeal *et al* (200), using Thatcher wheat seed produced at four different locations in Manitoba, concluded that test weight, above versus below fifty-five pounds per bushel, had little effect on yield. Bonnett and Woodworth (22) from a yield component study on barley, suggested that, if seeded at the same rate, a small seeded variety may outyield a large seeded one on account of the larger number of plants per unit area. Waldron (284), however, found that plots grown from larger seeds outyielded those grown from smaller seeds regardless of whether they were seeded by uniform weight grain or number of kernels per unit area.

There is a considerable amount of literature on the effect of initial seed size on plant development in other crops. Bartel and Martin (16) showed a significant effect of seed size on growth rate of soybeans. Black (18) has shown that early growth of subterranean clover is greater with large seeds but Donald and Black (62) reported that final dry matter was little affected by seed size. Similarly, Harkess (105) in an experiment involving pure stands of small and large seed of diploid and tetraploid Italian rye grass found that large seeds increased yield potential only during the first few weeks of growth. Hermann and Hermann (118) reported an advantage of large seed of crested wheatgrass over small seeds. In the same species Rogler (229) found high positive correlation between seed size and emergence. The studies