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

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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

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.

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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 $\underline{W} = (1-e^{-cx})$ where $\underline{W}$ = plant weight in absence of interference from neighbors, $\underline{x}$ = space available for each plant and $\underline{c}$ 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 $\underline{W}$ is the plant weight, $\underline{d}$ the crop density, $\underline{a}$ a competition index, showing intensity of competition and $\underline{k}$ 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 of Miller and Pammell (203) and Murphy and Arny (208) in legumes; and Kneebone and Cremer (165), Plummer (221) and Cummings (47) in grass species have shown that, within wide limits, plants grown from large seed had an advantage in seedling vigour over those grown from smaller seeds both among species and among strains within species.

Black (19) demonstrated competitive effects arising from differences in seed size of subterranean clover. In mixtures derived from small and large seeds of a single strain, large seeds showed definite competitive advantage for light interception through plant height. He inferred that care must be taken when comparing tetraploid and diploid plants of herbage legumes, because of differences in initial seed weight.

V. Competition in Plants

A. Definitions and Concepts:

Pavlychenko and Harrington (216) reported that the effects of competition among plants were noted in forest communities by DeCrescentiis in 1305 and in 1920 by DeCandolle in the plant kingdom. Milne (204) pointed out that the original meaning of the Latin verb *competere* which was: "to ask or sue for the same thing that another does", is fully preserved in the modern meaning of the word "competition". He discussed the various definitions suggested for competition between animals and pointed out that the need is not only for a strict definition of competition but also for discerning interpretation of such a definition.

Definitions of competition have been given by various workers in the field. Sakai (238) defined competition in a genetic context as "the effect of interaction operating between individuals of different genotypes within a population". Mather (192) pointed out that competition among organisms implied the presence of an individual as an effective part of the environment of other individuals and that competition will be expected prospectively whenever organisms share a need or an activity. Yamada and Horiuchi (296) defined competition as the interplant action and reaction as plants compete for water, nutrients and light. Chalbi (32) defined competition among genotypes as the biological interference among individuals of different genotypes belonging to the same population and coexisting in a given space. Edwards (68) sees that the term competition implies that the particular environment of an individual in a community is conditioned by the proximity of other individuals in ways that influence growth and reproductive capacity. Le Creg (173) referred to inter-row competition as the interference of adjacent rows of varieties which differ in growth habit, in plant development and yielding ability. Lysenko (183) looks at competition as involving an intraspecific relation only, while Gustafsson (98) finds competition involves any kind of struggle between individuals for water, light and nutrients. Clements et al (41) characterize competition between plants as a reaction-response phenomenon that gives one plant an initial advantage which is cumulative. They state: "Competition is a purely physical process; an actual struggle between competing plants never occurs. Competition arises from the action of one plant upon the physical factors about it and the effect of the modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other so long as the water content, the nutrient material, the light and the heat are in excess of the need of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins".

Milthorpe (205) uses the term competition to describe "those events leading to the retardation in growth of a plant which arise from association with other plants", while Welbank (291) uses the term "competitive ability of a plant" as its ability to depress the growth of other plants and the term "competitive potential" for the innate qualities that determine its actual ability to compete in particular circumstances. Such a differentiation was also recognized by Stern (262) and Helgason and Chebib (117) where the term "competitive influence" was used to denote the capacity of a type to exert competition on its neighbors, and the term "competitive ability" to denote the capacity of a type to withstand competition from its neighbors.

McGilchrist (197) gives a mathematical definition of competition between two species when sown in mixture as the average of the increase in yield of one competing species over its yield when grown in mono-culture, and the corresponding depression in the yield of the other. Harper (107 and 108) prefers to avoid the word "competition" altogether because he considers it lacks a precise scientific meaning. He uses the word "interference".

The view that competitive ability is a genetic character is held by Sakai (238), Jennings and his coworkers (138, 139 and 140) and by Stern (262). Sakai and Gotoh (241) have shown that competitive ability was independent of vigour. Sakai and Utiyamada (248) and Sakai and Suzuki (246) demonstrated in barley and rice that doubling the chromosome number in hybrids and in pure lines decreased their competitive ability. The very high competitive ability of hybrids was assumed to be due to overdominance of competitive ability genes in the heterozygous condition. Sakai and Suzuki (247) found that amphiploids of species hybrids in Abelmoschus and Nicotiana were superior in competitive ability to either parent. The amphiploid genus hybrid between Triticum and Secale was found to be superior to the Triticum parent but inferior to Secale in competitive ability. Sakai (238) reported significant superiority of Japonica over Indica rice varieties in plant weight, number of panicles and weight of panicles per plant. Significant differences in competitive ability among varieties of the same group were also reported. Sakai (237) illustrated in two wheat strains that it is possible to have different genotypes which when grown in mixture show no evidence of difference in competitive ability. Helgason and Chebib (117) found no evidence of competition among three varieties of barley differing in many agronomic characteristics. In an experiment involving twelve barley varieties differing in several agronomic properties, Sakai (238) reported differences in competitive ability but the relation between competitive ability and other plant characters such as plant height, maturity, seed size, growing habit, heading habit and grain yield was not significant. Similarly, Oka (212) could find no regular correlation between the competitive ability of Indica-Japonica crosses of rice and plant height, panicle number, seed number, earliness, grain shedding, germination speed or grain shape. Harper (108) disagreed with the absence of association between competitive ability and morphological characters and postulates that other characters not studied, such as extent and depth of root system, leaf area, height and time of appearance of first flag leaf would have a relationship to competitive ability. Sakai (240) and Oka (212) attempted to determine the inheritance of competitive ability as if it were a separate genetic character. They found that, in general, the heritability is very low. Yamada and Horiuchi (296) put many questions to Sakai's theory and explained competitive ability without having to assume the existence of independent genes.

There is not a great deal of published evidence on the characters with which competitive ability is associated. Pavlychenko and Harrington (216) studied competing ability of certain weeds and crop plants. It was shown that success in competition depends on readiness and uniformity of germination under adverse moisture conditions, the ability to develope a large assimilation surface in the early seedling stage and the possession of a large number of stomata and a root system with a large mass of fibre close to the surface but with its main root penetrating deeply. Black (20) has shown that length of petiole is an important competitive character in subterranean clover, for better light interception. Yamada and Horiuchi (295) concluded that an erect variety of wheat had a competitive advantage over a prostrate one in respect to tillers and leaf number and top growth when reared in a water culture solution. Suneson and Ramage (271) demonstrated in near isogenic lines that rough awned barley had a competitive advantage over smooth awned. Hartwig et al (110) found that border rows of soybeans differing in maturity, plant type or lodging offered different competition effects. Aaltonen (1) emphasized the importance of underground parts of field crops in competition relationships. Lee (174) and Edwards and Allard (69) have studied the biological basis for the better competitive ability of the barley variety Atlas when grown in mixture with Vaughn. They related this to the difference in root development at about the time of ear emergence, the time when competition begins. Grümmer (94) carried out experiments with flax and the weed *Camelina foetida* and concluded that *Camelina* produces some unknown matter which hampers the growth of flax. In another study Grummer (95) demonstrated toxic substances in four other genera.

Factors for which competition may occur are discussed by Donald (61). Competition for light has been demonstrated by Black

(19) in large seed of subterranean clover over small seed and is discussed in detail by Donald (60). Competition for water was demonstrated by Karper (149) and by Grimes and Musick (93) in grain sorghum and by Salter (249) in cauliflower. Competition for nutrients was studied by several workers. Donald (58), Lang et al (169) and Chipman and Mackay (34) demonstrated competition for nitrogen of equal genotypes of forage grasses, corn and sweet corn, respectively. Competition between grass and clover was demonstrated by Blaser and Brady (21) for potassium and by Walker and Adams (287) for sulphur. Drapala and Johnson (65) detected competitive effects between fertilized and unfertilized plots of sudangrass.

That competition is more intense at higher levels of soil fertility was demonstrated in barley by Sakai and Oka (245); in rice by Oka (212) and in forage crops by Blaser and Brady (21) and Walker and Adams (287). Sakai and Iyama (242) reported a rice variety of strong competitive ability to lose its competitive ability when heavily fertilized with nitrogen.

Clements et al (41) postulated that competition for each of two factors will involve an interaction, so that the aggressor species will gain competitive advantage exceeding the sum of the effects which occur when each factor operates alone. Both Clements et al (41) and Chippandale (35) tried to demonstrate this effect but their methods were open to objection. Donald (59) and Aspinall (12) studied this effect in competition between neighboring plants of two different species for light, nutrient and both light and nutrient.

In both cases an interaction intensifying the competition for either factor when operating alone was demonstrated in the treatments where competition was occurring for both factors.

B. Competition Among Equal Genotypes:

To investigate competition among equal genotypes, homogeneous seed stocks were planted at various densities. Such studies are presented by Kira *et al* (161) in soybeans, Puckridge and Donald (226) in wheat and de Wit (55a and 56) in various crops. The depression of yield per plant at higher sowing densities indicated an increase in intragenotypic competition. The changes of the individual plant yield or weight values within a population with changing density was used as a criterion whether intensified competition in this narrow sense accelerated the dominance of larger individuals over the smaller ones.

Hozumi *et al* (125) studied individual plant performance in corn. It was found that the weight of any plant in the row tended to be inversely related to the weight of its neighbor and directly related to the weight of its "next neighbor" in each direction.

C. Competition Among Associated Species:

Experiments of this type measured competition between two associated species, one of which was considered a weed. The degree of depression in yield of one species with the increased incidence of the weed measured the competitive aggressiveness of the weed. Such studies were reported by Donald (61), Mann and Barnes (186, 187, 188, 189 and 190), Pavlychenko and Harrington (216), Pendleton et al (218), Rydrych and Muzik (235), Santhirasegaram (250) and Staniforth and Weber (260). In these studies and others, yield of crops were shown to be depressed by the higher density of the weed. To compare competitive abilities of several weed species, Welbank (291) measured the effect of each on a common indicator. He assumed that the species being tested are affected by the indicator as little as possible. Jarvis et al (137), in a six-year study found that undersowing with grasses and legumes had no effect on the yield of a barley nurse crop. Tanner et al (274) have noted that a wheat variety with erect leaves, unable to suppress weeds effectively, gave the lowest yield in a variety yield trial in a weedy situation, but gave the highest yield on a site which was weed free; and conversely for varieties with floppy leaves. Pavlychenko and Harrington (216) classified cereal crops for competing ability with weeds as follows: barley, rye, wheat and oats, flax. Sakai (240) concluded, from experiments on rice, that wild species were inferior to cultivated species in respect of competitive ability.

D. Survivial in Mixed Populations:

The effect of competition on the ability of different genotypes to persist in mixed populations have usually been studied by growing two or more genotypes in mixtures and determining the success of various genotypes by means of generation-to-generation censuses.

Montgomery (206) working with wheat, barley and oats, initiated these studies in 1912. He concluded (p.22): "When left in competition, the variety which is the best yielder when placed alone, may not always dominate but, on the other hand, a less productive type may be able to survive competition". Gustafsson (98) collected experiments in which this effect was demonstrated. He termed this the "Montgomery Effect". In his study, he demonstrated that in barley, single gene mutants, which were less productive in pure-stand than the other strains, became more productive when they were competing with each other in segregating progenies of monoheterozygotes. The Montgomery Effect has shown itself to be of wide validity and is discussed by Dobzhansky (57) and Stebbins (261).

Harlan and Martini (106) observed the rate of natural selection in a mixture of eleven barley varieties grown in ten locations for a period of four to twelve years. They found that the less adapted varieties were eliminated rapidly at all stations. The variety dominating the mixture was soon evident, and varied from location to location. Suneson and Wiebe (273) observed a marked reduction in the percentage of Vaughn barley, the highest yielding variety, in a varietal mixture at the end of eight years. Suneson (269) extended this experiment to sixteen years and observed a further reduction to only 0.4% of Vaughn in the mixture. Jennings and de Jesus (140) demonstrated that a high yielding rice variety when placed in a mixture with other varieties is suppressed. Ghosh and Prakasha Rao (81) obtained an increase of twenty-one per cent in the yield of a rice variety when grown in alternating rows with other varieties. Jensen and Federer (142) found that competition accounted for sixty-three per cent of the apparent yield difference between a check variety and other strains in data from several nurseries of wheat. Laude and Swanson (170) have shown that the poorer variety of wheat may be almost eliminated from the original mixture of equal parts of two after ten years of cultivation. Wiebe _et al_ (293) studying the behavior of mixed barley isogenic lines in mixture, demonstrated a reversal in the relationship for yield of grain when pure stands and mixed populations were compared. Major shifts were also observed for number of heads per unit area and the number of kernels per head. Kernel weight was not disturbed. Similar results were reported by Bal _et al_ (15). Klages (164) observed a large increase in the durum component of a mixture with hard red spring wheat. A stem rust epidemic accounted for the decrease of the susceptible hard red spring wheat. Taylor and Kendall (279) concluded from experiments involving mixtures of polycross clones of red clover that performance in a mixture was not always related to performance when grown alone.

Suneson and Stevens (272) found in studies of bulked hybrid populations of barley that certain marker genes show poor survival in the bulked population. Suneson and Ramage (271) concluded, from a competition study of near isogenic genotypes of wheat, that yield and survival relations for alleles, hybrids and varieties are generally, but not universally, in accord. Jain and Allard (136) presented evidence for heterozygote advantage in competing populations of barley. Frank (77) found that one species of Daphnia caused the extinction of another, when cultivated together, through competition effect due to increased male production of the latter.

Equilibria in mixtures have been approached mathematically and graphically by Donald (61) and de Wit (55 and 56). de Wit (56) developed a theory to describe such competition phenomena quantitatively based on an analogy with theories underlining multi-component distillation and other exchange processes.

E. Intraplot Competition:

This type of competition studies investigated different seed typed in paired competition plots. The experimental design basically adopted was growing pure-culture plots and plots of pairs of the investigated types in competition within the row or between rows. Such designs were used by Christian and Gray (37), Helgason and Chebib (117), Lee (174), Pendleton and Seif (217), Waldron (286) and some of the work by Sakai (238 and 240). Statistical methods used to analyse these experiments varied considerably. Christian and Gray (37) and Waldron (285) compared the difference between the seed types when grown alone to that when grown in competition. Helgason and Chebib (117) suggested the construction of a two-way table whereby the rows constitute the competing seed types and the columns the tested seed types and applying a factorial analysis of variance to the data to measure the general competitive influence of each of the competing seed types by comparison of the row means. Lee (174) used this method in his competition study between Vaughn and Atlas barley. Two-way competition tables were also the basis of more sophisticated analyses based on the analysis of variance of diallel crosses as presented first by Yates (298) and modified later by the work of Jinks and Hayman (145), Hayman (115 and 116), Jinks (144) and Kempthorne (155).

Durrant (66) has given an analysis of reciprocal differences in genetic diallel tables and showed how the formulae may be modified for the analysis of reciprocal differences in competition diallels and also gave a graphical interpretation of various competitive effects as shown by reciprocal differences and means. Norrington-Davies (210) gave graphic and statistical analysis of two sets of competition data based on the methods described by Durrant (66).

McGilchrist (197) and Williams (294) presented mathematical and statistical studies regarding the method for analysis of competition experiments where the data may be arranged in a two-way diallel table. The analysis of variance presented was basically the same as that given by Cockerham (42) with addition of a whole plot term.

Sakai (240) grew nine wheat varieties alone and in pairs. He arranged his data in the manner of diallelic study to give a value for the general competing ability for each variety based on mean increment or decrement in yield when grown in all eight mixtures and for specific competing ability for each variety based on the performance of the variety in a particular mixture. Both general and specific competitive ability gave highly significant values. Jensen and Federer (143), using formulae supplied by Griffing (91) computed general, specific and reciprocal competing effects of four wheat genotypes. They were shown to differ considerably in competing ability under conditions of rod row culture. Indications of general and reciprocal but not specific competing ability were found for yield but not for height.

Chalbi (32) presented a biometrical study of genotypic competition in lucerne using the diallel crossing method of analysis. For each genotype he measured the general ability for competition, the general ability for aggressiveness and the specific ability for competition with each other genotype. Harper (108) also used the diallel method of analysis to analyse a competition experiment involving six varieties of *Linum*.

Eberhart *et al* (67) in a study of competition effects among maize single crosses stated that the diallel model is not appropriate when single cross means can be obtained separately from paired mixtures. He, therefore, proposed a competitional model. The performance of paired mixtures of two sets of single crosses with four or five single crosses in sets, respectively, were compared with their performance with pure stands.

Sakai (236 and 237) suggested that genotypic competition in mixed plant populations should bring about an increase in the error variance, i.e., in the mixed population, the variance of the characters that are affected by competition will be increased by an amount equal to the competitional variance. He found in a wheat population in which genotypic competition occurred, the competitional variance reached between twenty-five and forty per cent of the non-hereditary variance. Sakai (238) further developed the theory for partitioning variance components for quantitatively inherited characters when genotypic competition occurs. He subtracted from the variance of a mixed population a synthesized variance of the components to reach at the competitional variance. In most cases, the competitional variance was far greater than the genotypic one. Sakai and Mukaide (244) presented a similar method for the estimation of genetic parameters in forests where inter-tree competition occurs. Stern (262) postulated that competitive ability and competitive influence of different genotypes in a stand of competing plants are quantitative and heritable characters. The variance resulting from competition among different genotypes can be partitioned following a factorial plan. Covariances between neighboring plants can be divided in a similar manner.

Hanson et al (104) developed a similar model for competitional studies in soybeans. In both this and Sakai's work, the competing system was assumed to be an additive one, i.e., the increment of a particular genotype due to its superior competitive ability is equal to the decrement of its less competitive neighbor. Doney et al (63) obtained little evidence of additional variability due to genotypic competitional variance in experiments involving many genotypes of potatoes within plots. Another experiment in which plots consisted of alternating pairs of genotypes revealed strong non-additive competitive effects.

The effect of the number of competitors on a plant was studied by Schutz and Brim (251) in soybeans and Sakai (239) in rice. Both studies applied simple regression methods of the yield of a central tester plant on the number of competing plants in a surrounding ring. The effect on the central plant was in direct proportion with the number of competitors. Harper (107), however, supplied experimental data on two species of Bromus indicating no such linear relationship. The ability of one species to suppress the other was found to be some function of the degree of aggregation of the numbers surrounding any given individual.

F. Interplot Competition:

Studies concerned with the effect of competition of unlike plots and border effects in field experiments were carried out by Brown and Weibel (28), Hollowell and Heusinkveld (123), and Tysdal and Kiesselbach (281) in alfalfa; Gentner (80) and Smith (257) in corn; Christidis (38 and 39), Coombs (46), Green (90), Hancock (102), Hulbert et al (128), Hutchinson and Panse (129), Ligon (178), and Quinby et al (227) in cotton; Proebsting (225) in fruit trees; Down and Thayer (64) in navy beans; Meyers and Perry (202), Hudson and Bates (126), Jacob (135) and Wellhausen (292) in potatoes; Arny (9 and 10), Arny and Hayes (11), Hayes and Arny (111), Hulbert and Remsberg

(127), Kiesselbach (157 and 158), Klages (162 and 163), Love (180), Love and Craig (181), McClelland (193 and 194), Montgomery (206), Stadler (259), Stringfield (266) and Taylor (275) in small grains; Ross (231) in sorghum; Garber and Odland (79), Hanson et al (104), Hartwig et al (110), Hinson and Hanson (120), and Probst (222) in soybeans; Deming and Brewbaker (52) and Immer (131) in sugarbeets; Chittenden (36) in turnips; and by McRostie and Hamilton (201) in western ryegrass.

These investigations entail some discrepancies; but in general show, as summarized by LeCreg (173), (a) that competition among varieties exists in most studies; (b) competition is usually confined to one row on each side of the plot; (c) competition is negligible between varieties of similar growth habits; (d) a high-yielding variety is usually a strong competitor; (e) competition varies with environmental conditions so varieties can not be classified for competitive value and; (f) that competition may arise from differences in planting date, seeding rate, maturity, plant type, height or lodging habits.

G. Genotypic Blends:

Montgomery (206) has pointed out in 1912: "For some reason, in almost every case with both wheat and oats, two varieties in competition have given a greater number of plants at harvest and a greater yield than when either was sown alone". Early investigations concerning the effects of genotypic blends were reviewed by Frankel

(78). From the investigations of Engelke (71), Heuser (119), Nuding (211) and others, he concluded that generally, blends of varieties yield above the expected yields based on the performance of component varieties. In his experiment in wheat, Frankel (78) found that a variety of wheat depressed in every case the yield of the lines which it was blended with, and the total yield of the blend was not higher than the expected based on the average of the two blended lines. He advocated the use of blends in order to stabilize production.

Later studies by Jensen (141), Allard (6), Gustafsson (99), Allard and Hansche (8), Allard and Bradshaw (7), Pfahler (220) and Edwards (68) advocated the utilization of genetically diverse populations for greater stability of performance. Hayes et al (114) discussed multiline varieties and suggested ways of handling them in production. Jensen (141) presented a rather complete review of literature on the importance of diversification in plant breeding. Borlaug (23), Rosen (230) and Suneson (270) have suggested the use of multiline varieties in production to reduce the prevalence and severity of diseases.

Simmond (255) in a review article stated that most of the evidence seemed to be cumulatively powerful, at least in small grains, that there are interactions which result in mixtures that are frequently a few per cent higher in performance than the component means and occasionally higher than the better component.

In wheat and barley Orljanskaja and Poljakov (213), Gustafsson

(99) and Nasypajko (209) have shown that higher yields in a several years average are obtained from variety mixtures than from pure components. Borojevic and Misic (24), however, reported only a slight advantage of the mixture varieties. Gustafsson's best result was a gain of 5.5 per cent over the better component. Griffith (92) presented experimental evidence for the existence of over-compensatory as well as complementary and neutral effects in cereals. Jensen (141) observed in blending several varieties of oats that in all cases the yield of the field blend exceeded that of the average of the single varieties. Wiebe et al (293) studying mixtures of parental and heterozygous barley to simulate filial generations, found no net gain of the mixtures over the pure stands. Jensen and Federer (142) found that competitive effects associated with wheat nurseries enhanced the yields of taller wheats and depressed the yields of shorter wheats. Mixed plantings of tall and short strains produced a bonus. Kuz'min (168) found that mixtures of wheat varieties gave higher yields than pure sowings.

In rice, Grummer and Roy (96) reported that the yield of varietal mixtures was always higher than the mean of their components in pure stands. They suggested that this increase is due to a lower incidence of Helminthosporium oryza in the mixture. Roy (232) found that when two rice varieties are growing together, the effect is as often favorable as unfavorable.

In corn, Stringfield (267) tested forty two-pair hybrids separately and also in two hybrid mixtures and found that the grain yield per acre from the mixture showed remarkable equality to the mean yield of the two hybrids growing separately. Any absolute increase in yield by one of the hybrids in the mixture was compensated by an equal decrease in the other. Similarly, Pendleton and Seif (217) found no loss or gain when they mixed two corn genotypes differing markedly in stature. A single row of dwarf corn bordered by normal corn yielded thirty per cent less than when bordered by dwarf. Conversely a single row of normal bordered by dwarf yielded only six per cent more than when bordered by normal corn. Eberhart et al (67), found in maize single crosses that the average performance of any pair of single crosses grown in mixed stands was similar to their performance in pure stands.

In potatoes, Doney et al (63) demonstrated a gain in performance of a mixture of genotypes over the mean of the component genotypes when grown separately.

In soybeans, experimental evidence presented by Brim and Schutz (27), Caviness (31), Probst (224), and Mumaw and Weber (207) indicated that in general, mixtures perform slightly better than the appropriately weighted means of the component varieties when sown separately but no better than the higher component. Composites of unlike varieties exceeded the mean yield of the pure cultures by more than that for composites of similar varieties. The increase in productivity of the mixture was closely associated with the magnitude of the net competitive effects. Hanson et al (104), however, assumed that the competing system in soybeans was, as suggested by Sakai (238), primarily an additive one, i.e., the increment of a particular genotype due to its superior competitive ability is equal to the decrement of its less competitive neighbor. Experimental results supporting this assumption were presented by Hinson and Hanson (120), Fehr (74) and Torrie (280). Hinson and Hanson (120) in four varieties of soybeans, observed no superiority of mixtures over pure stands. Fehr (74) found that only one of twenty-six blends of 50:50 outyielded the better component. Torrie (280) reported that mixtures of three varieties in two years yielded similar to the average of the component pure lines.

Schutz and Brim (251) surrounded a tested genotype with a ring of 0-8 plants of a competing genotype and calculated the linear regression of the yield of the tested genotype on the number of competitors. By comparing the regression coefficients calculated from reciprocal rings, they defined complementary, overcompensatory and undercompensatory effects. Overcompensation was observed for certain pairs of genotypes and varied in magnitude for the different combinations. They further proposed a design for predicting yield of varietal blends. This design, however, was not effective in predicting mixture yield in the experiments reported by Fehr (74) due to excessive spacing among the hills.

In pasture plants, Donald (61) concludes from a review of experiments that there is no substantial evidence that two species can exploit the environment better than one. He presented an approach to measure whether the association of two species had a mutually harmful or beneficial effect, through the calculation of a "competition index". Papadakis (214) obtained a twenty-one per cent increase in the yield of cereal-legume mixture over that of the two species when grown separately with an increase in cereals and a slight decrease in legume yields. Guy (100) in a competition study in forage plants advocated growing mixtures of genotypes.

Ahlgren and Aamodt (3) suggested that when various common mesophytic pasture plants are associated in pairs, the yield per plant of both species in the mixture is less than the yield per plant in each of the corresponding pure cultures. They explained their experimental findings by "harmful root interactions" presumably of toxic excretions. According to Donald (61), there has been no further evidence to support that study suggesting a mutual depression in yield.

Simmond (255) in his review article stated that there was no real evidence as to the basic mechanism involved in the productive interaction of mixtures. Edwards (68) postulated that in a crop consisting of identical genotypes, there is likely to be competition among plants for the same environmental factors, whereas, if the genotypes are varied, they may make somewhat different demands on the environment and therefore, be less competitive with one another. Elton (70) explained the phenomenon of co-operation on the assumption that different components of a plant community occupy different "niches" from which the competition of others is countered with their own peculiar advantages.

H. Implications of Competition in Plant Breeding:

Sakai (238) concluded from the results of his experiments, that variation of plant characters due to competition must be taken into account and that estimation of heritabilities without considering competition could lead to erroneous results. Similarly, Hanson (103) and Hanson et al (104) presented evidence to show, that when inter-plant competition is introduced with genetic types, the variance among individual plants is doubled and erroneous heritability estimates are obtained. Hinson and Hanson (120) concluded: "A genetic analysis of individual-plant variability for yield can be extremely misleading when plant competition is a factor". Eberhart et al (67) found that estimates of within plot environmental variance for mixed stands of maize single crosses were less than the comparable estimates from pure stands for ear length, diameter and weight.

Christian and Gray (37) and Yamada and Horiuchi (296) have stressed the bias arising in plant selection due to interplant competition. Yamada and Horiuchi (296) proposed that efficient selection of characters correlated negatively with those governing competitive ability should be left to later generations. That plant competition, or lack thereof, has little effect on quality characteristics was demonstrated in soybeans by Hanson et al (104) for protein and oil content. Wiebe et al (293) concluded that, because of competitive effects among barley genotypes, one should save the poorest plants from the F_6 rather than the good ones. Doney et al (63) concluded from studies made using plots of (1) like genotypes and (2) unlike genotypes, that progeny evaluation of potato yields had no effect on selection for combining ability in plots of unlike genotypes.

Jennings and Aquino (138) advocated the rogueing of F_2 populations of rice to eliminate tall leafy and spreading types, which would otherwise shade the potentially more productive segregates. To reduce the bias arising from interplant competition due to unequal seed size in barley, Chebib (33) recommended sorting of seed of early generations according to size or weight before sowing and selecting from nurseries sown from equal seed sizes.

Edwards (68) postulated that competition among individual plants within a variety during critical stages of growth may be of value to the plant breeder by facilitating selection of the best genetic material from the population. Similarly, Degras (51) postulated from an analytical study of the yield of oats that the possibility of selection may be extended by growing populations of mixed genotypes.

MATERIALS AND METHODS

A field experiment was designed to examine the effect of differences in genotype, seed size and plant spacing on the intraplot variation of wheat plants.

Two seed sources were used; (a) a homogeneous population (the variety Manitou) and, (b) a mixture of segregating F_3 lines of the cross Manitou x Pembina.

Samples of small, large and unsorted seeds were obtained from each population by sieving and hand picking, excluding all broken, shrivelled or otherwise abnormal grain. The average seed weights for the two populations were as follows:

Population	Small	Large	Unsorted
Pure	21.2 mgm.	45.2 mgm.	30.3 mgm.
Segregating	20.8 mgm.	44.9 mgm.	30.1 mgm.

A factorial experiment was designed for the study involving three factors:

1. Plant spacing: 2, 4 and 6 inches within the row.
2. Genotype: Pure versus segregating.
3. Seed size: Small, large and unsorted.

The eighteen treatment combinations were arranged in a six replication split plot design with the plant spacings in the main plots. Each subplot consisted of four rows of fifty plants each. The lengths of the rows were 100, 200 and 300 inches for the 2", 4" and 6" spacing treatments respectively. All rows were twelve inches apart.

Due to the unequal lengths of the rows of the main plots, randomization of the main plots within each replication was restricted such that the six-inch spacing main plot was adjacent to the two-inch and four-inch spacing main plots which were laid end-to-end along the length of the row. A sample layout of the three main plots in a replication is shown in Fig. 1.

The experiment was sown on the University of Manitoba farm beginning on May 23rd., 1967.

Harvest data on eleven agronomic characteristics were obtained on a single-plant basis for the forty-six central plants of the two inner rows of each subplot. The eleven characteristics were:

1. Plant height (in inches).
2. Number of tillers.
3. Number of heads (number of head-bearing tillers).
4. Percent fertile tillers.
5. 1000-kernel weight (in grams).
6. Average number of seeds per head.
7. Average number of seeds per tiller.
8. Number of seeds produced.
9. Average yield per head (in grams).
10. Average yield per tiller (in grams).
11. Yield per plant (in grams).

If a plant within a test row were missing, the two adjacent plants were disregarded during the collection of data. The number of plants harvested from each subplot thus ranged between fifteen and seventy-nine for a total of 3,878 plants in the 108 subplots.

Statistical Analysis

In the hope that the eleven dimensions of variation could be

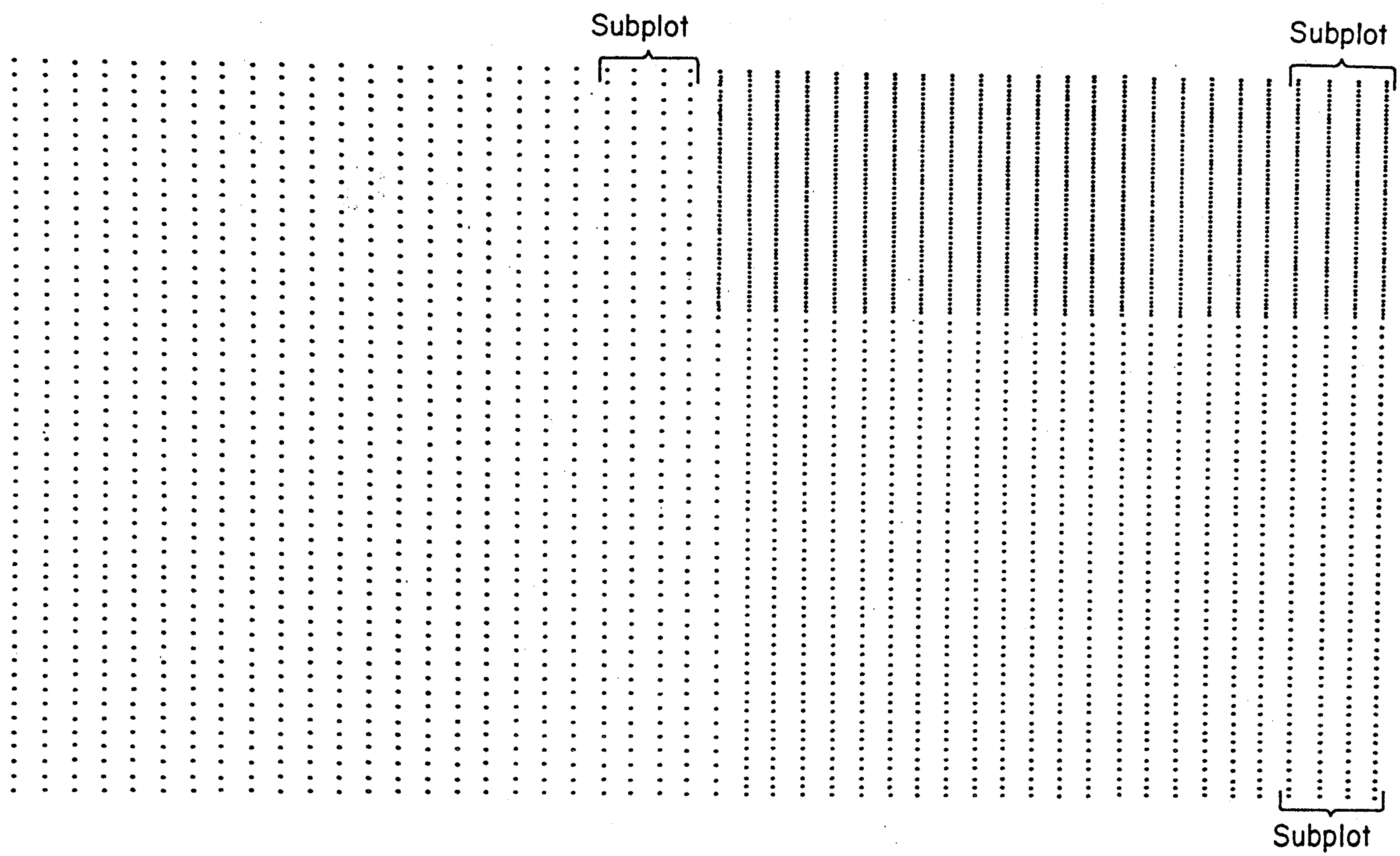

Fig. 1. Arrangement of the main plots within a replication

reduced, the conventional statistical analyses were preceded by a search for principal components from the single plant observations.

The intraplot variances for each of the eleven agronomic characteristics and the major components were then computed and subjected to an analysis of variance and to a multiple regression analysis. All computations were carried out by the use of the University of Manitoba IBM 360-65 computer system through programs developed by the author. A description of the analytical methods is as follows:

I. Principal Component Analysis:

The objective of this analysis was to reduce the number of agronomic characteristics studied to a fewer number of components, each component being a linear function of the eleven characteristics. The scores of the individual plants on each of the more important components will then be calculated and subjected to further statistical analyses.

Principal component analysis was devised in 1933 by Hotelling (124) and its techniques were described by Kendall (156) and Cooley and Lohnes (45). Briefly, and in the present context, it is a method to determine, from the observed agronomic characteristics of the single plants, a set of independent linear functions which could account for the observed variation in the plants, i.e., functions which involve no more than simple addition and subtraction of the observations, and such that the values of one function are not correlated with the values of any other. They are derived in such a way that the first principal component accounts for the largest possible proportion of the total variation in the plant characteristics, the second for the largest possible proportion of the remaining variation and so on until all the variation is accounted for. Thus the sum of the variances of the components equals the sum of the variances of the original characteristics.

In practice it is frequently found that the total variation can, for all practical purposes, be accounted for in terms of fewer components than the number of characteristics initially observed. In this way the analysis can lead to a considerable condensation of the data. Further, because they are independent of each other, the values of these functions are more amenable to study by the conventional statistical methods than are the original data.

The main limitation of this method is that some of the principal components, although derived following sound statistical procedure, may not have any physical meaning. In spite of this and other limitations biologists are more and more finding principal component analysis a useful tool in the study of multivariate data (see for example 30, 121, 122, 256 and 297).

Mathematically, and in this present context, the score of plant $\underline{i}$ on the $\underline{k}$ th. component, $\underline{f}_{ki}$, is a linear transformation of the data of the plant in question for the eleven agronomic characteristics ($\underline{y}_{ij}$, j=1,11), affected by a set of coefficients, or loadings (a_{kj}, j=1,11). These loadings are comparable to a set of standardized partial regression coefficients of component k on the eleven characteristics and may be written as:

$$f_{ki} = a_{k1}z_{1i} + a_{k2}z_{2i} + \dots + a_{k11}z_{11i}$$

$$= \sum_{j=1}^{11} a_{kj}z_{ji} \qquad \begin{matrix} i=1,n \\ k=1,p \end{matrix}$$

where z_{ji} is the standardized observation of plant i for characteristic j,

$$z_{ji} = \frac{y_{ji} - \mu_j}{\sigma_j} \qquad \begin{matrix} i=1,n \\ j=1,m \end{matrix}$$

μ_j and σ_j are the mean and standard deviation for characteristic j respectively, and n, m and p are the number of plants, the number of characteristics and the number of components, respectively.

This relationship may be written in matrix notation as:

$$F'_{(p,n)} = A'_{(p,m)}Z'_{(m,n)}.$$

The calculation of the factor loadings matrix $A \equiv a_{jk}$ was carried out through a principal component analysis of the eleven agronomic characteristics based on the 11 x 11 correlation matrix calculated for the observations taken on all plants. The method is described by Cooley and Lohnes (45). The major principal components, accounting for the largest amount of variability were interpreted and retained for further study. The component scores for each plant on each of the major components were then calculated according to the formula reported above and subjected to the following two statistical analyses.

II. Analysis of Variance

For each of the eleven agronomic characteristics studied and the major principal components retained, the intraplot variances were calculated from single-plant measurements and component scores respectively.

The intraplot variance observed among the plants of a subplot includes a spacing effect, a genotypic effect, a seed size effect and all possible interactions and may be written as:

$$V_{ijk\ell} = \mu + r_i + p_j + \alpha_{ij} + g_k + s_\ell + (gs)_{k\ell} + (pg)_{jk} + (ps)_{j\ell} + (pgs)_{jk\ell} + \varepsilon_{ijk\ell}$$

where $V_{ijk\ell}$ is the intraplot variance for the subplot of the ith. replication, jth. plant spacing, kth. genotype and ℓth. seed size and

$i = 1,6;\ j = 1,3;\ k = 1,2$ and $\ell = 1,3$.

The other symbols represent the contribution of the effect in question to the intraplot variance and are as follows:

μ is the general mean intraplot variance.

r_i is the contribution of the ith. replication.

p_j is the contribution of the jth. plant spacing.

α_{ij} is a random contribution of main plot ij.

g_k is the contribution of the kth. genotype.

s_ℓ is the contribution of the ℓth. seed size.

$(gs)_{k\ell}$ is the contribution of the kth. genotype of the ℓth. seed size.

$(pg)_{jk}$ is the contribution of the kth. genotype sown at the jth.

spacing.

$(ps)_{j\ell}$ is the contribution of the ℓth. seed size sown at the jth. spacing.

$(pgs)_{jk\ell}$ is the contribution of the ℓth. seed size of the kth. genotype under the jth. spacing.

and $\varepsilon_{ijk\ell}$ is a random contribution of the $ijk\ell$th. subplot.

The intraplot variances were subjected to a logarithmic transformation and the transformed data for each variable were subjected to an analysis of variance according to the following allocation of degrees of freedom:

Source of Variation	Degrees of Freedom	
Replication	5	
Plant spacing	2	
linear component		1
quadratic component		1
Main-plot error	10	
Genotype	1	
Seed size	2	
Genotype x seed size	2	
Spacing x genotype	2	
Spacing x seed size	4	
Spacing x genotype x seed size	4	
Subplot error	75	
Total	107	

All main effects and interactions were tested for significance.

On the assumptions that competition of unequal seed types increases the variance in the mixed population, and that it decreases with increased plant spacing, then competition effects may be investigated through an examination of the interactions involving plant spacing.

The effect of plant spacing on the intraplot variance was estimated by a linear regression coefficient of the intraplot variance on plant spacing for each of:

1) Pure genotype (b_{g1}).
2) Segregating genotype (b_{g2}).
3) Uniform seed size (small and large combined) (b_{s1}).
4) Unsorted seed size (b_{s2}).

The degree of competition due to genotype was then measured by the difference $b_{g2} - b_{g1}$, and that for competition due to seed size differences by the difference $b_{s2} - b_{s1}$. These differences were tested for significance by standard statistical procedures.

III. Multiple Regression

This analysis attempted to partition the intraplot variance into its assumed components. Two models, additive and multiplicative were recognized.

A. Additive Model:

Taking any agronomic characteristic such as yield, or any principal component, the total variance observed among the plants of a subplot, for any subplot may be written as:

$$V = V_o + V_1 + V_2 + V_3 + V_4 + V_5$$

where

V_o is the environmental variance.

V_1 is the variance added due to differences in genotype.

V_2 is the variance added due to differences in seed size.

V_3 is the variance added due to wider plant spacing.

V_4 is the variance added due to competition arising from differences in genotype.

and V_5 is the variance added due to competition arising from differences in seed size.

Each of the subplots utilized in this experiment contains, within its total variance V, the environmental variance V_o plus varying degrees of the other variances V_1 to V_5 depending upon its treatment combination. Plots of each treatment combination may, therefore, be described by a set of six independent variables x_o to x_5 to correspond with V_o to V_5 as is shown in Table 1.

The values selected for each of the independent variables x_o to x_5 shown in Table 1 range from 0, where the effect is not present to 1, where the effect is present to a full extent. The values of .5 were selected where the effect was assumed to have a moderate effect. The values of x_o are all fixed at one since all the plots contain the environmental variance.

The intraplot variance will then be a function of x_o to x_5 and may be written as a multiple regression equation of the type:

$$V' = b_o x_o + b_1 x_1 + b_2 x_2 + b_3 x_3 + b_4 x_4 + b_5 x_5$$

where the coefficients b_o to b_5 may be estimated by least squares methods such as:

$\Sigma(V - V')^2$ = minimum. The summation is over all plots.

TABLE 1

VALUES OF THE INDEPENDENT VARIABLES (x_o - x_5) ASSIGNED TO EACH TREATMENT COMBINATION IN THE MULTIPLE REGRESSION ANALYSES

Treatment combination			Source of variability					
Genotype	Spacing	Seed Size	Environment (x_o)	Genotype (x_1)	Seed Size (x_2)	Plant Spacing (x_3)	Genotypic Competition (x_4)	Seed size Competition (x_5)
Pure	2"	Small	1	0	0	0	0	0
Pure	2"	Large	1	0	0	0	0	0
Pure	2"	Unsorted	1	0	1	0	0	1
Pure	4"	Small	1	0	0	0.5	0	0
Pure	4"	Large	1	0	0	0.5	0	0
Pure	4"	Unsorted	1	0	1	0.5	0	0.5
Pure	6"	Small	1	0	0	1	0	0
Pure	6"	Large	1	0	0	1	0	0
Pure	6"	Unsorted	1	0	1	1	0	0
Segregating	2"	Small	1	1	0	0	1	0
Segregating	2"	Large	1	1	0	0	1	0
Segregating	2"	Unsorted	1	1	1	0	1	1
Segregating	4"	Small	1	1	0	0.5	0.5	0
Segregating	4"	Large	1	1	0	0.5	0.5	0
Segregating	4"	Unsorted	1	1	1	0.5	0.5	0.5
Segregating	6"	Small	1	1	0	1	0	0
Segregating	6"	Large	1	1	0	1	0	0
Segregating	6"	Unsorted	1	1	1	1	0	0

The partial regression coefficients b_1 to b_5 estimate the amount of variance added to the subplot variance as a result of a unit increase in the corresponding independent variable. Since the ranges of the independent variables x_1 to x_5 are all 0 to 1, the partial regression coefficients will estimate V_1 to V_5 as defined earlier. The definitions of V_3, V_4 and V_5 however, will have to be modified since they are dependent on the choice of the values for x_3, x_4 and x_5. The modified definitions are as follows:

V_3 is the variance added by increasing the plant spacing from 2" to 6". (V_3 is assumed to equal twice the variance added by increasing the plant spacing from 2" to 4" or from 4" to 6").

V_4 is the variance added due to competition arising from differences in genotype as a result of decreasing the plant spacing from 6" to 2". (V_4 is assumed to equal twice the variance added due to genotypic competition as a result of decreasing the plant spacing from 6" to 4" or from 4" to 2").

V_5 is the variance added due to competition arising from differences in seed size as a result of decreasing the plant spacing from 6" to 2". (V_5 is assumed to equal twice the variance added due to seed size competition as a result of decreasing the plant spacing from 6" to 4" or from 4" to 2").

Since the values of x_o in Table 1 are all fixed at one, and the values of x_1 to x_5 have all been set at 0 for the treatment combinations which do not contain the effect in question, the value of b_o, the intercept of the multiple regression equation, will estimate the environmental variance V_o.

The proportion of variance due to each of V_o to V_5 may therefore, be calculated directly from the coefficients of the multiple regression equation as:

$$P_i = \frac{b_i}{\sum_{j=0}^{5} b_j} \qquad (i=0,5)$$

The standard errors of b_o to b_5 provide tests of significance for these estimates. The square of the multiple correlation coefficient $R^2_{V.12345}$ provides an estimate of the percent of the total variability among the intraplot variances due to the five sources of variability x_1 to x_5 and may be used for comparisons between variables and with other studies.

For each agronomic characteristic studied, and for the major principal components retained, a multiple regression was fitted to measure the effect of the independent variables on the intraplot variance. The values of V_o to V_5 were calculated in each case and tested for significance. The data matrix for each analysis consisted of 108 plots, each containing one dependent variable, the intraplot variance, and five independent variables x_1 to x_5.

The subplot data were corrected for replication effect and for main plot x replication interaction prior to the multiple regression analyses. The correction factor added to the variance of all subplots of spacing _i_ of replication _j_ was

$$\overline{P}_i - \overline{M}_{ij}$$

where $\overline{P}_i$ is the mean variance of the _i_th. spacing and $\overline{M}_{ij}$ is the mean variance of main plot _ij_.

B. Multiplicative Model:

In this model the variance observed among the plants of any subplot (V) may be written as:

$$V = V_o.v_1.v_2.v_3.v_4.v_5$$

where V_o is the environmental variance, v_1, v_2, v_3, v_4 and v_5 are multipliers measuring the respective effects on the environmental variance of: genotypic differences, seed size differences, increased spacing, genotypic competition and seed size competition.

The variance of the plots of each type of treatment combination may be described by a similar equality depending upon the structure of the treatment combination. A list of the twelve equalities involved in this study is as follows:

Type of Treatment Combination

Genotype	Spacing	Seed size	
Pure	2"	Uniform	$V = V_o$
Pure	2"	Unsorted	$V = V_o.v_2.v_5$
Pure	4"	Uniform	$V = V_o.(v_3)^{\frac{1}{2}}$
Pure	4"	Unsorted	$V = V_o.v_2.(v_3)^{\frac{1}{2}}.(v_5)^{\frac{1}{2}}$
Pure	6"	Uniform	$V = V_o.v_3$
Pure	6"	Unsorted	$V = V_o.v_2.v_3$
Segregating	2"	Uniform	$V = V_o.v_1.v_4$
Segregating	2"	Unsorted	$V = V_o.v_1.v_2.v_4.v_5$
Segregating	4"	Uniform	$V = V_o.v_1.(v_3)^{\frac{1}{2}}.(v_4)^{\frac{1}{2}}$
Segregating	4"	Unsorted	$V = V_o.v_1.v_2.(v_3)^{\frac{1}{2}}.(v_4)^{\frac{1}{2}}.(v_5)^{\frac{1}{2}}$
Segregating	6"	Uniform	$V = V_o.v_1.v_3$
Segregating	6"	Unsorted	$V = V_o.v_1.v_2.v_3$

Extracting the logarithms of both sides of each of these equations generates on the right hand side, the independent variables x_o to x_5 presented in Table 1, where the unknowns are the logarithm of V_o and the logarithms of v_1 to v_5, and on the left hand side, the logarithms of the intraplot variance.

The multiple regression of the logarithm of the intraplot variance on the set of independent variables presented in Table 1 will therefore yield a set of coefficients b_o to b_5 measuring the logarithms of V_o and v_1 to v_5.

The net contribution of each source of variation to the total variance will be

$$V_i = V_o v_i - v_o \qquad (i=1,5)$$

and the proportional contribution to the total variance

$$P_i = \frac{V_i}{\sum_{j=0}^{5} V_j} \qquad (i=0,5)$$

where V_1 to V_5 are the variances added as defined for the additive model.

For each agronomic characteristic studied, and for each of the major principal components retained, an analysis similar to that presented for the additive model was performed. The dependent variable in each case was the logarithm of the intraplot variance. The coefficients of the resulting multiple regression equation were retransformed before calculating the variance proportions:

V_o was taken as the antilogarithm of b_o

and V_i was taken as $10^{(b_i + b_o)} - 10^{b_o}$ $(i \neq 0)$

EXPERIMENTAL RESULTS

I. Principal Component Analysis

The intercorrelations, Pearson product moment, among the eleven agronomic characteristics are presented in Table 2. Of the 55 possible correlation coefficients, 48 are significant at the 5% level, 46 of which are significant at the 1% or lower levels.

The correlation table shows high intercorrelations among number of tillers, number of heads, number of seeds and yield ($r \geq .90$); among the number of seeds per head, number of seeds per tiller, yield per head and yield per tiller ($.90 \geq r \geq .68$); and fairly strong intercorrelations among the 1000-kernel weight, yield per head and yield per tiller ($.90 \geq r \geq .66$). Plant height and per cent fertile tillers have no high correlations with any of the agronomic characteristics studied and may be independent.

Five principal components extracted from the 11 x 11 correlation matrix accounted for 99.27 per cent of the total variability and were retained for further analyses. Table 3 presents the principal component pattern. A brief description of these components is as follows:

The first component (C_I) is the most important component. It accounts for over forty-four per cent of the total variability. It is a general component common to all characteristics. Its highest loading is on yield and can, therefore, be defined as "yielding ability". It loads highly on those characteristics which are more logically

TABLE 2

PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS AMONG PAIRS OF ELEVEN AGRONOMIC CHARACTERISTICS (†)

Agronomic characteristic	1	2	3	4	5	6	7	8	9	10	11
1. Plant height											
2. Number of tillers	-02										
3. Number of heads	-02	97									
4. Per cent fertile tillers	02	-03	17								
5. 1000-kernel weight	40	-01	00	06							
6. Number of seeds per head	05	15	13	-07	14						
7. Number of seeds per tiller	06	12	21	49	16	82					
8. Number of seeds per plant	00	93	95	13	03	39	42				
9. Yield per head	27	10	09	-02	69	80	68	30			
10. Yield per tiller	26	07	15	41	66	68	83	33	90		
11. Yield per plant	07	90	91	14	23	40	43	97	43	46	

(†) Decimal points omitted.

TABLE 3

PRINCIPAL COMPONENT MATRIX FOR
ELEVEN AGRONOMIC CHARACTERISTICS (†)

Characteristics	C_I	C_{II}	C_{III}	C_{IV}	C_V
1. Plant height	18	31	60	34	-63
2. Number of tillers	67	-72	17	-03	01
3. Number of heads	71	-69	06	13	01
4. Per cent fertile tillers	26	12	-53	80	02
5. 1000-kernel weight	40	52	58	24	41
6. Number of seeds per head	68	40	-23	-52	-20
7. Number of seeds per tiller	74	41	-50	00	-16
8. Number of seeds per plant	84	-53	-01	-03	-05
9. Yield per head	73	60	18	-23	12
10. Yield per tiller	77	60	-06	14	11
11. Yield per plant	90	-40	11	02	05
Variability explained (%)	44.2	26.0	12.4	10.7	6.0

(†) Decimal points omitted.

related to yield viz. number of tillers, number of heads and number of seeds per plant.

C_{II} accounts for twenty-six per cent of the variability and is composed of a combination consisting of the number of heads and number of tillers in one direction, and the yield per head and yield per tiller in the other direction. Its loading on yield does not exceed .40. This relationship may define this component, after changing the signs of its loadings, as a measure of "physiologic homeostasis".

C_{III} is influenced mostly by plant height and the 1000-kernel weight in one direction and by the per cent fertile tillers and the number of seeds per tiller in the opposite direction. It accounts for 12.4% of the total variability. It is here termed "sterility" for further identification.

The fourth principal component (C_{IV}) accounts for 10.7% of the total variation. It loads highest (.80) on the per cent fertile tillers. It also loads negatively (-.52) on the number of seeds per head. This is probably a result of the arithmetic involved in the calculation of these two characteristics from the original observations and the independence of this component from the characteristic number of seeds per tiller. This component may therefore be referred to as a "mathematic artifice" component.

C_V is the least important principal component. It accounts for six per cent of the total variation. It loads highest (-.63) on plant height and, in the opposite direction, (.41) on the 1000-kernel weight.

It is here termed "shortness" for further identification.

A 3-dimensional representation of the relationship among the agronomic characteristics with the first three principal components as the reference axes is shown in Fig. 2. The distances in this 3-dimensional space between various pairs of characteristics are presented in Table 4.

A distance between two variables should be looked at as the distance between two points located close to the circumference of the unit circle (†). A distance of $\sqrt{2} = 1.414$, therefore, indicates a null relationship between the two variables because the two vectors representing them form a right angle between them. Distances smaller than 1.414 indicate positive correlations up to a distance of 0.0 representing identity of the two vectors or full correlation. Similarly, distances larger than 1.414 indicate negative relations up to a distance of 2.0 which indicates that the two vectors are at 180° angle or a complete negative correlation between the two variables concerned.

Figure 2 and Table 4 reveal the relative positions of the eleven agronomic characteristics. Three groups of characteristics could be recognized: Group 1 consists of the number of heads, number of tillers, number of seeds and the yield. The second group contains the number of seeds per head, the number of seeds per tiller, the yield per head and the yield per tiller. Plant height and 1000-kernel weight form the

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(†) The actual distance of a point from the centre of the circle is the sums of squares of the loadings for the characteristic concerned across the principal components defining the space.

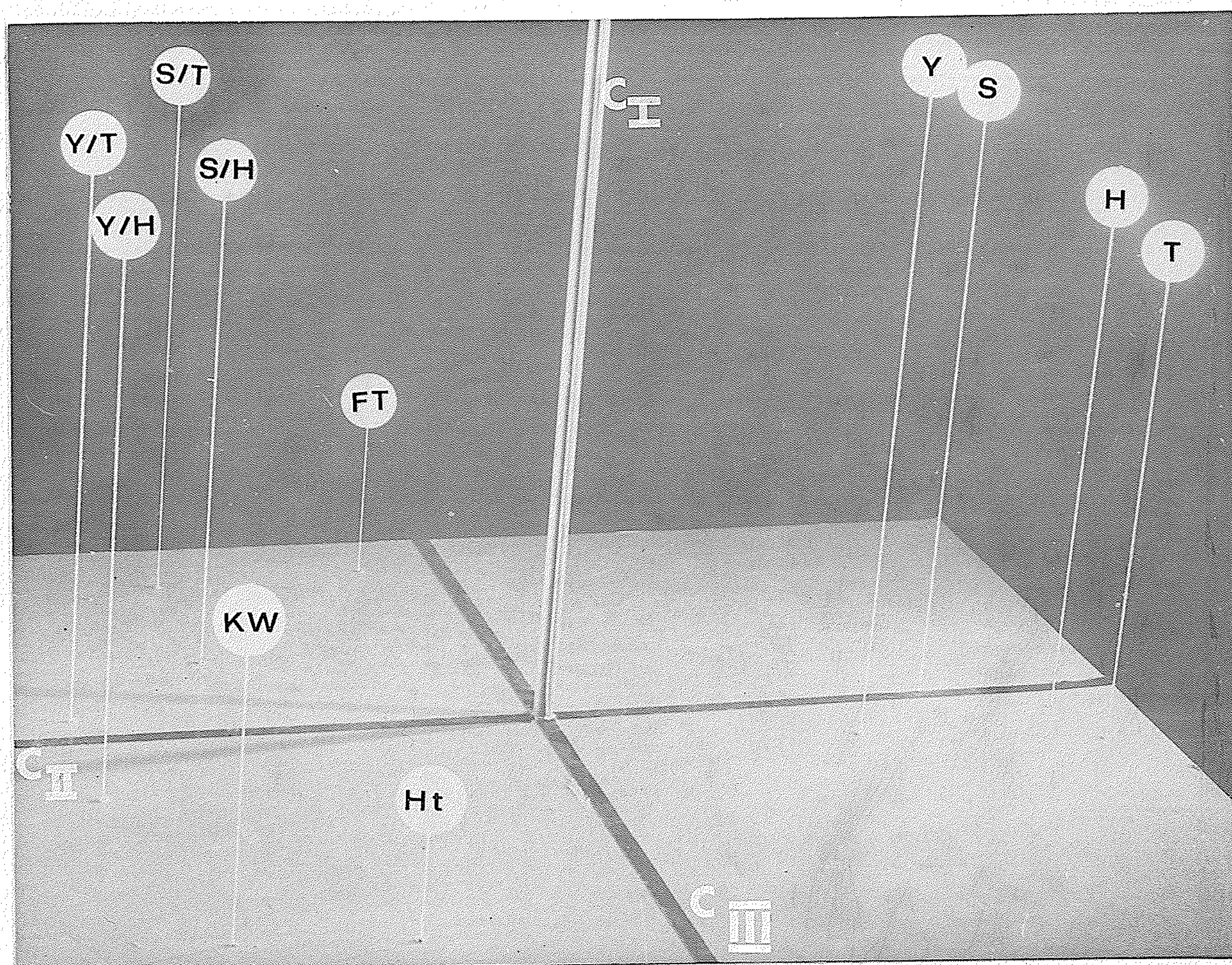

Fig. 2. Relative positions of eleven agronomic characteristics in 3-principal component space

Ht = Plant height. T = Number of tillers. H = Number of heads. FT = Per cent fertile tillers. KW = 1000-kernel weight. S/H = Number of seeds per head. S/T = Number of seeds per tiller. S = Number of seeds per plant. Y/H = Yield per head. Y/T = Yield per tiller. Y = Yield per plant.

TABLE 4

DISTANCES BETWEEN ALL POSSIBLE PAIRS OF CHARACTERISTICS IN 3-DIMENSIONAL SPACE

Agronomic characteristic	1	2	3	4	5	6	7	8	9	10	11
1. Plant height											
2. Number of tillers	1.22										
3. Number of heads	1.25	.12									
4. Per cent fertile tillers	1.15	1.17	1.10								
5. 1000-kernel weight	.31	1.33	1.35	1.19							
6. Number of seeds per head	.97	1.19	1.13	.59	.87						
7. Number of seeds per tiller	1.24	1.32	1.24	.56	1.14	.28					
8. Number of seeds per plant	1.23	.31	.22	1.02	1.28	.97	1.07				
9. Yield per head	.75	1.32	1.30	.98	.53	.46	.71	1.15			
10. Yield per head	.93	1.34	1.30	.84	.74	.28	.48	1.13	.24		
11. Yield per plant	1.12	.40	.35	1.04	1.15	.90	1.03	.19	1.02	1.02	

third group. Per cent fertile tillers does not fall into any distinct group although it is closest to the second group of characteristics.

Expanding the relationships shown in Fig. 2 to the fourth and fifth dimensions on the basis of the loadings of C_{IV} and C_V shown in Table 3, it will be clear that the characteristics of group 1 do not diverge from each other in these new dimensions. A small effect on the number of seeds per head of group 2 is evident in the fourth dimension, while the two characteristics of group 3, plant height and 1000-kernel weight are differentiated considerably in the fifth dimension.

II. Analysis of Variance

The intraplot variances for the 108 plots for each of the eleven agronomic characteristics studied are listed, with the number of plants from which each variance was calculated, in Appendix 1. Intraplot variances for the scores on each of the five principal components retained are shown in Appendix 2.

Intraplot variance means of the eighteen treatment combinations are presented for the eleven agronomic characteristics and for the five principal components in Appendices 3 and 4, respectively.

Results of the analyses of variance performed on the logarithms of the intraplot variances for the eleven characteristics and five components are presented in Tables 5 and 6, respectively.

These analyses revealed significant effects of plant spacing, especially the linear component, on the variances of all agronomic

TABLE 5

ANALYSES OF VARIANCE OF THE LOGARITHM INTRAPLOT VARIANCE FOR ELEVEN AGRONOMIC CHARACTERISTICS

		Mean Square										
Source of Variation	Degrees of freedom	Plant height	No. of tillers	No. of heads	Per cent fertile tillers	1000-kernel weight	No. of seeds per head	No. of seeds per tiller	No. of seeds per plant	Yield per head	Yield per tiller	Yield per plant
Replications	5	.337	.552	.511	.292*	.487	.087	.091	.536	.077	.064	.391
Plant spacing (P)	2	.470*	4.172**	4.584**	.454*	1.885**	.415*	.088	5.832**	.702**	.272*	6.032**
linear component	(1)	.939*	7.913**	8.640**	.163	3.536**	.611*	.131	10.827**	1.244**	.506*	11.379**
quadratic component	(1)	.002	.431	.527	.744*	.234	.219	.045	.822	.160	.038	.685
Main-plot error	10	.102	.256	.229	.085	.189	.076	.045	.248	.085	.059	.188
Genotype (G)	1	.069	.039	.081	.166	.085	.250**	.107*	.029	.321**	.202**	.026
Seed size (S)	2	.077	.066	.104*	.054	.124	.183**	.170**	.184**	.070*	.083*	.108
G x S	2	.086	.063	.034	.139	.069	.029	.004	.000	.026	.013	.006
P x G	2	.054	.025	.014	.077	.005	.026	.011	.005	.069*	.030	.024
P x S	4	.135*	.087*	.076	.100	.164*	.015	.007	.070	.006	.002	.033
P x G x S	4	.030	.001	.003	.120	.024	.044	.006	.015	.015	.004	.004
Subplot error	75	.039	.033	.033	.050	.064	.023	.017	.035	.019	.019	.036

* Significant at the 5% level.
** Significant at the 1% level.

TABLE 6

ANALYSES OF VARIANCE OF THE LOGARITHM INTRAPLOT VARIANCE FOR FIVE PRINCIPAL COMPONENTS

Source of variation	Degrees of freedom	Mean Square				
		C_I Yielding ability	C_{II} Homeostasis	C_{III} Sterility	C_{IV} Mathematic artifice	C_V Shortness
Replications	5	.295	.101	.393**	.205*	.429**
Plant spacing (P)	2	2.151**	.769**	.127*	.111	.433*
linear component	(1)	4.138**	1.298**	.253*	.032	.739**
quadratic component	(1)	.165	.239*	.001	.190*	.128
Main-plot error	10	.134	.042	.029	.037	.066
Genotype (G)	1	.097	.209**	.081*	.297**	.125
Seed size (S)	2	.104*	.040	.093*	.069	.081
G x S	2	.007	.018	.062*	.048	.079
P x G	2	.017	.058*	.007	.020	.088
P x S	4	.014	.027	.017	.042	.113
P x G x S	4	.003	.013	.024	.077	.019
Subplot error	75	.027	.018	.019	.033	.043

* Significant at the 5% level.
** Significant at the 1% level.

characteristics and principal components with the exception of the number of seeds per tiller and C_{IV}, the mathematic artifice component. Significant effects due to genotype, seed size and their interaction with plant spacing were also detected for some agronomic characteristics and principal components. The interaction genotype x seed size was significant in one instance only. The main effects are studied in Tables 7, 8 and 9, and the interactions involving plant spacing are studied in Tables 10 and 11.

Table 7 shows the mean intraplot variance of the three plant spacings for each of the variables studied. Except for per cent fertile tillers and C_{IV}, the mathematic artifice component, wider plant spacing increased the intraplot variance. A linear relationship between plant spacing and the logarithm intraplot variance was, in most of these cases, as shown from Tables 5 and 6, significant.

Table 8 shows, for each of the variables studied, a comparison between intraplot variances of the pure genotype and that for the segregating population. In every case, the mean intraplot variance for the segregating material was greater than the corresponding mean for the pure genotype. These differences, however, were significant only for the four agronomic characteristics measuring production of grain per unit head or tiller. The differences for the components C_{II}, C_{III} and C_{IV} were significant at the one per cent level as shown from Table 6.

Table 9 shows the mean intraplot variance for the three seed

TABLE 7

MEANS AND STANDARD ERRORS OF INTRAPLOT VARIANCES FOR PLOTS SOWN AT THREE PLANT SPACINGS FOR ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS (†)

Agronomic characteristic	2" spacing	4" spacing	6" spacing	Standard error
Plant height	4.776	6.331	8.081	1.130
No. of tillers	13.661	39.898	62.880	1.214
No. of heads	11.819	36.918	58.268	1.202
% fertile tillers	0.011	0.007	0.009	1.118
1000-kernel weight	5.521	11.546	15.320	1.182
No. of seeds per head	26.072	40.165	39.843	1.112
No. of seeds per tiller	32.525	39.628	39.590	1.085
No. of seeds per plant	14.122	52.811	84.228	1.210
Yield per head	0.037	0.060	0.068	1.118
Yield per tiller	0.042	0.056	0.062	1.098
Yield per plant	14.650	53.995	91.397	1.181
<u>Principal component</u>				
C_1 : Yielding ability	8.210	17.252	24.761	1.151
C_{II} : Homeostasis	3.304	5.664	6.132	1.081
C_{III}: Sterility	1.148	1.300	1.508	1.068
C_{IV} : Mathematic artifice	1.111	0.950	1.224	1.077
C_V : Shortness	0.231	0.345	0.368	1.103

(†) Retransformed data. Standard errors are applied to the means multiplicatively.

TABLE 8

MEANS AND STANDARD ERRORS OF INTRAPLOT VARIANCES FOR PURE AND SEGREGATING GENOTYPES FOR EACH OF ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS (†)

Agronomic characteristic	Pure	Segregating	Standard error
Plant height	5.899	6.626	1.064
No. of tillers	31.090	33.938	1.059
No. of heads	27.608	31.319	1.059
% fertile tillers	0.008	0.010	1.072
1000-kernel weight	9.302	10.582	1.083
No. of seeds per head	31.045	38.748	1.048
No. of seeds per tiller	34.498	39.880	1.042
No. of seeds per plant	38.735	40.796	1.061
Yield per head	0.047	0.060	1.045
Yield per tiller	0.047	0.058	1.045
Yield per plant	40.186	43.186	1.061
Principal component			
C_I : Yielding ability	14.180	16.279	1.052
C_{II} : Homeostasis	4.391	5.378	1.043
C_{III} : Sterility	1.230	1.396	1.045
C_{IV} : Mathematic artifice	0.965	1.229	1.059
C_V : Shortness	0.285	0.333	1.067

(†) Retransformed data. Standard errors are applied to the means multiplicatively.

TABLE 9

MEANS AND STANDARD ERRORS OF INTRAPLOT VARIANCES OF THREE SEED SIZES FOR ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS (†)

Agronomic characteristic	Small seed	Large seed	Unsorted seed	Standard error
Plant height	5.583	6.353	6.890	1.079
No. of tillers	32.516	29.414	35.836	1.073
No. of heads	29.063	26.147	33.457	1.072
% fertile tillers	0.008	0.009	0.009	1.089
1000-kernel weight	8.622	10.026	11.297	1.102
No. of seeds per head	29.772	33.963	41.263	1.060
No. of seeds per tiller	32.551	35.443	44.230	1.052
No. of seeds per plant	37.188	35.363	47.767	1.075
Yield per head	0.049	0.052	0.059	1.055
Yield per tiller	0.048	0.051	0.059	1.055
Yield per plant	39.620	37.958	48.075	1.075
Principal component				
C_{I} : Yielding ability	14.028	14.269	17.521	1.065
C_{II} : Homeostasis	4.630	4.669	5.308	1.052
C_{III}: Sterility	1.238	1.213	1.500	1.055
C_{IV} : Mathematic artifice	0.977	1.110	1.191	1.073
C_{V} : Shortness	0.272	0.321	0.335	1.083

(†) Retransformed data. Standard errors are applied to the means multiplicatively.

types studied, for each of the eleven characteristics and five principal components. It is noted that, in every case, the variance for the unsorted seed type is greater than the corresponding variance for the uniform size seed. These differences were, as shown from Tables 5 and 6, significant for six agronomic characteristics and two principal components.

The effects of competition, as measured by comparison of the linear regression of the logarithm of intraplot variance on plant spacing for the two compared seed types, are presented in Tables 10 and 11.

Table 10 shows the effect of competition due to differences in genotype on each of the variables studied. No significant effects of genotypic competition were detected for any of the agronomic characteristics and principal component studied.

Table 11 shows the effect of competition arising from differences in seed size on each of the variables studied by comparing the regression coefficients for the uniform seed size with those for the unsorted seed. The effect of competition due to seed size was found to be significant for five agronomic characteristics and one principal component.

III. Multiple Regression Analysis

The intraplot variances for the 108 plots for each of the eleven agronomic characteristics studied and the five principal components

TABLE 10

EFFECT OF COMPETITION DUE TO DIFFERENCES IN GENOTYPE ON ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS

Agronomic characteristic	Regression coefficient (†) For pure genotype	For segregating genotype	Genotypic competition (difference)
Plant height	.0558	.0583	-.0025
No. of tillers	.1640**	.1553**	.0087
No. of heads	.1698**	.1642**	.0056
% fertile tillers	-.0269	-.0237	-.0032
1000-kernel weight	.1060*	.1055*	.0005
No. of seeds per head	.0389	.0335	.0054
No. of seeds per tiller	.0152	.0147	.0005
No. of seeds per plant	.1945**	.1851**	.0094
Yield per head	.0580*	.0472*	.0108
Yield per tiller	.0343	.0304	.0039
Yield per plant	.1995**	.1868**	.0127
Principal component			
C_{I} : Yielding ability	.1157**	.1103**	.0054
C_{II} : Homeostasis	.0647**	.0475*	.0172
C_{III} : Sterility	.0262	.0263	-.0001
C_{IV} : Mathematic artifice	.0007	.0109	-.0102
C_{V} : Shortness	.0518	.0453	.0065

(†) Slope of linear regression on plant spacing of logarithm intraplot variance.
* Significant at the 5% level.
** Significant at the 1% level.

TABLE 11

EFFECT OF COMPETITION DUE TO DIFFERENCES IN SEED SIZE ON ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS

Agronomic characteristic	Regression coefficient (†) For uniform size seed	Regression coefficient (†) For unsorted seed	Seed size competition (difference)
Plant height	.0750*	.0213	.0537*
No. of tillers	.1839**	.1294**	.0545*
No. of heads	.1912**	.1373**	.0539*
% fertile tillers	-.0356	-.0002	-.0354
1000-kernel weight	.1354**	.0616	.0738*
No. of seeds per head	.0502*	.0377	.0125
No. of seeds per tiller	.0278	.0085	.0193
No. of seeds per plant	.2138**	.1542**	.0596*
Yield per head	.0682**	.0609*	.0073
Yield per tiller	.0440*	.0377	.0063
Yield per plant	.2109**	.1745**	.0364
<u>Principal component</u>			
C_I : Yielding ability	.1295**	.1006**	.0289
C_{II} : Homeostasis	.0777**	.0460	.0317
C_{III}: Sterility	.0364	.0161	.0203
C_{IV} : Mathematic artifice	.0054	.0209	-.0155
C_V : Shortness	.0687*	.0145	.0542*

(†) Slope of linear regression on plant spacing of logarithm intraplot variance.
* Significant at the 5% level.
** Significant at the 1% level.

retained are presented, with the number of plants from which each variance was calculated, in Appendices 1 and 2. Results of the multiple regression analyses according to the additive and multiplicative models were as follows:

A. Additive Model:

Table 12 presents, for each of the eleven agronomic characteristics studied, the values of the multiple correlation coefficient and the partial regression coefficients measuring the effects of the independent variables presented in Table 1 on the intraplot variance. The coefficients of the multiple regression equation, b_o to b_5 estimate the amount of variance contributed by each of the environment V_o, and the other five effects under study, V_1 to V_5. It is noted that, except for one characteristic, per cent fertile tillers, a significant effect of the sources of variation on the intraplot variance was found. The multiple correlation coefficients for the number of tillers, number of heads, number of seeds per plant and yield exceeded .70. A large part of this effect was the contribution of wider plant spacing which was the major factor in most of the characteristics under study. Genotypic differences did not show any significant effect on the intraplot variance in any of the agronomic characteristics studied. Seed size differences increased the intraplot variance significantly in two characteristics, number of seeds per head and number of seeds per tiller. Increased variance due to competition was not revealed in any characteristic studied.

TABLE 12

RESULTS OF THE MULTIPLE REGRESSION ANALYSES
FOR ELEVEN AGRONOMIC CHARACTERISTICS
ACCORDING TO THE ADDITIVE MODEL

Agronomic characteristic	Multiple correlation coefficient (R)	Environmental effect (b_o)	Genotypic effect (b_1)	Seed size effect (b_2)	Spacing effect (b_3)	Genotypic competition effect (b_4)	Seed size competition effect (b_5)
Plant height	0.38*	4.35**	1.14	-1.35	4.85**	0.49	3.30
Number of tillers	0.73**	15.71**	5.63	-4.00	57.92**	-3.86	11.81
Number of heads	0.76**	12.34**	9.05	-0.35	53.00**	-6.44	8.88
Per cent fertile tillers	0.29	0.01**	0.001	0.003	-0.003	0.001	-0.003
1000-kernel weight	0.49**	5.68**	1.39	1.43	12.05**	1.09	2.10
Number of seeds per head	0.50**	23.69**	6.73	11.66*	14.46*	3.86	-1.52
Number of seeds per tiller	0.50**	29.17**	2.85	10.34*	9.37	2.58	2.46
Number of seeds per plant	0.77**	16225*	5782	6505	77319**	-4458	8604
Yield per head	0.63**	0.034**	0.007	0.007	0.034**	0.009	-0.004
Yield per tiller	0.54**	0.037**	0.006	0.006	0.023**	0.007	-0.002
Yield per plant	0.77**	14.44*	7.00	7.00	83.75**	-3.16	3.12

* Significant at the 5% level.
** Significant at the 1% level.

The percentages of the intraplot variance due to each source, as calculated from the coefficients derived from the additive model, are presented, for the eleven agronomic characteristics studied, in Table 13. Wider plant spacing was the major source contributing to the intraplot variance. It accounted for over 72 per cent of the variance for yield. This source, however, had little effect on the four characteristics which measure production per unit head or unit tiller viz., number of seeds per head, number of seeds per tiller, yield per head and yield per tiller. The contribution of the environment ranged from 12.4 per cent for yield to 67.2 per cent for the per cent fertile tillers. The genetic contribution to the variance was in all cases low and ranged between 5 and 11 per cent. Effect of genotypic competition was negligible in most cases while competition arising from seed size differences accounted for over 23 per cent of the variance in plant height.

Results of the multiple regression analyses of the principal component scores variances are shown, for each of the five components retained, in Table 14. The coefficients of the multiple regression equation b_o to b_5 estimate the amount of variance contributed, to the component scores variance, by each of the environment, V_o, and the other five effects under study, V_1 to V_5. It is noted that there exists a significant effect of the sources of variation on the variances of all components. The multiple correlation coefficients decreased with the decreasing importance of the components:

TABLE 13

PER CENT VARIANCE DUE TO THE VARIANCE COMPONENTS FOR ELEVEN AGRONOMIC CHARACTERISTICS (ADDITIVE MODEL)

Agronomic characteristic	Environmental effect	Genotypic effect	Seed size effect	Spacing effect	Genotypic competition effect	Seed size competition effect
Plant height	30.76	8.08	0.0(†)	34.33	3.46	23.37
Number of tillers	17.25	6.18	0.0	63.60	0.0	12.97
Number of heads	14.82	10.87	0.0	63.65	0.0	10.66
Per cent fertile tillers	67.22	7.97	20.28	0.0	4.53	0.0
1000-kernel weight	23.92	5.85	6.01	50.78	4.58	8.86
Number of seeds per head	39.23	11.14	19.30	23.94	6.39	0.0
Number of seeds per tiller	51.37	5.03	18.22	16.51	4.54	4.33
Number of seeds per plant	14.18	5.05	5.69	67.56	0.0	7.52
Yield per head	35.83	7.90	11.06	36.03	9.18	0.0
Yield per tiller	44.71	6.66	12.32	28.11	8.20	0.0
Yield per plant	12.42	6.02	6.83	72.05	0.0	2.68

(†) Negative contributions were considered zero.

TABLE 14

RESULTS OF THE MULTIPLE REGRESSION ANALYSES FOR FIVE PRINCIPAL COMPONENTS ACCORDING TO THE ADDITIVE MODEL

Principal component	Multiple correlation coefficient (R)	Environmental effect (b_o)	Genotypic effect (b_1)	Seed size effect (b_2)	Spacing effect (b_3)	Genotypic competition effect (b_4)	Seed size competition effect (b_5)
C_I - Yielding ability	0.72**	8.01**	2.58	3.51	17.73**	-1.45	0.31
C_{II} - Homeostasis	0.65**	2.88**	0.24	-0.15	3.85**	1.18	1.16
C_{III} - Sterility	0.47**	1.02**	0.10	0.20	0.52**	0.07	0.21
C_{IV} - Mathematic artifice	0.36*	0.96**	0.33	0.34	0.06	0.05	-0.25
C_V - Shortness	0.35*	0.22**	0.05	-0.01	0.20*	0.04	0.11

* Significant at the 5% level.
** Significant at the 1% level.

$R_{I.12345} = .72$, $R_{V.12345} = .35$. The change in the intraplot variance of the component scores, however, was solely due to wider plant spacing in all components with the exception of C_{IV}, the mathematic artifice component.

The percentages of the score intraplot variance due to each source, for each of the five components, as calculated from the coefficients derived from the additive model are presented in Table 15. Wide plant spacing was the major source of variance for the first two principal components. It accounted for 55% of the variance of the scores on C_I, yielding ability, and 41% of the variance of the scores on C_{II}, homeostasis. It also contributed a large proportion to the variance of the scores on C_{III} and C_V. C_{IV}, the mathematic artifice component, was not affected by wider plant spacing. Environmental contribution to all components was appreciable and ranged between 24 and 54 per cent. The genetic and seed size effects were low for all components with the exception of C_{IV}, where each contribution approached 20 per cent. Competition effects were generally low; each of seed size competition and genotypic competition contributed about 13 per cent to the variance of C_{II} scores, and seed size competition contributed 17 per cent to the variance of C_V scores which measure plant height.

B. Multiplicative Model:

Results of the multiple regression analyses for the multiplicative model are presented in Table 16. The coefficients v_1 to v_5 are the

TABLE 15

PER CENT VARIANCE DUE TO THE VARIANCE COMPONENTS
FOR FIVE PRINCIPAL COMPONENTS (ADDITIVE MODEL)

Principal component	Environmental effect	Genotypic effect	Seed size effect	Spacing effect	Genotypic competition effect	Seed size competition effect
C_{I} - Yielding ability	24.93	8.04	10.91	55.16	0.0 (†)	0.96
C_{II} - Homeostasis	30.96	2.54	0.0	41.34	12.72	12.44
C_{III} - Sterility	48.04	4.87	9.31	24.37	3.44	9.97
C_{IV} - Mathematic artifice	54.85	19.11	19.68	3.37	2.99	0.0
C_{V} - Shortness	35.73	8.35	0.0	31.96	6.23	17.33

(†) Negative contributions were considered zero.

TABLE 16

RESULTS OF THE MULTIPLE REGRESSION ANALYSES FOR ELEVEN AGRONOMIC CHARACTERISTICS ACCORDING TO THE MULTIPLICATIVE MODEL (†)

Agronomic characteristic	Multiple correlation coefficient (R)	Environmental effect (v_o)	Genotypic effect (v_1)	Seed size effect (v_2)	Spacing effect (v_3)	Genotypic competition effect (v_4)	Seed size competition effect (v_5)
Plant height	0.51**	4.00**	1.14	0.90	1.98**	0.98	1.64
Number of tillers	0.85**	12.09**	0.99	0.90	5.99**	1.21	1.65*
Number of heads	0.86**	10.29**	1.04	0.95	6.32**	1.18	1.64*
Per cent fertile tillers	0.26	0.01**	1.20	1.24	0.72	1.00	0.72
1000-kernel weight	0.65**	4.56**	1.08	0.87	3.66**	1.10	1.97*
Number of seeds per head	0.59**	21.32**	1.11	1.23	1.78**	1.26	1.12
Number of seeds per tiller	0.54**	26.96**	1.09	1.19	1.37**	1.13	1.20
Number of seeds per plant	0.87**	12678**	0.97	1.00	7.77**	1.18	1.73*
Yield per head	0.71**	0.03**	1.08	1.14	2.22**	1.41**	1.07
Yield per tiller	0.60**	0.04**	1.10	1.16	1.67**	1.24	1.06
Yield per plant	0.88**	13.40**	0.96	1.05	7.79**	1.25	1.40

* Significant at the 5% level.
** Significant at the 1% level.
(†) Retransformed coefficients.

antilogarithms of the partial regression coefficients and they represent multipliers affecting the environmental variance V_o which is the antilogarithm of b_o. A v value of unity does not contribute to the total variance while values larger than one increase the variance multiplicatively. The tests of significance of v_1 to v_5 are, therefore, for differences from unity rather than from zero. It is noted from Table 16, that the multiplicative model revealed, for all agronomic characteristics studied with the exception of per cent fertile tillers, significant effects of the sources of variation on the intraplot variance and larger multiple correlation coefficients than the corresponding coefficients derived from the additive model. The effect of wider plant spacing was highly significant in all these cases and increased the variance by from 1.37 to 7.79 times the environmental variance. No significant effect of genotype or seed size was detected in any agronomic characteristic. The effect of genotypic competition was significant for yield per head. Seed size competition showed significant effects on the variances for the number of tillers, number of heads, 1000-kernel weight and the number of seeds per plant.

Table 17 shows the percentages of the total variance due to each source for each of the eleven characteristics as calculated from the results of the regression analyses according to the multiplicative model. Wider plant spacing is the major source contributing to the total variance. Its contribution to the variance of the 1000-kernel weight was 55 per cent. The environmental contribution was the next major

TABLE 17

PER CENT VARIANCE DUE TO THE VARIANCE COMPONENTS FOR ELEVEN AGRONOMIC CHARACTERISTICS (MULTIPLICATIVE MODEL)

Agronomic characteristic	Environmental effect	Genotypic effect	Seed size effect	Spacing effect	Genotypic competition effect	Seed size competition effect
Plant height	36.36	4.91	0.0 (†)	35.44	0.0	23.29
Number of tillers	14.58	0.0	0.0	72.80	3.10	9.52
Number of heads	13.91	0.61	0.0	74.02	2.52	8.94
Per cent fertile tillers	69.44	13.77	16.79	0.0	0.0	0.0
1000-kernel weight	20.76	1.73	0.0	55.14	2.14	20.23
Number of seeds per head	39.97	4.46	9.00	31.29	10.41	4.87
Number of seeds per tiller	50.60	4.44	9.69	18.86	6.56	9.85
Number of seeds per plant	11.53	0.0	0.01	78.00	2.03	8.43
Yield per head	34.24	2.86	4.74	41.85	13.92	2.39
Yield per tiller	44.95	4.42	7.32	30.01	10.58	2.72
Yield per plant	11.79	0.0	0.57	80.03	2.91	4.70

(†) Negative contributions were considered zero.

contributor. Its contribution reached approximately 70 per cent for the per cent fertile tillers and over 34 per cent for each of the variances in plant height, number of seeds per head, number of seeds per tiller, yield per head and yield per tiller. The contributions of genotypic differences, seed size differences and competition were small in all but a few cases.

Results of the multiple regression analyses for the multiplicative model for each of the five principal components are presented in Table 18. The coefficients v_1 to v_5 are the antilogarithms of the partial regression coefficients and they represent multipliers affecting the environmental variance, V_o, which is the antilogarithm of b_o. With the exception of C_{IV}, the mathematic artifice component, the multiple correlation coefficients were significant at the one per cent level and larger than the corresponding coefficients of the additive model. Spacing effect was significant in four components. Genotypic competition showed significant effects on C_{II} while seed size competition affected C_{II} and C_V significantly.

Table 19 shows the percentages of the total variance in the scores of each component due to each variance source calculated according to the multiplicative model. Wider plant spacing was the major contributory source to the variance of the first two components. It also contributed heavily to the variances of C_{III} and C_V. The contribution of the environment ranged between 23 and 64 per cent. Genotype and seed size differences contributed 14 to 18 per cent to the variance of C_{IV}.

TABLE 18

RESULTS OF THE MULTIPLE REGRESSION ANALYSES FOR FIVE PRINCIPAL COMPONENTS ACCORDING TO THE MULTIPLICATIVE MODEL (†)

Principal component	Multiple correlation coefficient (R)	Environmental effect (V_o)	Genotypic effect (v_1)	Seed size effect (v_2)	Spacing effect (v_3)	Genotypic competition effect (v_4)	Seed size competition effect (v_5)
C_I - Yielding ability	.82**	6.96**	1.05	1.08	3.60**	1.19	1.30
C_{II} - Homeostasis	0.71*	2.68**	1.02	0.99	2.45**	1.44**	1.34*
C_{III} - Sterility	0.49**	0.96	1.10	1.12	1.44**	1.06	1.21
C_{IV} - Mathematic artifice	0.34*	0.90	1.28	1.23	1.05	0.99	0.87
C_V - Shortness	0.46**	0.19	1.11	0.88	1.98**	1.10	1.65**

* Significant at the 5% level.
** Significant at the 1% level.
(†) Retransformed coefficients.

TABLE 19

PER CENT VARIANCE DUE TO THE VARIANCE COMPONENTS
FOR FIVE PRINCIPAL COMPONENTS (MULTIPLICATIVE MODEL)

Principal component	Environmental effect	Genotypic effect	Seed size effect	Spacing effect	Genotypic competition effect	Seed size competition effect
C_{I} - Yielding ability	23.63	1.21	1.99	61.42	4.55	7.20
C_{II} - Homeostasis	30.78	0.68	0.0(†)	44.67	13.41	10.46
C_{III} - Sterility	51.98	5.23	5.98	22.91	3.24	10.66
C_{IV} - Mathematic artifice	64.37	17.88	14.72	3.03	0.0	0.0
C_{V} - Shortness	35.15	3.98	0.0	34.42	3.67	22.78

(†) Negative contributions were considered zero.

Genotypic competition constituted 13% of the variance of C_{II}, homeostasis; while seed size competition accounted for 10 to 23 per cent of the variance of three components.

DISCUSSION AND CONCLUSIONS

With the exception of the principal component analysis, the statistical analyses in this study were all performed on the intraplot variances for each of the plant characteristics and on the intraplot variances for the components' scores, which are functions of these characteristics. Analyses of the actual magnitudes of the characteristics, which are adopted in conventional analyses, do not contribute to the objectives of this study and were therefore ignored. These are presented for reference, in Appendix 5, as treatment combination means computed for each agronomic characteristic over the six replications.

It is assumed that the intraplot variance provides an adequate measure of the amount of variability existing in a plot and encompasses more or less equal range of each of the various variance components. It is however recognized, that due to the relatively small sample size, an average of 36 plants per plot, and due to the complex inheritance of most of the characteristics under study, each plot may encompass a lesser amount of the genetic and the genetic competitional variances than of the other types of variance viz.: those due to environment, spacing, seed size and seed size competition. If this is the case, the former two types of variance may be underestimated.

The natural limitations in the scope of this study should be noted. The results obtained are based on one year's data and, therefore, are dependent on the environmental conditions which prevailed in 1967 and their interactions with a specific set of experimental material, i.e., one cross in one species. The repeatability of the results can not be determined. As a consequence, emphasis is placed in the following discussion on the analytical methods. The procedures devised in measuring the effects under study may be of importance in providing an approach which can be used in similar situations.

I. The Principal Components

The use of the multivariate analysis method, principal component analysis, was effective in fully describing the eleven agronomic characteristics by means of the five functions C_I to C_V. The percentage variability left unexplained does not exceed 1% of that in the eleven characteristics. Further it provided a simplified picture of the interrelationships among yield and the morphological yield components. An arrow diagram illustrating the effect of the five principal components on the eleven agronomic characteristics, based on the principal component matrix shown in Table 3, is presented in Fig. 3.

The first principal component, termed "yielding ability", accounts for 44 per cent of the variance in the eleven agronomic characteristics and may be written as:

$$C_I = .18z_1 + .67z_2 + .71z_3 + .26z_4 + .40z_5 + .68z_6 + .74z_7 + $$
$$+ .84z_8 + .73z_9 + .77z_{10} + .90z_{11}$$

where $\underline{z_1}$ to $\underline{z_{11}}$ are the standard deviates for the eleven agronomic characteristics in the order listed in Table 3.

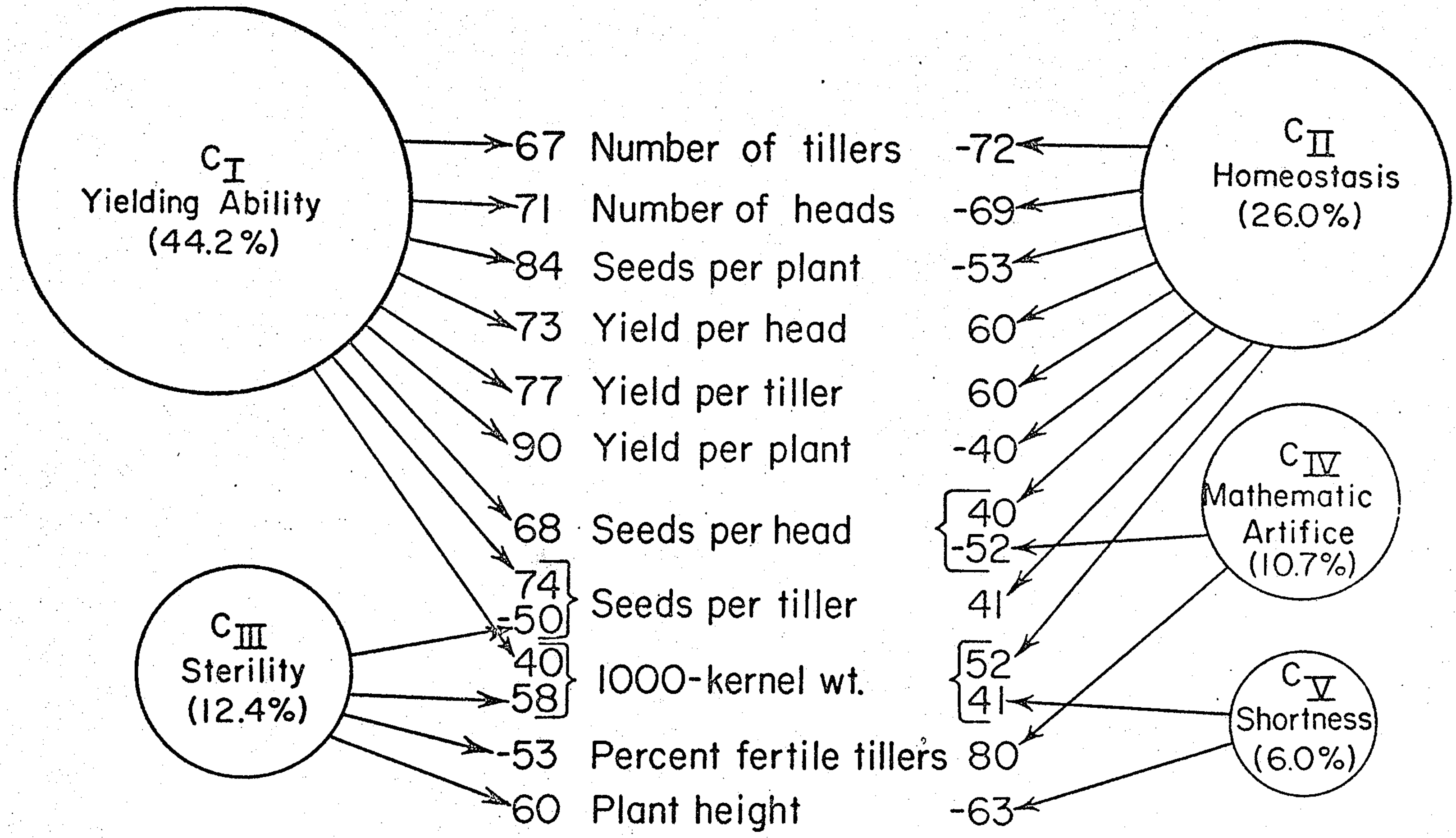

Fig. 3. Major interrelationships of eleven agronomic characteristics and five principal components

(loadings ≥ 0.40 are illustrated)

The score of any plant on this component is greatly affected by its yield and the other characteristics related to yield *viz.*, number of tillers, number of heads, number of seeds per head, number of seeds per tiller and number of seeds per plant. Plant height and per cent fertile tillers contribute little to the plant score on this component. The interrelationships of yield and the major contributors to yield are fully expressed in this function.

The second principal component, termed "physiologic homeostasis", accounts for 47% of the variability remaining after the first component is extracted. As seen from its loadings on the various characteristics, this bipolar component describes a quantitative balance between the number of producing units and the amount of production per unit, *i.e.*, as the number of tillers, heads and total number of seeds produced increase, there is a corresponding decrease in the number of seeds per tiller, number of seeds per head, yield per tiller and yield per head with total yield little affected. This relationship conforms with the theory of physiologic homeostasis as outlined by Lerner (176). Further, since principal components are mutually orthogonal, yielding ability, as described by the first component, and physiologic homeostasis, as defined by this component, are not correlated.

The term "sterility" was chosen for the third principal component for lack of a better descriptive term. This bipolar component is affected by plant height and 1000-kernel weight in one direction and by the per cent fertile tillers and number of seeds per tiller in the opposite direction. It indicates that taller plants, with heavier kernels, produced a smaller number of head bearing tillers and consequently a smaller number of seeds per tiller. This may be an effect of breakage and loss of heads with shrivelled or light seeds before and during harvest.

The fourth component was termed "mathematic artifice". It shows a negative association between the per cent fertile tillers and the number of seeds per head and is independent of the number of seeds per tiller. These three characteristics were computed for each plant from the harvest data by the possible ratios of number of heads, number of tillers and number of seeds per plant. For any plant, the product of the per cent fertile tillers by the number of seeds per head is arithmetically equivalent to the number of seeds per tiller which is, as far as this component is concerned, a constant. This resulted in the observed negative but spurious relationship between the two characteristics comprising this component.

The fifth principal component was termed "shortness" for lack of a better agronomic expression. It is a bipolar component, affected negatively by plant height and positively by the 1000-kernel weight. Short, plump-seeded plants will, therefore, have high scores on this component. Being the least important component, accounting for no more than 6% of the total variability, conclusions drawn about it should be given little concern.

The relative distances of the agronomic characteristics from each other in 3-dimensional space, presented in Table 4, are a by-product of the principal component analysis. They provide another aspect for examining the interrelationships among the variables and a method of grouping them on the basis of these relationships.

The distances among the agronomic characteristics, in the 5-dimensional space defined by the five principal components, have been computed from the principal component matrix and are presented in Appendix 6. Any discrepancy between these distances and the theoretical distances in the 11-dimension space, which may be computed from the individual correlation coefficients as $\sqrt{2\ (1-r)}$, will be due to diversions in the sixth to the eleventh dimensions. Those, however, are negligibly small, indicating again the adequacy of describing the eleven characteristics by five principal components.

A comparison of the conclusions drawn from the analyses of the eleven characteristics and of the five principal components will follow the discussion of the results of each of the two analytical methods, the analysis of variance and the multiple regression.

II. Analysis of Variance

The analyses of variance of the logarithms of the intraplot variances presented in Tables 5 and 6 emphasize that the major factor affecting plant-to-plant variability within a plot is plant spacing. Wider plant spacing was found to increase the intraplot variance significantly for ten agronomic characteristics and four principal components. The variation in the number of seeds per tiller was little affected by plant spacing, although, as seen from Table 7 it increased from the 2-inch to the 4-inch plant spacing. The variance of the scores on the fourth principal component, mathematic artifice, was also independent of plant spacing and the mean variances for the three plant spacing treatments studied followed no regular pattern. The effect of plant spacing on the logarithm of the intraplot variance was found to be of a linear nature indicating an exponential effect of plant spacing on the intraplot variance. An examination of the retransformed mean intraplot variances reported in Table 7, however, indicates a better fit to a straight linear relationship for most of the agronomic characteristics and major components. These relationships are presented for the eleven agronomic characteristics in Figs. 4 and 5, and for the five principal components in Fig. 6.

Yield and C_I, yielding ability, are agronomically the most important variables studied. The intraplot variance for yield ranged from 14.6 for the 2-inch plant spacing to 91.4 for the 6-inch plant spacing averaging an increase of 19.2 units in the intraplot variance for every one inch increase in plant spacing. This represents 131% of the variance in yield of plants sown at 2-inch spacing. The corresponding figures for C_I are an increase from 8.2 to 24.8 averaging 4.1 units for every inch increase in plant spacing which is equivalent to 50% of the initial variance observed for the 2-inch spacing.

A segregating population is expected to show a larger plant-to-plant variability than a more homogeneous one. This was observed in

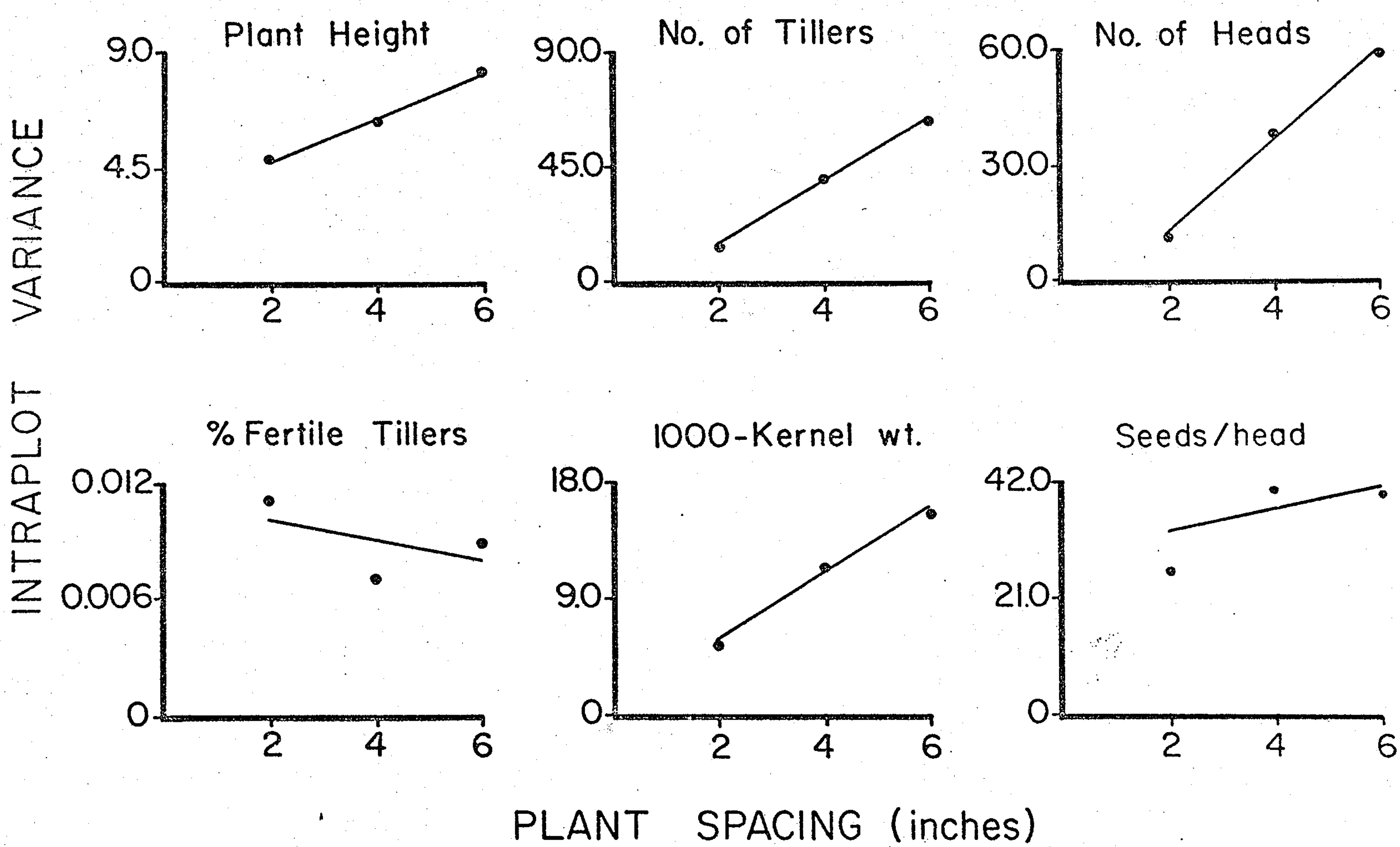

Fig. 4. Effect of plant spacing on the intraplot variance of six agronomic characteristics

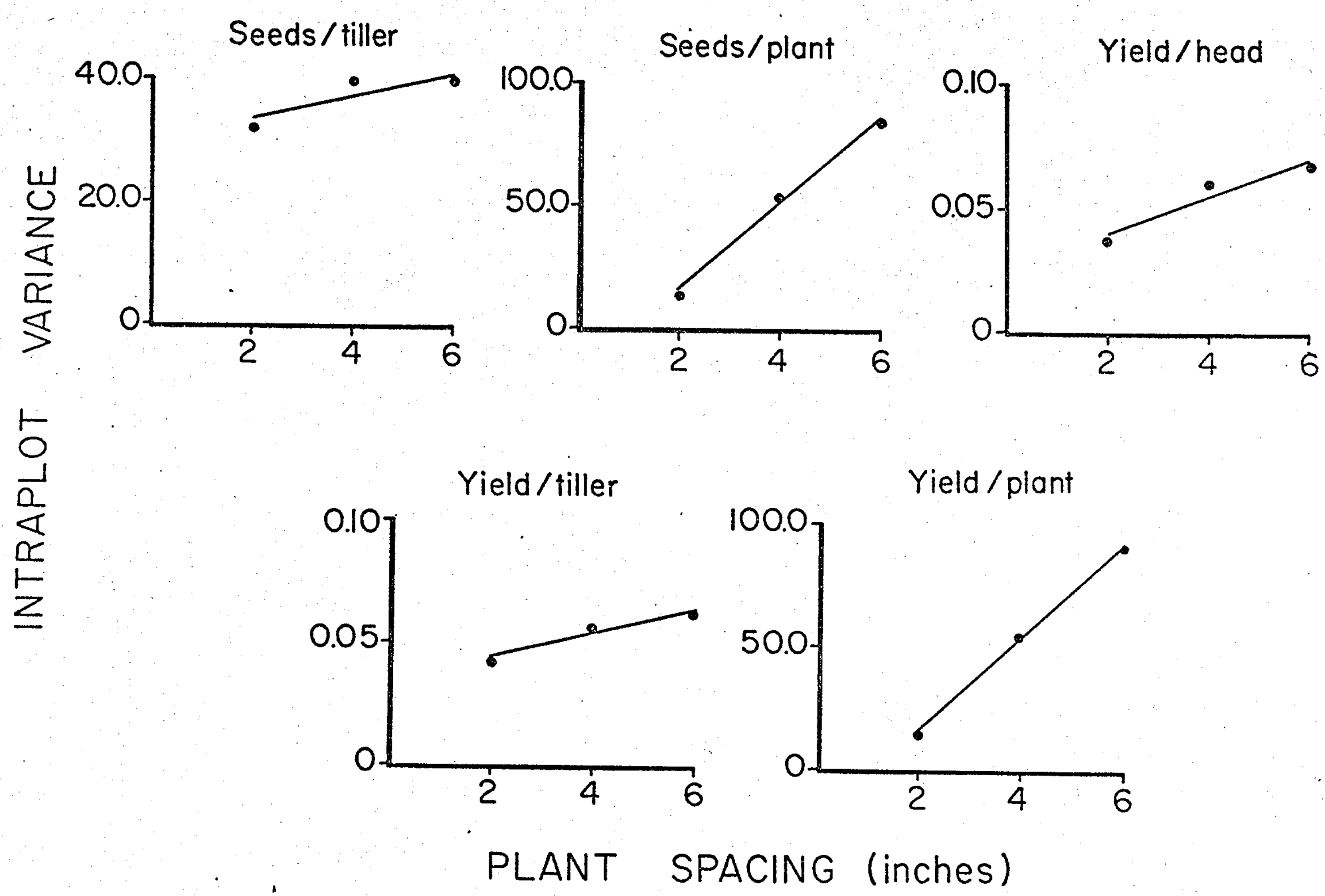

Fig. 5. Effect of plant spacing on the intraplot variance of five agronomic characteristics

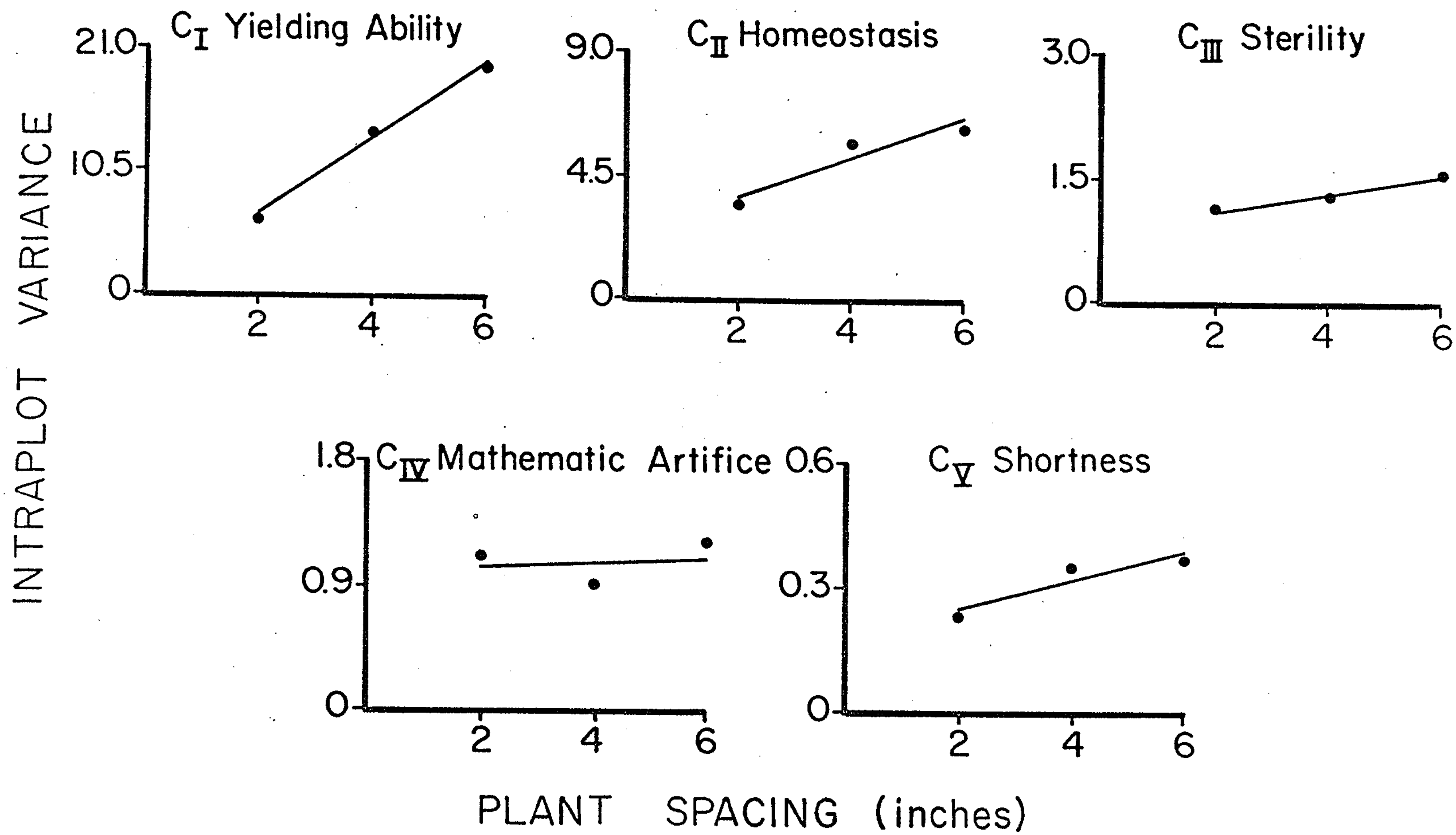

Fig. 6. Effect of plant spacing on the intraplot variance of the scores on five principal components

the experimental results for all agronomic characteristics and principal components. These differences, however, were significant only for four agronomic characteristics and three principal components excluding C_I, yielding ability and its major contributors. The variables for which this effect was significant are the agronomic characteristics measuring production per head or tiller and the principal components comprising these characteristics viz.: number of seeds per head, number of seeds per tiller, yield per head, yield per tiller, C_{II}, C_{III} and C_{IV}. The failure to detect significance of this effect for the other agronomic characteristics and principal components is attributed to their larger experimental errors in the analyses of variance. This is evident from an examination of the standard errors reported in Table 8. Furthermore, the large variations in the three plant spacing treatments may cause the inability of detecting significance of smaller differences such as those between the two genotypic types.

The unsorted seed, as reported in Table 9, gave in all cases larger intraplot variances than the uniform sized seed. The differences among variances for the three seed types were found to be highly significant for the agronomic characteristics number of seeds per head, number of seeds per tiller and number of seeds per plant and significant at the 5% level for the number of heads, yield per head and yield per tiller. Significant differences among the variances of the three seed types were also detected for yielding ability as measured by the first principal component where the mean variances were 14.0, 14.3 and 17.5

for the small, large and unsorted seed, respectively. A similar effect was also found for the variances of C_{III} which is a function of plant height and sterility. When the variances of the small and the large seed types are combined and compared to the variance of the unsorted seed, the other agronomic characteristics also show significant differences with the exception of plant height, per cent fertile tillers, 1000-kernel weight C_{IV} and C_V. The compared mean variances for yield were 38.8 and 48.1 for the uniform and the unsorted seed types, respectively.

The measurement of the degree of competition used in this analysis is based on comparison of two regression coefficients of the logarithm intraplot variance on the plant spacing. The difference between the two regression coefficients for the two compared seed types measures the degree of competition. This is illustrated in Fig. 7 for some hypothetical cases.

In Fig. 7, wider plant spacing is illustrated to increase the variance in the mono-culture plots. Competition is non-existent if the magnitude of the slope applicable to this relationship holds for the mixed culture plots, whereas competition effects will decrease the slope of the line representing the relationship in the mixed culture plots. A "negative competition" effect is represented in the case where the slope of the line for the mixed culture plots is greater than that for the mono-culture plots. These arguments hold true regardless of the direction of the line representing the effect of

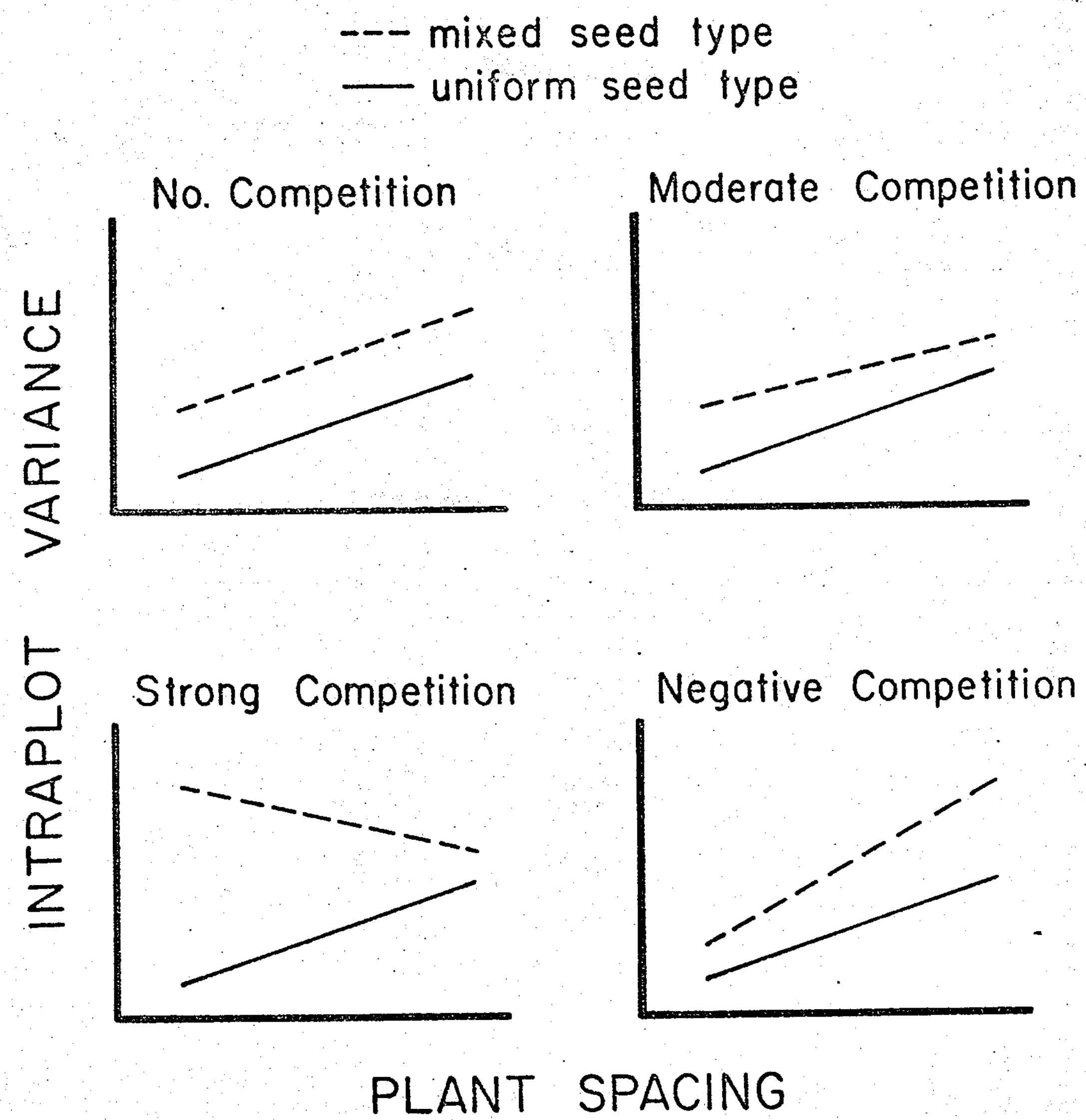

Fig. 7. Effect of plant spacing on intraplot variance of mono- and mixed-cultures for hypothetical competition cases

plant spacing on the variance in the mono-culture plots.

The slopes of the regression lines representing such relationships for each of the agronomic characteristics and principal components have been calculated and the differences between the slopes in the pure and segregating genotype and in the uniform and unsorted seed sizes were tested for significance and reported in Tables 10 and 11, respectively. The test of significance for the difference between the slopes of the two lines representing pure and mixed seed types is equivalent, in an analysis of variance, to that for the interaction: linear spacing component x pure vs. mixed seed, with one degree of freedom.

Although most of the values measuring genotypic competition were positive, none was statistically significant. Two agronomic characteristics and two principal components showed negative, but non-significant genotypic competition effects. Furthermore, with the exception of two variables, none of the spacing x genotype interactions tested in the analyses of variance approached statistical significance. An individual examination of the variance means of these two variables, yield per head and C_{II}, showed that the interactions were due to a larger increase in the variance of the mixed population from the 2- to the 4-inch spacing treatments as compared to the corresponding increase in the pure population. This indicates a possible genotypic competition effect at the closest plant spacing only.

Competition due to differences in seed size were more pronounced than genotypic competition effects. For all agronomic characteristics and principal components, with the exception of per cent fertile tillers and the mathematic artifice component, the slope of the regression line representing the effect of plant spacing on the intraplot variance of plots sown with uniform size seed was greater than the slope of the corresponding line calculated from variances of plots sown with unsorted seed indicating a positive competition effect. The significance of these effects, however, did not exceed the 1% level and exceeded the 5% level for six variables only viz.: plant height, number of tillers, number of heads, 1000-kernel weight, number of seeds per plant and the fifth principal component which is a function of plant height and the 1000-kernel weight. The analyses of variance showed significant spacing x seed size interactions for only two of these six variables. This discrepancy is due to the fact that the analysis of variance measures the interaction with plant spacing of the three seed size types: small, large and unsorted while in Table 11, the variances of the small and large seed sizes were combined into one category: uniform seed size and the test of significance involved is for the interaction: linear spacing component x uniform vs. unsorted seed.

The conclusions drawn from the analyses of variance of the variances of the eleven agronomic characteristics compare favourably with those drawn from the analyses of variance of the variances of the five principal components scores. A comparison of significant results obtained from the analyses of variance for the two types of variables, as summarized from Tables 6, 7, 9 and 10, is presented in Table 20.

It is noted that, in general, a significant effect for an agronomic characteristic resulted in a corresponding significant effect for the principal component on which the characteristic loads highly. An example is the quadratic effect of plant spacing for the characteristic per cent fertile tillers resulting in a similar quadratic effect on the fourth principal component with which the characteristic is related with a loading of 0.80. In some instances, such as the effects of seed size and of genotype on the third principal component, only one of the variables comprising the component was enough to produce the significant effect. In one case, the effects of each of the agronomic characteristics studied separately was not large enough to show statistical significance, but when combined in a principal component, the effects accumulated to reveal a significant effect. This is illustrated by the significance of the genotype x seed size interaction for the third principal component.

III. Multiple Regression

The use of regression methods, rather than analysis of variance, for the analysis of data categorized into non-continuous groups or treatments is not a common practice in statistical analysis. A discussion of the application of regression methods to such data is, therefore, presented prior to the discussion of the experimental

TABLE 20

COMPARISON OF SIGNIFICANCE OF RESULTS OBTAINED FROM THE ANALYSES OF VARIANCE FOR ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS

Agronomic characteristic	Plant spacing (P) linear	Plant spacing (P) quadratic	Genotype (G)	Seed Size (S)	G x S Inter-action	P x G Inter-action	P x S Inter-action	Genotypic competition	Seed size competition
Plant height	*						*		*
No. of tillers	**						*		*
No. of heads	**			*					*
% fertile tillers		*							
1000-kernel weight	**								*
No. of seeds per head	*		**	**					
No. of seeds per tiller			*	**					
No. of seeds per plant	**			**					*
Yield per head	**		**	*		*			
Yield per tiller	*		**	*					
Yield per plant	**								
Principal component									
C_I : Yielding ability	**			*					
C_{II} : Homeostasis	**		**			*			
C_{III} : Sterility	*		*	*	*				
C_{IV} : Mathematic artifice		*	**						
C_V : Shortness	**								*

* Significant at the 5% level.
** Significant at the 1% level.

results obtained by the multiple regression analyses.

A. Methodology:

Considering two alternate levels of a factor such as pure versus segregating genotype, the intraplot variance of plots sown with the segregating genotype, for a given agronomic characteristic or principal component, includes the environmental variance plus the genotypic variance; the intraplot variance of plots sown with the pure genotype represents the environmental variance. The object of the analysis is to arrive at an estimate for each of these two types of variance. The intraplot variance for each plot may be represented on an X-Y scatter diagram by a point whose ordinate is the observed variance and abscissa an arbitrary dichotomous scale of 0, for plots sown from pure genotype, to 1, for plots sown from segregating seed. The resulting scatter diagram satisfies the requirement for a simple regression analysis in that the X is an error-free independent variable and the Y is the dependent, continuous variable. The coefficients of the resulting regression equation, of the type $Y' = b_o + bX$, which best fits the points in the scatter diagram yields the best estimates of the required parameters, the environmental variance and the genetic variance, respectively. This is illustrated diagramatically in Fig. 8.

In comparison with a one-way analysis of variance or the student-t test, applicable to this example, it can mathematically be proven that: (1) the value of the intercept of the regression line which results

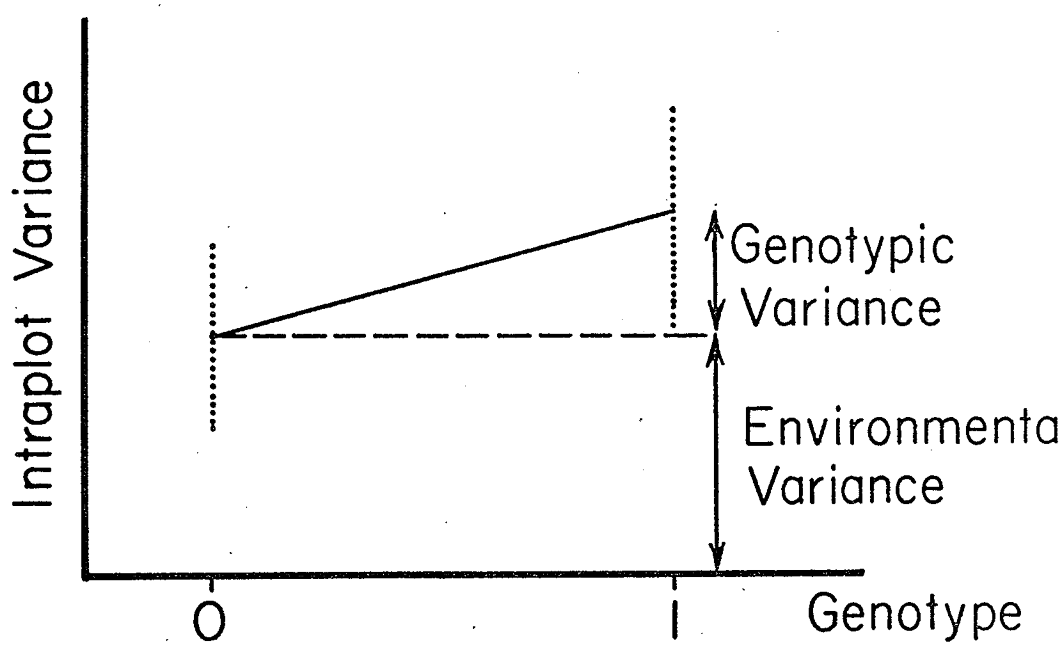

Fig. 8. Regression of intraplot variance on genotype, a nominal-type variable

from the regression analysis, $\underline{b_o}$, equals the mean of the data for the treatment coded 0, i.e., the mean intraplot variance of the pure genotype; (2) the slope of the regression line, b, equals the difference between the means of the two treatments involved and; (3) the significance level for the slope, b, is equivalent to that of the difference between the two means. Regression analysis is therefore, in this simple case, equivalent to an analysis of variance.

This method, however, is applicable only to data where the factors may assume two alternate levels such as pure versus unsorted seed size. In the case where the factor assumes more than two levels,

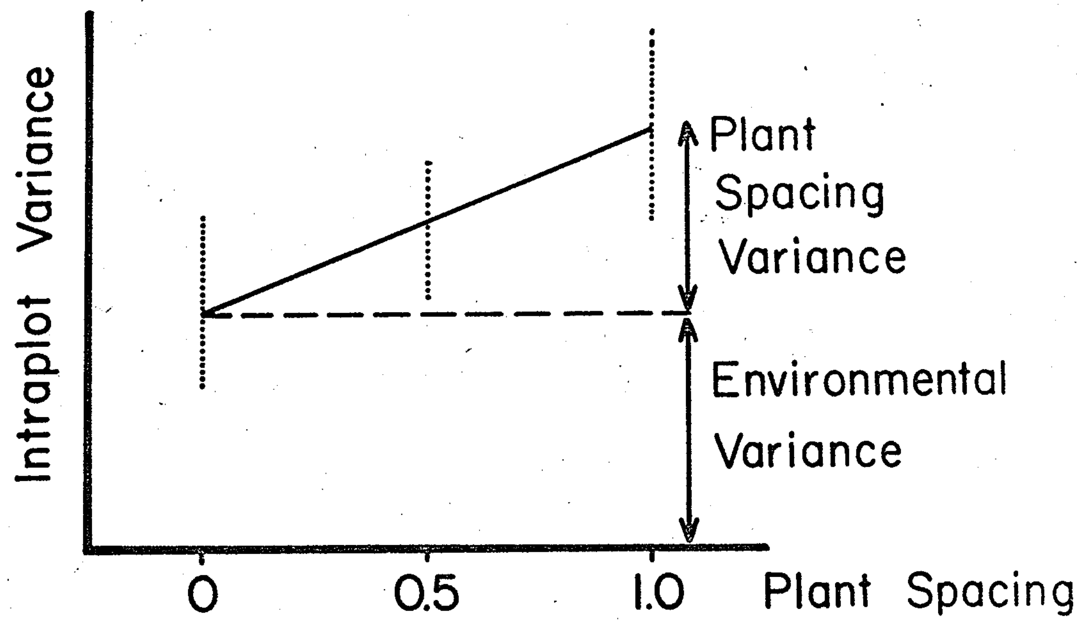

Fig. 9. Regression of intraplot variance on plant spacing, an interval-type variable

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it is necessary, in order that the X values have a logical meaning, that the levels are not of a nominal-type scale. This was applied in this study to estimate the effects of plant spacing and of competition by coding the levels of these effects to the interval scales presented in Table 1. Fig. 9 illustrates a hypothetical example for the regression of the intraplot variance on plant spacing.

In such cases the choice of the coding scale affects the value of b, the slope of the regression line, and consequently its interpretation. The 0 to 1 scale for the two- to six-inch plant spacings used in this study yields b values measuring the amount of variance, added to the environmental variance, due to increasing plant spacing from two to six inches.

In experiments where more than one effect is investigated, separate regression analyses may be substituted by a multiple regression analysis which yields a function whose coefficients, being partial regression coefficients, measure the effect of each factor when all other factors are held constant, provided that the levels of each factor investigated have been properly coded to logical interval scales and that proper corrections are applied to correct for effects which may not be so coded, such as the effect of blocks.

Interaction effects may be included in the multiple regression analysis by creating additional independent variables, each measuring a one-degree-of-freedom interaction effect, by multiplying corresponding values of the independent variable for the main effects involved in the interaction. This, however, will yield estimates of the partial regression coefficients for the main effects which are confounded with the interaction effects. Conversely, ignoring interaction effects will result in correct estimates of the partial regression coefficients but will produce an error variance which includes the ignored interaction effect. This is equivalent to a factorial analysis of variance where the interactions are pooled with the experimental error.

In general, the fact that the multiple regression analysis does not require a balanced design makes it a flexible analytical method and, in many cases a desirable substitute for the analysis of variance. It will be superior to the analysis of variance for the analysis of factorial experiments where not all possible treatment combinations have been included in the design due to their complexity, and where the nature of the treatments makes it impossible to have a balanced design such as in the case of an a + b x c factorial, where a, b and c are the levels of the factors involved. It may also substitute the analysis of covariance in which case both the covariates and the treatments will be considered as independent variables. Its limitations lie in the inability to measure interaction effects without affecting the estimates of the main effects and the necessity to correct for all effects which may not be coded into interval-type scales.

In spite of these limitations, the multiple regression analysis as used in this study, compared with the conventional analysis of variance, had an advantage in the possibility of arriving at direct independent estimates for each effect studied with considerably less amount of computations. Furthermore, it was possible to combine the data obtained of plots sown from small and from large seed into one category, uniform seed size, without encountering the difficulty of unequal subclass numbers. The effects of competition were directly measurable, in the regression analysis, by proper coding of the treatment combinations for genotypic and seed size competition while, in the analysis of variance, these effects were originally masked in the spacing x genotype and spacing x seed size interactions, and it was necessary to compute the differences in the regression coefficients of the effect of plant spacing on the investigated seed types.

The correction factor added to the variance of the subplots, to correct for main plot effects and reported on page 51, was derived so as to make the variance mean of each main plot equal to that of its spacing treatment. This had the effect of eliminating variation among replications and among mainplots of the same spacing treatment without affecting the variability among subplots.

In order to perform a detailed comparison of the two methods of analysis as used in this study, it is necessary to further partition the allocation of degrees of freedom in the analysis of variance shown on page 46, and study the destination of each source of variation in the multiple regression analysis as follows:

Source of Variation	Degrees of freedom	Handling in multiple regression analysis
Replication	5	Corrected for
Plant spacing		
linear component	1	Spacing effect
quadratic component	1	Deviations from regression
Replication x plant spacing	10	Corrected for
Genotype	1	Genotypic effect
Seed size		
small vs. large	1	Deviations from regression
uniform vs. unsorted	1	Seed size effect
Spacing x genotype		
linear component x genotype	1	Genotypic competition
quadratic component x genotype	1	Deviations from regression
Spacing x seed size		
Spacing x (small vs. large)	2	Deviations from regression
linear component x (uniform vs. unsorted)	1	Seed size competition
quadratic component x (uniform vs. unsorted)	1	Deviations from regression
Spacing x genotype x seed size	4	Deviations from regression
Replications x subplots	75	Deviations from regression
Total	107	Total

The multiple regression analysis of variance is therefore as follows:

Source of variation	Degrees of freedom
Due to regression	5
Deviations from regression	87
Total	92

with 15 degrees of freedom lost by correction for replication and replication x plant spacing effects.

Thus, the multiple regression analysis provided a simplified method for measuring selected effects with individual degrees of freedom. Effects of no interest to the study were assumed to be small and were, therefore, pooled with the error term. These effects were: small versus large seed and its interaction with plant spacing, genotype x seed size interaction, the quadratic effect of plant spacing and its interactions with genotype and with seed size and the third order interaction. Dealing with intraplot variances, none of these effects are agronomically interpretable and were all assumed to be of small magnitudes. This assumption was, for the most part, confirmed by the results of the analyses of variance.

A comparison of the conclusions obtained from the results of the analyses by the two methods will follow a discussion of the results of the multiple regression analyses.

B. Results:

Results of the multiple regression analyses indicate that wider plant spacing is the major contributor to the intraplot variance. This effect was significant, for the multiplicative model, in all agronomic characteristics and principal components with the exception of per cent fertile tillers and the mathematic artifice component. The additive model produced similar significant effects with one exception, the number of seeds per tiller. The increase in plant spacing from two to six inches caused an increase in the intraplot variance for yield from

14.4 to 98.2 according to the multiplicative model and plots sown at 6-inch plant spacing had an average intraplot variance 7.8 times that of plots sown at 2-inch plant spacing. The per cent of yield intraplot variance due to wide plant spacing was calculated as 72% and 80% for the additive and multiplicative models, respectively. Similar large effects of plant spacing on the intraplot variance were noted for most of the agronomic characteristics and principal components studied.

Compared to the effect of plant spacing, other effects contributing to the intraplot variance were found to be of little significance. Other controllable, non-genetic effects are seed size, seed size competition and genotypic competition. The analysis revealed only few instances where significance of such effects could be detected. According to the additive model, significant competition effects could not be detected for any of the agronomic characteristics or principal components studied, and seed size effect was found to be significant for only two agronomic characteristics, number of seeds per head and number of seeds per tiller and no principal components. The multiplicative model was more effective in detecting significant competition effects. Competition due to genetic differences was found to be significant for yield per head and for the homeostasis component. Seed size competition was found to be significant for the number of tillers, number of heads, 1000-kernel weight and number of seeds per plant in addition to the second and fifth principal components, homeostasis and shortness. Seed size effect was not found to be significant in any case.

Under the conditions of this experiment, the effect of genotype on the intraplot variance did not approach the 5% significance level for any of the agronomic characteristics or principal components studied and was negative in three of the 32 cases tested. This indicates that the natural inaccuracies inherent in handling the experimental material, although all methods were of a quantitative nature, together with the differential random variations in plants due to wide plant spacing, introduced an amount of variability larger than the measurable amount which exists in the segregating experimental material.

The percentages of variance due to each effect, although many are not of statistical significance, provide a picture of the contributions of each source to the total variance for each variable. These were averaged, for each of the two models assumed, to obtain estimates of the effect of each source on the total variance of all variables. The vector representing the percentages of total variance explained by each of the principal components reported in Table 3 was post-multiplied by each of the matrices of the percentage variance due to each effect reported in Tables 17 and 19. The results are reported, after correction for the amount of variability unexplained by the five principal components, in Table 21 and Fig. 10.

The multiple correlation coefficients obtained for the multiplicative model reported in Tables 16 and 18 were larger than the corresponding coefficients for the additive model reported in Tables 12 and 14 for ten agronomic characteristics and four principal components.

TABLE 21

PER CENT OF THE TOTAL VARIANCE IN ELEVEN AGRONOMIC CHARACTERISTICS DUE TO EACH OF THE VARIANCE COMPONENTS FOR TWO MODELS

Variance component	Per cent variance	
	Additive model	Multiplicative model
Environment	33.28	34.13
Genotype	7.42	3.54
Seed size	8.14	3.22
Spacing	40.72	44.30
Genotypic competition	4.46	6.16
Seed size competition	5.98	8.65

The exceptions are those for per cent fertile tillers, which were not statistically significant under any model and for C_{IV}, the mathematic artifice component. This indicates that the multiplicative model is, in general, more adequate in describing the relationships between the independent variables and the intraplot variance. A detailed comparison of the standardized partial regression coefficients for the two models, however, indicated that the effects of genotype and of seed size tend to follow an additive model whereas those for plant spacing, genotypic competition and seed size competition tend to have a multiplicative effect on the environmental variance. This comparison is presented in Table 22 which shows, for each effect studied, the number of cases, out of the 16 comparisons involved, where the standardized partial regression coefficient calculated from the multiplicative model was larger than the corresponding coefficient for the additive

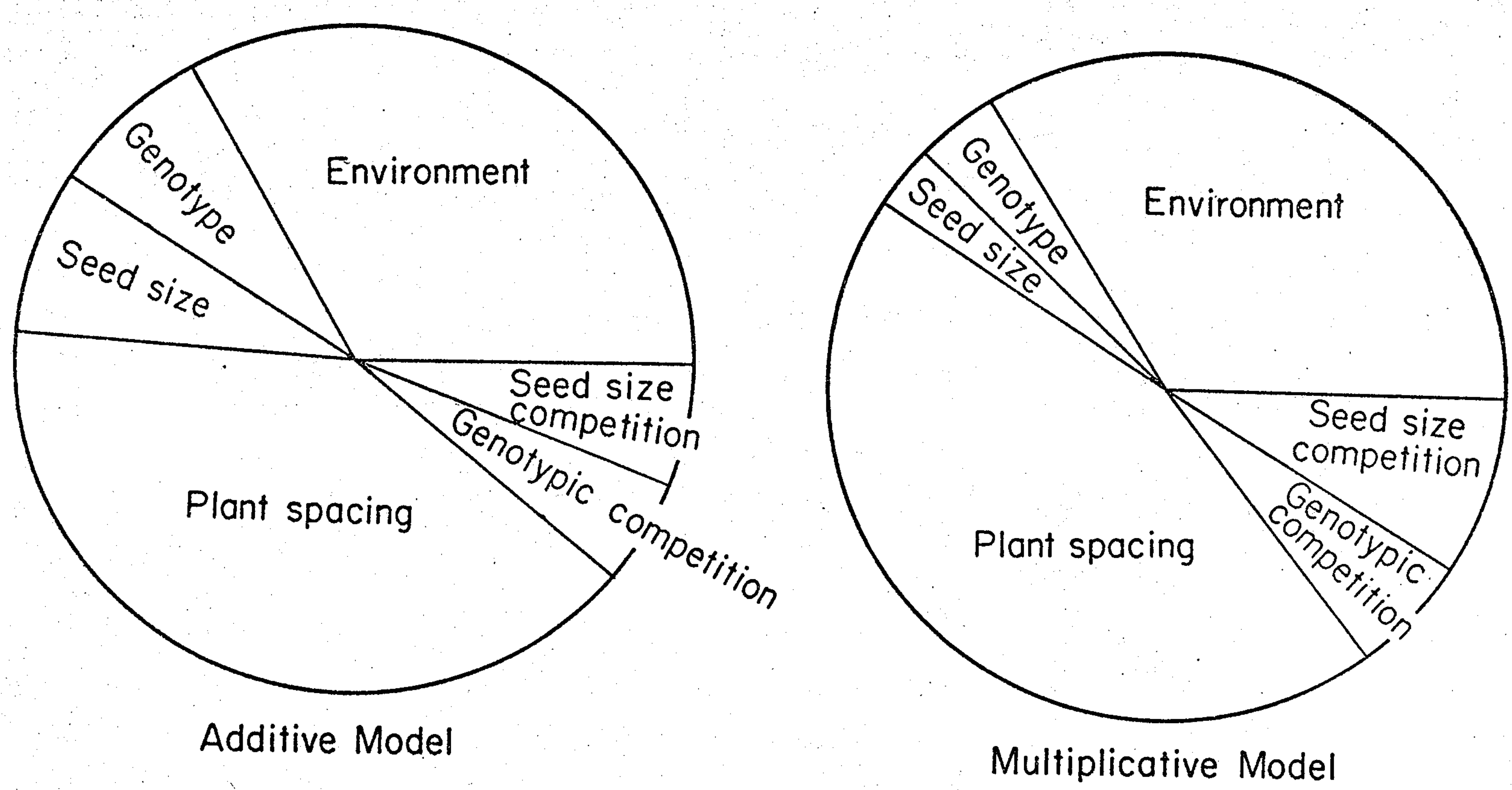

Fig. 10. Proportions of the total variance in the eleven agronomic characteristics due to each of the variance components for two models

TABLE 22

NUMBER OF CASES WHERE THE STANDARDIZED PARTIAL REGRESSION COEFFICIENT FOR THE MULTIPLICATIVE MODEL EXCEEDED THAT FOR THE ADDITIVE MODEL FOR EACH OF FIVE EFFECTS (†)

Effect	Number of cases
Genotype	5
Seed size	5
Plant spacing	15
Genotypic competition	13
Seed size competition	15

(†) Total of sixteen agronomic characteristics and principal components.

model. Furthermore, analyses according to the additive model revealed significant effect of seed size in two cases and those according to the multiplicative model revealed competition effects in eight cases where analyses according to the alternate models failed to detect any significant effects. A comparison of the significant results obtained by the two models is presented in Table 23.

The results of the multiple regression analyses for the eleven agronomic characteristics showed close agreement with those for the five principal components regardless of the model assumed, as seen in Table 24. The only discrepancy is that the analyses of the component scores failed to reveal seed size effects detected for the number of seeds per tiller and number of seeds per head. The significance level for the effect of seed size on C_I, which loads highest on these two agronomic characteristics was between 20 and 30%. This is probably

TABLE 23

SIGNIFICANT EFFECTS REVEALED BY THE MULTIPLE REGRESSION ANALYSES FOR ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS FOR TWO MODELS

	Additive model		Multiplicative model	
Effect tested	Agronomic characteristics	Principal components	Agronomic characteristics	Principal components
Genotype	None	None	None	None
Seed size	Seeds per tiller Seeds per head	None	None	None
Plant spacing	All but per cent fertile tiller and no. of seeds per tiller	All but C_{IV}	All but per cent fertile tillers	All but C_{IV}
Genotypic competition	None	None	Yield per head	C_{II}
Seed size competition	None	None	No. of tillers No. of heads 1000-kernel weight Seeds per plant	C_{II} C_V

due to the inclusion in C_I, of a large proportion of the variability in other agronomic characteristics which are not affected by seed size. The effect of plant spacing was significant for all agronomic characteristics studied except the per cent fertile tillers. Similarly it was significant on all principal components with the exception of C_{IV} which loads highly (0.80) on this characteristic. The effect of genotypic competition on yield per head, as detected by the analysis according to the multiplicative model, was reflected on the homeostasis component showing a similar effect. Similarly, the effects of competition due to seed size differences on the number of tillers, number of heads and number of seeds per plant were reflected on C_{II}, and its effect on the 1000-kernel weight was reflected on C_{V}.

Because the intraplot variances were logarithmically transformed for the analyses of variance, only results derived from the multiple regression analyses according to the multiplicative model may be compared with those from the analyses of variance. This is presented, for significant effects detected, in Table 24. This comparison indicates that the analysis of variance is the more effective method in detecting statistical significance of the effects studied. Genotypic and seed size effects, which were significant for a number of agronomic characteristics and principal components in the analyses of variance, showed no significance for any variable in the multiple regression analyses. This is due to a combination of two reasons: (1) the value of a partial regression coefficient underestimates the difference in the two means involved by one-half the interaction of the effect in question with the linear component of plant spacing which was included in the multiple regression analyses to estimate competition and; (2) the deviations from regression mean square includes all effects ignored in the multiple regression analysis. These facts make the analysis of variance the better method of handling analyses of experiments where interactions are to be included.

TABLE 24

COMPARISON OF SIGNIFICANT RESULTS OBTAINED BY TWO METHODS OF STATISTICAL ANALYSIS FOR ELEVEN AGRONOMIC CHARACTERISTICS AND FIVE PRINCIPAL COMPONENTS

	Plant spacing (linear component)		Genotype		Seed size (uniform vs. unsorted)		Genotypic competition		Seed size competition	
Agronomic characteristic	Analysis of variance	Multiple regression	Analysis of variance	Multiple regression	Analysis of variance	Multiple regression	Analysis of variance	Multiple regression	Analysis of variance	Multiple regression
Plant height	*	**							*	
No. of tillers	**	**			*				*	*
No. of heads	**	**			*				*	*
% fertile tillers										
1000-kernel weight	**	**							*	*
No. of seeds per head	*	**	**		**					
No. of seeds per tiller		**	*		**					
No. of seeds per plant	**	**			**				*	*
Yield per head	**	**	**		*			*		
Yield per tiller	*	**	**		*					
Yield per plant	**	**								
Principal component										
C_I : Yielding ability	**	**			*					
C_{II} : Homeostasis	**	**	**		*			**		*
C_{III} : Sterility	*	**	*		*					
C_{IV} : Mathematic artifice			**							
C_V : Shortness	**	**							*	**

* Significant at the 5% level.
** Significant at the 1% level.

IV. General Conclusions

The efficiency of single plant selection for improvement of quantitative characters may be looked at as a function of three limiting factors: (1) the proportion of superior genotypes present in the segregating population; (2) the skill of the plant breeder in recognizing superior genotypes and; (3) the degree of manifestation of genotype in the phenotype of a single plant.

The first factor has been examined elsewhere (252) and may be partially overcome by increasing the size of the population grown. The skill of the plant breeder in recognizing superior genotypes may be improved by the use of quantitative, rather than visual methods, in the selection procedure. The results of this study, however, tend to indicate that, in spite of the standardized quantitative methods used in collecting data, the amount of natural inaccuracies inherent in individual plant determinations is, in many cases, larger than that existing among the tested seed types.

Factors affecting the degree of the expression of the genotype in the phenotype, were examined quantitatively in this study. It has been demonstrated by a number of workers (14, 76, 132, 219, 278) that in many segregating populations in cereals, the actual yields of plants bear very little relation to the yield of their progenies. The lack of such correlation has been explained on the basis of environmental factors influencing growth and reducing heritability estimates.

The degree of correlation between yield of single plants in segregating populations and the mean of the plant progeny rows is directly proportional to the product of the heritability estimates in the selection and the progeny row nurseries. Heritability in the selection nursery is defined by: $\frac{G}{G + E}$ where G and E are the variances, based on individual plant variation in the selection nursery, due to genetic and non-genetic effects, respectively.

In this study, the variations in genotype of the material used was very low when compared to the total variation among individual plants for most of the agronomic characteristics and principal components studied. The per cent variance due to genotype for yield and yielding ability as defined by a principal component were estimated, according to the additive model, to be 6 and 8%, respectively. Estimates for other agronomic characteristics and principal components ranged between 0 and 19%. The weighted averages over all agronomic characteristics were 7.42 and 3.54% for the additive and multiplicative models, respectively. These estimates may be increased by designs of selection nurseries in which sources of non-genetic variation are controlled.

The components of non-genetic variance considered in this study are micro-environment, plant spacing, initial seed size and competition effects due to differences in genotype and in initial seed size. The degree to which each contributes to the total variability among the plants was estimated for each of several agronomic characteristics and component scores. The results indicate that, in general, the most important controllable non-genetic contributor is wide plant spacing followed by differences in seed size, seed size competition and genotypic competition in decreasing order.

These sources of environmental variation may be controlled by proper design of the selection nursery. Sorting seed according to size or weight and planting selection nurseries from seed of uniform size should reduce the effects of both initial seed size and competition arising from seed size differences. Closer plant spacing will reduce variation due to space-planting but will magnify that due to genotypic competition. Competition due to difference in genotype, at a given plant spacing, may be a function of the amount of variability in genotype and may differ from population to population. It will, therefore, be necessary to select a plant spacing where the combined variability due to spacing and genotypic competition is a minimum. Space planting will confound single plant selection as long as the amount of variability introduced due to wider plant spacing *per se* is greater than the amount of genotypic competition removed.

The efficiency of selection in various designs of the nursery may be compared by calculating an estimate of heritability under each sowing condition. This is demonstrated in Table 25 for the combined variances in the eleven agronomic characteristics for the analyses according to the additive model based on the figures reported in Table 21.

TABLE 25

CALCULATION OF HERITABILITY ESTIMATES UNDER FOUR SOWING CONDITIONS BASED ON THE TOTAL VARIABILITY IN ELEVEN AGRONOMIC CHARACTERISTICS (ADDITIVE MODEL)

	Sowing conditions			
	6" plant spacing		2" plant spacing	
Effect	Unsorted seed	Sorted seed	Unsorted seed	Sorted seed
Environment	33.28	33.28	33.28	33.28
Genotype	7.42	7.42	7.42	7.42
Seed size	8.14		8.14	
Space planting	40.72	40.72		
Genotypic competition			4.46	4.46
Seed size competition			5.98	
Total	89.56	81.42	59.28	45.16
Heritability (%)	8.28	9.11	12.52	16.43

The efficiency of single-plant selection, relative to the standard 6-inch space-planted nurseries sown with seed unsorted as to size, may be doubled by sowing uniform-size seed in close-planted nurseries. Sorting seed alone will increase the efficiency by 10%, while close-spacing alone will increase the efficiency by 51%.

SUMMARY

A field experiment was carried out to investigate the effects of variation in plant spacing, seed size, genotype and interplant competition on the plant-to-plant variability in wheat and their relationship with selection procedures.

Small, large and unsorted seed of each of a genetically segregating and a pure population were sown in plots at 2-, 4- and 6-inch plant spacing in a split plot arrangement with six replications. Harvest data on eleven agronomic characteristics were obtained on individual plant basis. Five additional variables were calculated as plant scores on the major components extracted in a principal component analysis.

The intraplot variances for each of the sixteen variables were subjected to two methods of statistical analysis. Results obtained were discussed and the analytical methods compared.

The main findings from the experimental results were as follows:

1. The principal component analysis was effective in fully describing the eleven agronomic characteristics by means of five principal components.

2. Results obtained from analysis of component scores compare favourably to those obtained from analyses of the agronomic characteristics.

3. The analysis of variance method is more effective than the multiple regression analysis in detecting significant results where interactions are present.

4. The natural inaccuracies inherent in single plant determinations are, in many cases, larger than the differences which exist in the tested material.

5. The major factor affecting intraplot variability is wide plant spacing.

6. Heritability estimated from single plant measurements is low.

7. Differences in initial seed size have a direct effect on the intra-plot variability as well as an indirect effect as a source of interplant competition.

8. The degree to which genotypic competition confounds selection procedures is much less than the error introduced by wide plant spacing.

It was concluded that the effectiveness of single plant selection could be doubled by grading the seed from segregating generations of a cross according to size or weight, and sowing only seed of approximately the same size together in close-planted selection nurseries.

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Appendix 1. Intraplot variances for eleven agronomic characteristics in 108 subplots

Plant Spacing	Genotype	Seed Size	Replication	No. of Plants	Plant Height	No. of Tillers	No. of Heads	Per cent Fertile Tillers	1000-kernel Weight	No. of Seeds per Head	No. of Seeds per Tiller	No. of Seeds per Plant	Yield per Head	Yield per Tiller	Yield per Plant
2"	Pure	Small	1	54	4.25	7.42	8.05	0.0191	3.50	26.03	43.05	13235	0.0389	0.0597	14.67
2"	Pure	Small	2	55	4.82	15.08	11.45	0.0098	4.58	17.99	25.95	11813	0.0269	0.0348	11.02
2"	Pure	Small	3	28	6.33	42.00	29.51	0.0152	10.73	34.52	39.14	53338	0.0431	0.0410	39.07
2"	Pure	Small	4	67	3.26	4.95	4.99	0.0070	1.39	11.40	16.70	4996	0.0162	0.0215	5.36
2"	Pure	Small	5	26	1.21	7.60	7.29	0.0069	1.56	8.30	10.44	8495	0.0144	0.0152	10.39
2"	Pure	Small	6	64	2.92	2.95	3.31	0.0158	1.89	22.73	25.85	3304	0.0302	0.0352	4.06
2"	Pure	Large	1	51	7.05	7.45	4.54	0.0149	9.18	19.85	35.47	4799	0.0271	0.0478	5.57
2"	Pure	Large	2	38	3.54	9.25	7.01	0.0083	6.40	24.50	26.34	9653	0.0451	0.0432	10.92
2"	Pure	Large	3	27	10.41	25.20	16.38	0.0088	9.40	28.02	33.27	23923	0.0452	0.0419	26.59
2"	Pure	Large	4	42	6.54	11.34	9.68	0.0132	3.74	15.56	24.06	13556	0.0155	0.0225	10.68
2"	Pure	Large	5	24	2.09	25.97	24.46	0.0111	6.47	18.14	26.18	22729	0.0171	0.0252	25.81
2"	Pure	Large	6	41	3.64	5.90	6.60	0.0079	2.03	15.21	17.30	7001	0.0217	0.0243	7.99
2"	Pure	Unsorted	1	48	7.37	12.66	12.00	0.0284	6.19	14.87	40.14	12732	0.0220	0.0447	12.80
2"	Pure	Unsorted	2	40	7.02	15.56	12.89	0.0110	6.85	35.08	34.28	16233	0.0472	0.0447	14.91
2"	Pure	Unsorted	3	26	7.56	31.30	24.04	0.0114	17.12	56.56	61.71	36132	0.0551	0.0569	32.08
2"	Pure	Unsorted	4	25	9.53	31.75	28.39	0.0072	8.98	39.17	42.79	54308	0.0407	0.0431	32.61
2"	Pure	Unsorted	5	17	5.01	16.53	13.01	0.0124	5.90	20.32	29.03	12614	0.0201	0.0236	12.94
2"	Pure	Unsorted	6	79	4.54	7.07	6.99	0.0046	5.73	24.62	28.46	8883	0.0447	0.0486	11.36
2"	Segregating	Small	1	49	4.77	10.87	10.51	0.0217	6.71	35.39	33.78	10248	0.0517	0.0458	12.75
2"	Segregating	Small	2	27	2.33	16.99	14.64	0.0068	12.52	22.05	23.30	17165	0.0445	0.0430	17.53
2"	Segregating	Small	3	17	4.51	42.50	30.99	0.0201	10.57	70.91	53.69	38626	0.0733	0.0411	41.97
2"	Segregating	Small	4	33	1.90	14.94	9.28	0.0240	1.14	16.85	31.61	7414	0.0221	0.0403	7.94
2"	Segregating	Small	5	34	3.18	9.72	7.64	0.0099	1.92	30.58	29.39	8915	0.0466	0.0432	11.69
2"	Segregating	Small	6	47	4.28	6.43	6.52	0.0096	3.32	24.83	30.94	6724	0.0444	0.0516	8.44
2"	Segregating	Large	1	46	7.97	11.37	8.93	0.0106	9.36	34.96	40.37	9235	0.0525	0.0601	11.54
2"	Segregating	Large	2	41	14.09	11.55	11.29	0.0055	2.50	21.89	24.45	12479	0.0341	0.0347	14.19
2"	Segregating	Large	3	39	4.60	48.30	37.66	0.0095	12.53	51.15	43.68	37781	0.0853	0.0750	40.87
2"	Segregating	Large	4	33	4.31	10.58	8.06	0.0112	2.46	34.82	45.89	9939	0.0508	0.0649	12.15
2"	Segregating	Large	5	24	1.07	16.26	16.60	0.0124	7.71	20.40	22.31	20092	0.0361	0.0369	22.92
2"	Segregating	Large	6	48	5.85	6.40	5.88	0.0109	4.29	20.03	34.86	5825	0.0324	0.0509	6.72
2"	Segregating	Unsorted	1	42	24.41	10.19	9.16	0.0179	6.90	42.44	50.53	9009	0.0556	0.0568	10.91
2"	Segregating	Unsorted	2	16	9.05	34.38	29.98	0.0166	5.51	28.87	31.46	33977	0.0354	0.0328	34.28
2"	Segregating	Unsorted	3	31	4.78	49.37	43.88	0.0113	8.58	60.98	59.43	72683	0.0901	0.0813	69.21
2"	Segregating	Unsorted	4	30	3.21	16.65	17.86	0.0112	8.34	39.04	57.54	34636	0.0518	0.0718	24.32
2"	Segregating	Unsorted	5	31	4.40	10.59	9.65	0.0164	26.11	15.72	29.29	11304	0.0337	0.0391	7.42
2"	Segregating	Unsorted	6	48	6.31	13.40	11.76	0.0031	11.28	45.18	46.22	14737	0.0587	0.0625	14.57

Appendix 1 (continued)

Plant Spacing	Genotype	Seed Size	Replication	No. of Plants	Plant Height	No. of Tillers	No. of Heads	Per cent Fertile Tillers	1000-kernel Weight	No. of Seeds per Head	No. of Seeds per Tiller	No. of Seeds per Plant	Yield per Head	Yield per Tiller	Yield per Plant
4"	Pure	Small	1	33	3.67	111.29	97.48	0.0024	19.31	40.21	40.00	116412	0.0548	0.0493	96.29
4"	Pure	Small	2	21	11.85	123.16	91.49	0.0130	22.80	47.79	61.82	115844	0.0808	0.0769	104.01
4"	Pure	Small	3	30	5.68	37.27	31.57	0.0075	13.16	44.66	45.54	49284	0.0689	0.0649	58.87
4"	Pure	Small	4	37	5.30	40.72	33.70	0.0104	8.26	35.45	21.64	44462	0.0637	0.0429	49.32
4"	Pure	Small	5	49	4.87	27.10	21.62	0.0066	4.57	25.15	28.73	28738	0.0439	0.0448	35.03
4"	Pure	Small	6	46	3.15	8.88	8.83	0.0028	4.52	22.88	20.42	14156	0.0270	0.0244	14.64
4"	Pure	Large	1	23	10.54	102.02	90.70	0.0069	16.56	41.33	48.73	153844	0.0689	0.0684	152.45
4"	Pure	Large	2	32	7.02	45.50	42.38	0.0102	28.72	50.50	61.92	74889	0.1261	0.1131	95.53
4"	Pure	Large	3	18	2.64	30.33	34.81	0.0191	17.00	18.44	42.31	47254	0.0300	0.0385	32.52
4"	Pure	Large	4	34	4.77	34.80	30.36	0.0078	8.33	34.19	31.20	43323	0.0537	0.0477	46.10
4"	Pure	Large	5	30	8.28	16.33	12.13	0.0076	12.35	41.50	34.01	20176	0.0512	0.0496	28.46
4"	Pure	Large	6	47	1.87	16.21	13.88	0.0038	2.35	19.40	14.94	19404	0.0249	0.0193	22.70
4"	Pure	Unsorted	1	18	10.38	113.63	111.91	0.0027	32.21	50.85	53.63	163297	0.0737	0.0716	129.56
4"	Pure	Unsorted	2	29	5.83	51.17	38.81	0.0077	15.32	57.25	55.91	77350	0.0858	0.0814	77.79
4"	Pure	Unsorted	3	28	8.72	49.51	44.19	0.0086	14.11	21.16	21.56	55023	0.0548	0.0442	54.15
4"	Pure	Unsorted	4	35	4.18	27.29	27.25	0.0028	12.89	83.28	89.08	46328	0.0689	0.0755	38.96
4"	Pure	Unsorted	5	37	8.12	58.18	57.73	0.0036	14.57	74.01	66.90	82142	0.0987	0.0870	67.28
4"	Pure	Unsorted	6	41	2.84	21.27	20.30	0.0006	1.95	22.87	23.85	30746	0.0371	0.0376	41.67
4"	Segregating	Small	1	47	19.25	99.99	91.51	0.0111	20.86	21.72	31.42	94423	0.0366	0.0397	81.55
4"	Segregating	Small	2	22	7.86	55.83	54.11	0.0062	18.21	51.80	47.83	92641	0.0929	0.0762	86.29
4"	Segregating	Small	3	23	33.70	49.35	52.07	0.0070	9.92	19.60	23.48	65045	0.0319	0.0255	40.73
4"	Segregating	Small	4	16	8.27	107.30	95.30	0.0031	53.48	29.39	38.02	115787	0.1010	0.0998	136.31
4"	Segregating	Small	5	37	9.03	38.30	36.42	0.0044	13.54	39.12	39.28	59328	0.0643	0.0628	60.62
4"	Segregating	Small	6	54	3.19	14.32	13.39	0.0058	1.59	21.60	27.86	15123	0.0325	0.0379	18.16
4"	Segregating	Large	1	46	4.13	84.94	80.89	0.0206	24.54	129.90	42.51	90242	0.0889	0.0474	78.39
4"	Segregating	Large	2	33	9.53	38.40	35.73	0.0038	10.44	44.56	43.37	55606	0.0626	0.0582	58.58
4"	Segregating	Large	3	15	12.52	30.92	32.74	0.0191	15.25	68.08	31.61	50936	0.0729	0.0402	48.46
4"	Segregating	Large	4	51	11.97	22.67	21.01	0.0091	10.60	63.83	59.16	31099	0.0771	0.0693	27.08
4"	Segregating	Large	5	53	5.65	12.48	12.29	0.0045	17.90	36.79	37.50	21370	0.0844	0.0829	29.50
4"	Segregating	Large	6	31	2.69	22.61	20.38	0.0040	9.93	37.43	43.39	28455	0.0870	0.0921	38.48
4"	Segregating	Unsorted	1	23	8.24	72.64	71.20	0.0052	10.87	50.96	54.59	113048	0.0579	0.0584	94.74
4"	Segregating	Unsorted	2	36	5.32	33.74	30.77	0.0182	16.08	28.25	52.07	38334	0.0522	0.0694	42.31
4"	Segregating	Unsorted	3	22	7.37	60.54	74.82	0.0355	2.64	81.86	64.77	100831	0.0965	0.0730	106.44
4"	Segregating	Unsorted	4	20	8.88	145.04	133.52	0.0171	63.03	65.41	40.58	191165	0.1099	0.1030	220.12
4"	Segregating	Unsorted	5	36	4.15	17.34	15.84	0.0081	9.72	83.48	66.92	26499	0.0661	0.0580	29.59
4"	Segregating	Unsorted	6	46	3.73	17.49	16.77	0.0065	3.96	27.85	30.80	18280	0.0315	0.0355	22.58

Appendix 1 (continued)

Plant Spacing	Genotype	Seed Size	Repli-cation	No. of Plants	Plant Height	No. of Tillers	No. of Heads	Per cent Fertile Tillers	1000-kernel Weight	No. of Seeds per Head	No. of Seeds per Tiller	No. of Seeds per Plant	Yield per Head	Yield per Tiller	Yield per Plant
6"	Pure	Small	1	33	11.06	134.77	121.88	0.0084	12.87	36.86	45.88	163856	0.0606	0.0611	140.99
6"	Pure	Small	2	33	5.84	92.26	82.52	0.0067	26.86	29.07	29.98	119349	0.0771	0.0705	129.07
6"	Pure	Small	3	38	4.26	38.40	36.17	0.0126	19.57	60.02	63.44	71865	0.1027	0.0979	84.31
6"	Pure	Small	4	53	12.32	69.95	65.77	0.0034	17.65	47.60	50.97	101673	0.0845	0.0869	115.23
6"	Pure	Small	5	38	2.72	55.70	54.59	0.0050	6.35	39.56	26.80	82441	0.0454	0.0286	95.86
6"	Pure	Small	6	45	3.65	20.94	21.26	0.0036	6.93	20.05	20.87	36244	0.0346	0.0361	44.98
6"	Pure	Large	1	39	7.40	134.02	121.89	0.0060	20.85	48.71	31.17	157946	0.0761	0.0557	175.66
6"	Pure	Large	2	34	16.76	71.33	46.70	0.0181	6.50	30.15	43.08	59042	0.0395	0.0511	67.04
6"	Pure	Large	3	41	5.55	58.62	57.17	0.0127	24.69	32.29	34.53	72269	0.0516	0.0488	84.65
6"	Pure	Large	4	28	15.77	37.44	36.30	0.0126	12.88	44.18	28.74	55115	0.0754	0.0438	53.47
6"	Pure	Large	5	35	11.36	46.33	40.49	0.0086	8.90	32.98	36.53	75346	0.0514	0.0480	74.87
6"	Pure	Large	6	22	8.11	88.73	72.92	0.0092	15.28	34.95	42.59	94133	0.0751	0.0804	108.05
6"	Pure	Unsorted	1	31	13.98	81.08	83.69	0.0182	24.73	46.21	51.42	104363	0.0702	0.0698	102.39
6"	Pure	Unsorted	2	31	7.17	83.39	73.92	0.0052	8.70	29.06	26.47	96707	0.0537	0.0454	103.30
6"	Pure	Unsorted	3	33	6.91	60.30	55.48	0.0132	21.74	27.42	40.27	89156	0.0529	0.0573	103.47
6"	Pure	Unsorted	4	53	17.79	110.17	94.69	0.0261	59.76	71.74	76.80	170040	0.1412	0.1301	175.32
6"	Pure	Unsorted	5	39	9.59	34.06	36.71	0.0091	13.11	39.62	41.93	59804	0.0580	0.0545	58.90
6"	Pure	Unsorted	6	32	4.38	34.20	29.22	0.0043	8.60	31.82	22.65	48563	0.0525	0.0400	60.04
6"	Segregating	Small	1	44	7.76	233.18	210.01	0.0147	37.79	36.11	44.05	276242	0.0901	0.0823	295.27
6"	Segregating	Small	2	30	11.62	73.86	64.79	0.0085	16.82	37.25	34.24	86141	0.0419	0.0415	68.34
6"	Segregating	Small	3	22	9.45	63.07	57.61	0.0086	21.72	25.45	32.11	60933	0.0538	0.0569	87.86
6"	Segregating	Small	4	40	17.16	50.34	47.31	0.0073	19.87	35.65	35.21	77982	0.0811	0.0694	99.09
6"	Segregating	Small	5	28	6.07	82.39	77.14	0.0016	16.55	51.34	48.97	50276	0.0766	0.0738	68.35
6"	Segregating	Small	6	22	5.40	50.09	38.64	0.0121	10.36	31.81	27.16	56246	0.0473	0.0405	54.42
6"	Segregating	Large	1	48	28.81	136.05	136.97	0.0165	33.28	57.76	66.34	183258	0.1116	0.1010	197.28
6"	Segregating	Large	2	29	7.85	83.82	90.19	0.0126	15.87	32.92	37.43	135296	0.0573	0.0523	128.79
6"	Segregating	Large	3	28	7.50	62.77	53.82	0.0101	23.27	46.30	41.49	71060	0.0891	0.0741	79.61
6"	Segregating	Large	4	38	8.73	34.75	30.58	0.0060	11.54	29.73	30.59	52495	0.0481	0.0497	52.45
6"	Segregating	Large	5	31	7.19	40.25	37.13	0.0047	17.57	54.25	44.81	73025	0.1009	0.0827	73.90
6"	Segregating	Large	6	43	3.25	48.39	48.77	0.0107	8.12	31.88	35.05	58260	0.0525	0.0475	49.18
6"	Segregating	Unsorted	1	38	18.08	194.01	193.28	0.0147	35.37	38.30	53.16	254945	0.0800	0.0852	259.13
6"	Segregating	Unsorted	2	43	7.15	39.66	42.82	0.0177	10.03	83.99	103.96	78871	0.0914	0.1129	89.79
6"	Segregating	Unsorted	3	41	5.57	23.19	24.65	0.0139	5.03	63.32	44.15	37580	0.0760	0.0558	40.79
6"	Segregating	Unsorted	4	46	6.14	43.56	40.40	0.0056	17.81	57.57	48.03	67210	0.1145	0.0927	88.58
6"	Segregating	Unsorted	5	17	6.19	61.01	52.60	0.0126	14.53	76.35	37.41	84588	0.1105	0.0635	89.76
6"	Segregating	Unsorted	6	45	5.91	61.25	60.31	0.0085	10.96	26.01	32.15	76751	0.0525	0.0589	92.53

Appendix 2. Intraplot variances for five principal component scores in 108 subplots

Plant Spacing	Genotype	Seed Size	Replication	No. of Plants	C_I Yielding Ability	C_{II} Homeostasis	C_{III} Sterility	C_{IV} Mathematic Artifice	C_V Shortness
2"	Pure	Small	1	54	11.49	2.84	1.36	1.38	0.14
2"	Pure	Small	2	55	6.28	3.09	1.09	0.77	0.16
2"	Pure	Small	3	28	16.31	3.69	1.49	1.40	0.34
2"	Pure	Small	4	67	3.76	1.38	0.73	0.53	0.13
2"	Pure	Small	5	26	3.61	1.23	0.38	0.66	0.06
2"	Pure	Small	6	64	5.11	1.94	0.99	1.55	0.12
2"	Pure	Large	1	51	5.66	3.22	1.65	1.05	0.40
2"	Pure	Large	2	38	7.41	3.25	0.70	0.81	0.24
2"	Pure	Large	3	27	11.36	3.26	1.54	0.88	0.45
2"	Pure	Large	4	42	4.65	1.88	1.15	1.30	0.30
2"	Pure	Large	5	24	6.89	2.87	1.32	0.91	0.17
2"	Pure	Large	6	41	4.44	1.74	0.52	0.90	0.15
2"	Pure	Unsorted	1	48	8.33	2.40	2.10	2.05	0.35
2"	Pure	Unsorted	2	40	9.87	3.67	0.96	1.31	0.31
2"	Pure	Unsorted	3	26	18.86	3.46	1.94	1.29	0.49
2"	Pure	Unsorted	4	25	10.91	5.71	1.56	0.83	0.55
2"	Pure	Unsorted	5	17	3.64	2.77	1.75	1.28	0.17
2"	Pure	Unsorted	6	79	8.72	3.40	0.43	0.58	0.16
2"	Segregating	Small	1	49	7.67	3.28	1.55	2.34	0.21
2"	Segregating	Small	2	27	7.75	3.98	0.73	0.68	0.28
2"	Segregating	Small	3	17	15.04	4.90	1.89	2.75	0.45
2"	Segregating	Small	4	33	4.21	2.88	1.46	2.16	0.09
2"	Segregating	Small	5	34	7.51	3.30	0.70	1.17	0.13
2"	Segregating	Small	6	47	7.39	3.63	0.79	0.92	0.14
2"	Segregating	Large	1	46	8.94	4.82	1.23	1.26	0.29
2"	Segregating	Large	2	41	5.66	3.46	1.15	0.68	0.55
2"	Segregating	Large	3	39	12.88	10.04	1.31	1.28	0.18
2"	Segregating	Large	4	33	8.20	4.87	1.11	1.16	0.18
2"	Segregating	Large	5	24	10.73	1.75	0.77	1.20	0.10
2"	Segregating	Large	6	48	7.56	3.20	0.98	0.93	0.18
2"	Segregating	Unsorted	1	42	11.08	3.98	2.70	1.84	0.79
2"	Segregating	Unsorted	2	16	12.20	3.45	1.52	1.67	0.33
2"	Segregating	Unsorted	3	31	25.11	7.15	1.29	1.37	0.20
2"	Segregating	Unsorted	4	30	14.60	4.68	1.52	0.86	0.19
2"	Segregating	Unsorted	5	31	4.96	3.69	2.03	1.12	0.56
2"	Segregating	Unsorted	6	48	12.45	5.02	0.84	0.55	0.29
4"	Pure	Small	1	33	28.44	7.54	1.35	0.40	0.38
4"	Pure	Small	2	21	38.60	6.38	2.19	1.07	0.74
4"	Pure	Small	3	30	20.00	5.33	0.96	1.00	0.32
4"	Pure	Small	4	37	11.12	5.89	1.33	1.40	0.20
4"	Pure	Small	5	49	8.93	4.88	1.04	0.74	0.18
4"	Pure	Small	6	46	5.77	2.13	0.53	0.49	0.21
4"	Pure	Large	1	23	43.81	4.30	1.32	0.49	0.69
4"	Pure	Large	2	32	36.32	5.80	1.45	0.92	0.47
4"	Pure	Large	3	18	9.84	4.81	1.53	1.71	0.46
4"	Pure	Large	4	34	11.88	5.96	1.14	1.07	0.14
4"	Pure	Large	5	30	12.80	3.36	1.04	1.11	0.41
4"	Pure	Large	6	47	4.93	2.55	0.52	0.67	0.08
4"	Pure	Unsorted	1	18	41.57	6.69	2.65	0.77	0.27
4"	Pure	Unsorted	2	29	25.51	7.16	1.66	1.02	0.11
4"	Pure	Unsorted	3	28	11.03	7.28	1.51	0.92	0.41
4"	Pure	Unsorted	4	35	20.19	6.61	1.46	0.93	0.40
4"	Pure	Unsorted	5	37	25.04	10.96	1.18	0.78	0.38
4"	Pure	Unsorted	6	41	9.67	3.68	0.46	0.21	0.12

Plant Spacing	Genotype	Seed Size	Repli-cation	No. of Plants	C_I Yielding Ability	C_{II} Homeostasis	C_{III} Sterility	C_{IV} Mathematic Artifice	C_V Short-ness
4"	Segregating	Small	1	47	21.40	7.53	1.81	1.33	1.05
4"	Segregating	Small	2	22	21.41	10.11	1.89	0.95	0.27
4"	Segregating	Small	3	23	8.88	7.75	2.17	1.10	1.23
4"	Segregating	Small	4	16	36.76	7.99	3.05	0.38	0.67
4"	Segregating	Small	5	37	21.26	5.07	1.30	0.55	0.29
4"	Segregating	Small	6	54	7.26	3.18	0.54	0.68	0.15
4"	Segregating	Large	1	46	26.15	6.98	1.37	4.06	0.71
4"	Segregating	Large	2	33	20.88	4.75	1.10	0.74	0.33
4"	Segregating	Large	3	15	14.50	4.96	2.15	2.63	0.69
4"	Segregating	Large	4	51	16.81	6.19	1.49	1.32	0.50
4"	Segregating	Large	5	53	15.25	5.79	0.78	0.59	0.32
4"	Segregating	Large	6	31	15.18	7.56	0.61	0.42	0.16
4"	Segregating	Unsorted	1	23	27.46	7.00	1.12	0.85	0.50
4"	Segregating	Unsorted	2	36	16.96	4.74	2.24	1.21	0.30
4"	Segregating	Unsorted	3	22	27.98	7.06	1.89	4.80	0.38
4"	Segregating	Unsorted	4	20	47.06	9.19	2.58	3.06	1.54
4"	Segregating	Unsorted	5	36	15.20	5.05	1.27	1.54	0.44
4"	Segregating	Unsorted	6	46	6.01	3.95	1.10	0.91	0.12
6"	Pure	Small	1	33	33.29	10.99	2.09	1.04	0.30
6"	Pure	Small	2	33	31.29	7.47	1.80	0.86	0.19
6"	Pure	Small	3	38	29.65	7.58	1.05	1.12	0.24
6"	Pure	Small	4	53	33.67	6.70	1.45	0.57	0.48
6"	Pure	Small	5	38	18.11	5.19	0.72	1.02	0.26
6"	Pure	Small	6	45	11.96	2.64	0.39	0.51	0.26
6"	Pure	Large	1	39	37.54	8.65	1.58	1.39	0.44
6"	Pure	Large	2	34	17.38	5.42	2.13	1.95	0.67
6"	Pure	Large	3	41	18.97	5.29	1.84	1.71	0.51
6"	Pure	Large	4	28	17.36	4.93	1.75	1.84	0.54
6"	Pure	Large	5	35	19.35	4.61	1.54	0.97	0.51
6"	Pure	Large	6	22	29.98	9.01	0.85	0.99	0.20
6"	Pure	Unsorted	1	31	27.11	7.43	2.82	2.20	0.73
6"	Pure	Unsorted	2	31	21.66	7.99	1.35	0.59	0.19
6"	Pure	Unsorted	3	33	20.25	5.91	2.36	1.33	0.55
6"	Pure	Unsorted	4	53	61.41	6.48	3.82	2.05	0.97
6"	Pure	Unsorted	5	39	21.80	3.41	1.31	1.11	0.40
6"	Pure	Unsorted	6	32	13.82	4.43	0.88	0.78	0.16
6"	Segregating	Small	1	44	67.11	10.68	2.78	1.67	0.41
6"	Segregating	Small	2	30	18.70	6.16	1.74	1.55	0.49
6"	Segregating	Small	3	22	18.19	6.09	2.19	1.10	0.47
6"	Segregating	Small	4	40	29.16	2.98	1.44	1.29	0.87
6"	Segregating	Small	5	28	18.04	10.00	1.76	0.79	0.22
6"	Segregating	Small	6	22	14.62	4.79	1.40	1.41	0.26
6"	Segregating	Large	1	48	57.73	7.72	3.66	1.86	0.86
6"	Segregating	Large	2	29	30.80	6.40	1.67	1.69	0.18
6"	Segregating	Large	3	28	22.65	9.19	1.33	1.42	0.28
6"	Segregating	Large	4	38	18.65	3.18	1.05	0.67	0.38
6"	Segregating	Large	5	31	24.25	6.98	0.95	0.86	0.48
6"	Segregating	Large	6	43	15.00	6.02	1.01	1.16	0.26
6"	Segregating	Unsorted	1	38	70.38	7.87	1.93	1.48	0.77
6"	Segregating	Unsorted	2	43	32.83	6.86	2.25	1.84	0.42
6"	Segregating	Unsorted	3	41	14.67	4.72	1.26	2.17	0.31
6"	Segregating	Unsorted	4	46	29.25	6.07	1.09	1.06	0.28
6"	Segregating	Unsorted	5	17	20.81	8.27	2.03	2.49	0.22
6"	Segregating	Unsorted	6	45	24.49	5.12	0.78	1.03	0.21

Appendix 3. Mean intraplot variance of eleven agronomic characteristics for eighteen treatment combinations (†)

Plant Spacing	Genotype	Seed Size	Plant Height	No. of Tillers	No. of Heads	Per cent Fertile Tillers	1000-kernel Weight	No. of Seeds per Head	No. of Seeds per Tiller	No. of Seeds per Plant	Yield per Head	Yield per Tiller	Yield per Plant
2"	Pure	Small	3.38	8.97	8.30	0.011	2.99	18.07	24.12	10263	0.026	0.032	10.61
2"	Pure	Large	4.84	12.02	9.66	0.010	5.48	19.70	26.40	11586	0.026	0.033	12.36
2"	Pure	Unsorted	6.63	16.85	14.58	0.011	7.77	28.86	37.98	18890	0.036	0.042	17.56
2"	Segregating	Small	3.31	13.94	11.41	0.014	4.31	29.85	32.66	12022	0.044	0.044	13.94
2"	Segregating	Large	4.91	13.83	12.00	0.010	5.36	28.68	33.98	13104	0.046	0.052	15.24
2"	Segregating	Unsorted	6.74	18.56	17.03	0.011	9.64	35.70	44.10	22459	0.051	0.055	20.21
4"	Pure	Small	5.21	41.36	34.91	0.006	9.98	34.72	33.57	47861	0.053	0.048	49.61
4"	Pure	Large	4.93	33.02	29.69	0.008	11.18	31.93	35.57	45803	0.051	0.049	49.16
4"	Pure	Unsorted	6.09	46.20	42.78	0.003	11.69	45.34	45.77	65820	0.067	0.063	62.50
4"	Segregating	Small	10.33	50.31	47.83	0.006	12.78	28.60	33.71	62412	0.053	0.051	59.19
4"	Segregating	Large	6.69	29.40	28.16	0.008	13.95	57.09	42.15	41118	0.078	0.062	43.57
4"	Segregating	Unsorted	5.95	43.23	42.40	0.012	10.19	51.16	49.88	58592	0.064	0.063	63.07
6"	Pure	Small	5.69	58.22	55.03	0.006	13.18	36.66	36.81	86774	0.063	0.058	95.58
6"	Pure	Large	10.00	66.47	57.16	0.011	13.43	36.63	35.71	80065	0.060	0.054	86.92
6"	Pure	Unsorted	8.96	61.16	57.16	0.010	17.77	38.64	39.84	87354	0.066	0.061	93.74
6"	Segregating	Small	8.84	78.02	69.28	0.007	19.00	35.47	36.25	82692	0.063	0.059	93.15
6"	Segregating	Large	8.38	60.37	57.68	0.009	16.51	40.67	41.28	85602	0.072	0.065	85.32
6"	Segregating	Unsorted	7.38	55.44	54.48	0.011	13.11	53.44	49.15	83116	0.085	0.076	94.19

(†) Retransformed data.

Appendix 4. Mean component score intraplot variance for eighteen treatment combinations (†)

Plant Spacing	Genotype	Seed Size	C_I Yielding Ability	C_{II} Homeo-stasis	C_{III} Sterility	C_{IV} Mathematic Artifice	C_V Short-ness
2"	Pure	Small	6.59	2.18	0.92	0.96	0.14
2"	Pure	Large	6.38	2.62	1.06	0.06	0.26
2"	Pure	Unsorted	9.02	3.43	1.29	1.14	0.30
2"	Segregating	Small	7.70	3.61	1.10	1.47	0.19
2"	Segregating	Large	8.70	4.08	1.08	1.06	0.22
2"	Segregating	Unsorted	12.05	4.52	1.55	1.14	0.34
4"	Pure	Small	15.25	5.00	1.13	0.78	0.30
4"	Pure	Large	15.08	4.28	1.11	0.92	0.30
4"	Pure	Unsorted	19.63	6.73	1.32	0.69	0.25
4"	Segregating	Small	16.88	6.51	1.59	0.77	0.47
4"	Segregating	Large	17.71	5.96	1.15	1.17	0.40
4"	Segregating	Unsorted	19.56	5.92	1.61	1.66	0.41
6"	Pure	Small	24.67	6.20	1.09	0.82	0.28
6"	Pure	Large	22.35	6.09	1.55	1.42	0.45
6"	Pure	Unsorted	24.57	5.70	1.85	1.20	0.41
6"	Segregating	Small	23.66	6.21	1.83	1.26	0.41
6"	Segregating	Large	25.47	6.27	1.42	1.20	0.36
6"	Segregating	Unsorted	28.23	6.35	1.45	1.59	0.33

(†) Retransformed data.

Appendix 5. Means of eleven agronomic characteristics for eighteen treatment combinations

Plant Spacing	Genotype	Seed Size	Plant Height	No. of Tillers	No. of Heads	Per cent Fertile Tillers	1000-kernel Weight	No. of Seeds per Head	No. of Seeds per Tiller	No. of Seeds per Plant	Yield per Head	Yield per Tiller	Yield per Plant
2"	Pure	Small	39.43	10.59	9.61	0.916	32.37	30.94	28.30	300	1.002	0.918	9.54
2"	Pure	Large	39.63	9.85	8.98	0.919	32.34	32.97	30.29	296	1.066	0.979	9.55
2"	Pure	Unsorted	37.96	10.59	9.64	0.918	30.33	33.42	30.66	323	1.016	0.933	9.76
2"	Segregating	Small	39.38	10.35	9.21	0.903	33.49	32.73	29.40	298	1.098	0.985	9.93
2"	Segregating	Large	38.93	10.64	9.78	0.924	32.91	33.39	30.81	322	1.104	1.020	10.63
2"	Segregating	Unsorted	37.77	11.60	10.50	0.910	30.12	32.54	29.61	344	0.984	0.894	10.36
4"	Pure	Small	37.83	16.79	15.50	0.934	29.37	35.65	33.25	552	1.060	0.988	16.56
4"	Pure	Large	38.04	16.95	15.52	0.920	30.55	35.87	32.98	560	1.103	1.015	17.30
4"	Pure	Unsorted	37.18	16.08	15.33	0.959	28.82	37.71	36.11	578	1.097	1.052	16.93
4"	Segregating	Small	37.74	15.27	14.43	0.945	28.86	36.04	34.03	521	1.049	0.989	15.39
4"	Segregating	Large	37.47	15.24	14.10	0.925	28.99	36.76	33.73	516	1.070	0.987	15.07
4"	Segregating	Unsorted	38.12	17.75	16.06	0.899	29.86	37.16	33.17	586	1.106	0.989	17.66
6"	Pure	Small	37.49	21.07	19.71	0.939	30.31	36.05	33.84	714	1.103	1.036	22.00
6"	Pure	Large	37.74	21.54	19.47	0.906	29.40	36.59	32.98	708	1.082	0.975	21.28
6"	Pure	Unsorted	36.98	20.20	18.57	0.918	29.02	36.95	33.83	690	1.083	0.993	20.84
6"	Segregating	Small	37.21	20.94	19.23	0.921	28.79	36.22	33.30	694	1.048	0.965	20.53
6"	Segregating	Large	37.23	20.98	19.26	0.915	29.36	35.98	32.85	698	1.067	0.976	20.77
6"	Segregating	Unsorted	37.91	19.18	17.77	0.921	30.67	36.24	33.33	647	1.127	1.040	20.51

Appendix 6. Distances between all possible pairs of characteristics in a 5-dimensional space

Agronomic characteristic	1	2	3	4	5	6	7	8	9	10	11
1. Plant height											
2. Number of tillers	1.43										
3. Number of heads	1.42	.20									
4. Per cent fertile tillers	1.40	1.43	1.29								
5. 1000-kernel weight	1.09	1.42	1.42	1.37							
6. Number of seeds per head	1.37	1.30	1.32	1.46	1.30						
7. Number of seeds per tiller	1.37	1.33	1.25	.99	1.30	.59					
8. Number of seeds per plant	1.41	.32	.28	1.31	1.39	1.10	1.07				
9. Yield per head	1.20	1.34	1.35	1.42	.76	.63	.79	1.18			
10. Yield per tiller	1.21	1.36	1.30	1.08	.81	.78	.57	1.16	.44		
11. Yield per plant	1.35	.40	.37	1.30	1.22	1.08	1.05	.22	1.05	1.03	