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Title: COMPENSATING EFFECTS AND GENE ACTION ESTIMATES FOR THE COMPONENTS OF GRAIN YIELD IN WINTER WHEAT (TRITICUM AESTIVUM, L.EM THELL.)

Abstract Approved: Redacted for Privacy
(Warren E. Kronstad)

Five winter wheat cultivars and their diallel crosses were evaluated for plant height, harvest index, deading-maturity duration, the components of yield, (spikes per plant, spikelets per spike, kernel weight and kernels per spikelet) and total plant yield. Two diverse locations, Moro, a dryland site (250 mm annually) located in central Oregon and the Hyslop Agronomy Farm, a high rainfall site (over 1000 mm annually) located in the Willamette Valley, were utilized for one and two cropping seasons, respectively. Three rates of seeding were used as main plots in a split-plot design that was replicated four times. A modified blend method of seeding was used to simulate solid seeding conditions. Experimental seeds were planted 30.5 centimeters apart within the row over a filler cultivar in equally spaced (30.5 centimeters) rows. The data were analyzed by analysis of variance, Griffing's diallel analysis (Method 4, Model

1), correlation, path-coefficient analysis and by parent progeny regression.

The correlation between grain yield, its components, harvest index, maturity-duration and plant height was dependent on the particular environment of the test. There was poor correlation between yield, tiller number and seed size under all the conditions of these studies. Negative associations between the components of yield indicated the sequential compensatory behavior of these characters under all environments. It would be very hard to select for large grain and short stature wheat because of the positive correlation between plant height and seed size within this population. The low correlations of yield with tiller number and seed size were mainly caused by indirect negative effects through one or more of the other yield components. Harvest index, maturity-duration and plant height had very small direct or indirect influences on grain yield.

It was concluded that maximum yield would be obtained from a plant type which produces enough tillers to cover a particular unit of field area with large, fertile spikes, having medium to large kernels and semi-dwarf stature.

No significant differences existed between parents and single crosses in the expression of the yield components. Nevertheless, hybrids outyielded their parents in grain yield and demonstrated that heterosis for complex traits was a consequence of multiplicative relationships among the components of these traits.

Significant interactions between the genotypes and locations, seeding rates and years were observed in the expression of all characters studied. These interactions indicated that using data from non-competitive conditions to assess performance under competitive conditions could not be justified. Also, limiting the number of testing sites may lead to unsound generalizations and erroneous recommendations regarding gene action estimates of yield and the components of grain yield and three associated characters.

Under non-competitive conditions, estimates of the additive type of gene action were more significant and contributed larger effects than the non-additive type for all traits. As competition increased at higher seeding rates, the effects of specific combining ability became more important in the expression of yield, number of spikes, spikelets per spike, and plant height. Heritability estimates confirmed these results except for yield.

Of the agronomic characters, harvest index, maturity-duration and plant height, only harvest index showed some promise as a selection criterion under noncompetitive conditions.

A breeding procedure utilizing the component approach consisted of selecting early generations under spaced planting with emphasis on avoiding extreme values in any of the components of yield. The balanced combinations of the components of yield should be tested under solid seeding conditions.

Compensating Effects and Gene Action Estimates
for the Components of Grain Yield in Winter
Wheat (*Triticum aestivum*, L. em Thell.)

by

Michel Abi-Antoun

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Typed by A & S Bookkeeping/Typing for Michel Abi-Antoun.

Dedicated to

My wife, Samia, and my sons,

Walid and Nadim

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INTRODUCTION

Wheat improvement has been carried on since the dawn of civilization. Scientific breeding started during the early part of the present century and the development of high yielding cultivars has contributed to the rapidly changing agricultural technology. However, an ameliorated understanding of yield component compensation and gene action estimates must be developed if advancements in grain yield are to be continued. Previous advances have resulted from breeding for specific traits which indirectly affect grain yield such as disease and lodging resistance and if yield increases were realized it was frequently quite by chance. Breeding for grain yield per se has been more controversial because yield in the wheat plant is a complex character which is highly influenced by the environment. It is also the product of several morphological components which are in turn influenced by genetic and environmental factors. The primary components of yield are considered as the spikes per plant, spikelets per spike, kernels per spikelet and kernel weight.

A second factor complicating selecting directly for yield is the fact that wheat is commercially grown under competitive conditions (solid seeding), while selection of the desirable plants in early generations is usually practiced under non-competitive conditions (space planting). This raises the question whether genetic parameters and selection based on space plantings are valid and result in maximum grain yield capacity for solid seeding as well.

Negative correlations have been observed among several of the components of grain yield in wheat which include tiller number, spikelet number, kernel number and kernel weight. This is apparent when plants are grown under environmental stress. Early generation selection practiced under space-planted conditions may cause a loss of the most competitive genotypes and does not take into account any biological limitations that may exist among yield components. However, selections made during the early generations under solid seeded conditions may not accurately evaluate the yield potential of a genotype. Under a selection program anticipated gains may be offset by negative correlations resulting from the compensatory behavior of the components of yield. Such reactions limit the value of early generation selection for grain yield in terms of yield components. Nonetheless, possible improvement may be achieved either by changing the lowest component of a cultivar, or by compromise selection among yield components that leads to better balance and consequently lower compensating effects.

This study was conducted to determine the nature of the compensating effects when stresses are applied to a diallel set of crosses involving five divergent winter wheat cultivars. The characters studied were grain yield, the primary components of yield, which are tiller number, spikelet numbers, kernel number and kernel weight, plant height, harvest index and heading-maturity duration in two solid seeding and 30.5 centimeters space planted conditions. The experiment was repeated over two diverse environments and two consecutive years. A second objective of this investigation was to study the nature of genetic variation in terms of gene action estimates for grain yield and the other characters measured and to determine the effectiveness of selection under the various competitive conditions. The third objective was to measure the influence of environment on the expression of agronomic traits and genetic parameters by determining if results obtained under a given set of environmental conditions can be extrapolated to other environments. An additional objective was to determine if plant height, harvest index or heading-maturity duration might serve as reliable selection criteria in breeding for increased grain yield.

LITERATURE REVIEW

Genotype-Environment Interactions

A genotype will not express the same phenotype under all environments nor will all genotypes react the same under a given set of environmental conditions. This lack of consistency has been termed genotype-environment interaction. The breeder bases his selection on phenotypic expression of agronomic traits which are the product of interaction between the genotype and the environment. Thus, he can develop either widely adapted cultivars or cultivars specifically adapted to fit particular environments (Frankel, 1958). In pursuing the first objective he must obtain information on adaptation and yield of different cultivars when grown under a wide range of soil, climatological and biological conditions (Salmon, 1951; Reitz and Salmon, 1959). However, even cultivars that are bred for specific areas must possess a considerable degree of general adaptability because of the marked fluctuations of climatic conditions from year to year (Finlay and Wilkinson, 1963) which can be more than four times as large as the variation from location to location (Rasmussen and Lambert, 1961). To develop the most appropriate scheme for evaluation of genotypes according to their environmental response, most cultivated crops have been studied in relation to genotype-environment interactions (Abou-El-Fittouh et al. 1969; Baker, 1968; Stroike and Johnson, 1972). Various techniques have been used to determine the behavior of individual cultivars under fluctuating environmental conditions. The procedures commonly used are: (1) analysis of performance tests over a series of environments, (2) linear regression of the mean yield of individual varieties on the mean yield of all varieties in a nursery, and (3) combining ability studies conducted over a series of environments. A new approach was proposed by Boyd and Konzak, 1976, who gave consideration to the analyses of relative deviations from the highest yielding genotype in each environment over which tests are conducted. Using the highest yielding genotype as reference index reduces bias against superior genotypes.

In a detailed review of the implications of genotype x environment interaction in applied plant breeding, Allard and Bradshaw (1964) classified environmental variations into two types: predictable and unpredictable. The first includes genotype x location interactions, while the latter contains genotype x year interactions. Comstock and Moll (1961) developed a model by which variances for the different interactions of genotype x location, genotype x year and genotype x year x location could be partitioned by utilizing an analysis of variance.

Several workers using the analysis of variance technique (Liang *et al.* 1966; Rasmusson and Glass, 1967; Baker, 1968, 1969; Kaltsikes, 1971, and Boyd and Konzak, 1976) have reported on genotype x environment interactions.

Cultivar x year interactions were small and nonsignificant, whereas cultivar x location and cultivar x year x location interactions were highly significant and of considerable magnitude according to Liang *et al.* (1966) who tested varieties of wheat, oats and barley. Grouping of locations reduced location interactions considerably. In barley, Rasmusson and Glass (1967) reported significant variances for genotype x location interactions even when error variances were high. Baker (1968) considered the ratio of genotype x location interaction variance to the variance associated with experimental error as a measure of stability of cultivars in certain geographic areas. In 1969 Baker concluded that stability of a given cultivar was proportional to the genotype x location variance.

The matrix approach was used by Kaltsikes (1971) and the cultivar that had the lowest contribution to genotype x location variance was considered the most stable one. Deviations from the highest yielding cultivars, measured in percent values, over a set of environments were claimed by Boyd and Konzak (1976) to give unbiased estimates of adaptability. The cultivar that contributed the lowest variance was considered to be the most adaptable.

The linear regression technique was developed by Finlay and

Wilkinson (1963). They regressed the mean yield of individual cultivars on the mean yield of all cultivars in a nursery over a range of environments. Average phenotypic stability was indicated by a regression coefficient of one. A regression coefficient smaller than one was an indication of above average stability; that is, the cultivar in question was widely adaptable. St. Pierre et al. (1967) and Johnson et al. (1968) also used linear regression. The adaptability of selected barley strains was estimated from yield trials conducted in the F_7 and F_8 generations at two locations. The widest adaptability was obtained in strains which were selected at alternate locations in successive years (St. Pierre et al. 1967). Widely adapted wheat cultivars reported by Johnson et al. (1968) had improved stability of performance and higher potential yields over previous varieties. These cultivars yielded well under poor conditions and respond to favorable environments with high yield potential. Eberhart and Russell (1966) regressed varietal means over environmental indeces. The environmental index was defined as the deviation of each environmental mean from the grand mean over all environments. Stability was measured by the regression coefficient as well as by the deviation mean square value which was used as a measure of predictability. The deviation mean square was a more important stability parameter because it reflected changes in cultivars resulting from specific changes in environment (Eberhart and Russell, 1969). Joppa *et al.* (1971) considered this latter parameter a measure of specific genotype x environment interaction. Hardwick and Wood (1972) and Boyd and Konzak (1976) showed that the regression model suffered a bias. Environmental means were assumed to be measured without error which is not always true (Hardwick and Wood, 1972). The regression of cultivar means on environmental variables through simulation and multiple regression techniques should reduce the bias, especially with a large number of genotypes. Boyd and Konzak (1976) argue that "average of all genotypes" is not only an unnatural index for plant breeding purposes, but it introduces a bias which discriminates against genotypes that are agronomically superior.

Combining ability studies, conducted over a series of environments, were introduced by Rojas and Sprague (1952) using corn as a test crop. Jordaan and Laubscher (1968) partitioned G. C. A. and S. C. A. x location interactions for eleven winter wheat cultivars. Boyd *et al.* (1976) presented evidence to support the possibility of discriminating between crosses as early as F_2 derived bulks following selection for agronomically appropriate characteristics. The use of small plot replication over environment leads to savings in resources and collaboration between breeding programs. Walton (1968) considered that phenotype stability has proved universally difficult to achieve and suggested that attempts to produce cultivars with wide adaptation are less likely to succeed than programs designed to produce varieties for specific management problems. Finlay (1968) used the widespread semi-dwarf Mexican spring wheat cultivars to refute such arguments. The use of stability parameters assists plant breeders in the selection of potential parents and in the evaluation of crosses in early generations for high yielding segregates with wide adaptability.

Components of Yield

A successful breeding program is based on the effectiveness of selection. Early generation selection is the least expensive and most rapid. Selection for a complex trait as yield may not give higher yielding progenies. Efforts to break down yield into component traits started over fifty years ago with the work of Engledow and Wadham (1923) and others working with many different crops. Many investigations have pointed out that yield per plant may be interpreted as a product of number of tillers, number of grains per tiller and grain weight. Possible use of these components for practical plant breeding purposes was not very clear due to their close interrelations and high fluctuations. Grafius (1956, 1964) applied a geometric approach to simplify the complexity of yield by proposing that yield is an artifact and may be considered as an end product of three components; X, number of ears; Y, average number of kernels per ear and Z, average kernel weight. Each of the components is quantitatively inherited. Thus, there can be no genes for yield, no dominance or overdominance effects, no additive effects, no heritability and no combining ability estimates. The total yield (W) may be visualized geometrically as a rectangular parallelipiped with edges X Y Z and volume W. Thus, there is no way in which yield can be changed without changing one or more of the components X Y Z. The highest volume change is obtained by changing the shortest edge of a good cultivar. This was accomplished in oats (Grafius, 1964) and in spring wheat (Knott and Talukdar, 1971).

Independent gene systems governing the different yield components have been demonstrated when correlations among yield components were found to tend toward zero under minimum plant competition (Grafius, 1964). In field beans, leaf area components were reported to be independent by Duarte and Adams (1963). Functional genes were primarily due to the components of leaf area and not to the complex trait itself. Parents complemented each other in components of leaf area and this complementation, combined with favorable dominance resulted in heterosis in excess of the better parent. Duarte and Adams (1963) proposed that such heterosis resulting from multiplicative relationships among components is potentially fixable in true breeding genotypes. McNeal et al. (1974) used spring wheat yield nursery data to calculate correlations between the components of yield. R^2 values were very small, suggesting that compensating effects among yield components were very small. In animal experimentation, Sheridan and Barker (1974) failed to detect compensating effects while selecting for two concurrent traits after 22 generations.

Plants at different densities compete for certain environmental factors at different intensities. The existing negative correlation among the yield components makes it more complicated to attribute the results to individual agronomic traits (Kirby, 1967). Occurrence of negative correlations among yield components contrasts with the hypothesis of genetic independence among those components. Adams (1967) concluded from a study of yield in field beans under different competitive conditions, that these correlations arose in response to developmental rather than genetic influences. The development of yield components in a sequential pattern varies in response to the input of metabolites that are limiting at critical stages in the sequence. This was known as the concept of sequential development of components. Based on this concept, Adams (1967) suggested that selections be practiced under environmental conditions that favor the full expression of genes relevant to yield components. Rasmusson and Cannel (1970) attributed negative responses to a linkage of genes controlling the components. They related effectiveness of selection to compensatory effects determined by both environment and genetic history of the populations. Adams and Grafius (1971) refuted the linkage theory and attributed negative associations among yield components to an oscillatory response of components. This response is caused by the sequential nature of component development and a limitation of environmental resources. In this oscillatory component compensation system plants reach a compromise in use of available resources thus their development is a contrast between immediate fittness and long-term flexibility. Thomas et al. (1971) supported this latter concept. Because components develop in sequence, resources used at one stage of development may not be available for later use. Under environmental stresses, the genetic control of the last component to develop in the sequence would be replaced by indirect control of the most influential component developed under better environmental resources. The increase in the flow of environmental resources throughout the developmental stages allows the plant breeder to predict more accurately what yield component will be the most influential in early segregating populations.

The components of yield and other associated characters have also been investigated using other approaches. Genes behaving additively were controlling the expressions of all yield components and other related characters (Kronstad and Foote, 1964; Fonseca and Patterson, 1968; Lee and Kaltsikes, 1972; Edwards et al. 1976, Ketata et al. 1976). Dominance and epistatic effects were detected for grain yield and some yield components. The expression of kernel weight was partially controlled by dominance effects (Chapman and

McNeal, 1971; Sun et al. 1972). Epistasis affected the expression of kernels per spikelet and grain yield (Bitzer and Fu, 1972; Ketata et al. 1976) and kernel weight (Sun et al. 1972; Widner and Lebsock, 1973).

Reports using narrow sense heritability estimates as an index of gene action has lead to contradictory results. Fonseca and Patterson (1968) and Lee and Kaltsikes (1972) found the number of tillers per plant to be highly heritable. This character showed low heritabilities in the studies of Kronstad and Foote (1964) and Johnson et al. (1966). The latter studies reported high heritability values for kernel weight while the former studies reported otherwise. Kernel weight had relatively high narrow sense heritability estimates even when the environment played a large role according to Singh and Anand (1972). It generally has a higher heritability value than the other yield components (Bhatt, 1972). The number of kernels per spike had high heritabilities according to most of these studies but Gandhi et al. (1964) showed low heritability values for this trait. The inconsistencies of heritability estimates for and among various agronomic traits were related to (1) the method used in calculating the heritability estimates (Johnson et al. 1966), (2) the genetic background of the parental lines (Schmalz, 1972), (3) the intensity of the environmental variations (Singh and Anand, 1972) and environmental stresses which could have affected the expression of the different components during their sequential development (Adams, 1967; Grafius and Thomas, 1971), and (4) failure to meet the theoretical assumptions underlying the use of these techniques.

Association Among Agronomic Traits

The study of the relationships among various agronomic traits may indicate significant associations between highly heritable traits and economically important ones that are of complex nature. This allows the breeder to practice indirect selection (Gandhi *et al.* 1964). Characters which are independent of each other at the environmental and genetic levels facilitate the interpretation of genetic analyses (Whitehouse *et al.* 1958). Research to discover morphological characters which are indicators of adaptability was urged by Finlay (1970) and Syme (1970, 1972).

Due to the independent development of the yield components, they are used very often to explain the structure of economic grain yield in wheat (Baier and Robertson, 1967). Associations which show most consistency are those between the components of yield with grain yield. Tiller number per plant or per unit area is the most consistent. Kernel weight and number per head are less consistent. The assumption that yield components are independent of each other does not always hold true due to environmental effects as well as the nature of the genotypes studied (Anand *et al.* 1972; Khan *et al.* 1972).

Phenotypic and genotypic correlations have been used to refine the estimates of association between different traits. In general, phenotypic and genotypic correlations have the same sign but differ in magnitude (Singh et al. 1969; Khadr, 1971).

Morphological characters in spring wheat influenced plot yields indirectly in that leaf area, flag leaf width and total photosynthetic area above the flag leaf node were associated with yield per ear (Nass, 1973). Thus, ears per plant, yield per ear and harvest index considered together should be an effective means of selecting for increased yield. The duration of green material of the flag leaf and the peduncle gave a significant correlation with grain yield (Spiertz et al. 1971). Fischer and Kestesz (1976) concluded that harvest index measurements in spring wheat offered promise as predictors of yielding ability when the seeds available are limited.

Path coefficient analysis was useful in that it revealed the true nature of cause and effect relationships of heading time, plant height, spike number and kernel weight with grain yield. Kernel weight had the greatest direct and indirect effects on grain yield. Spike number had a direct effect but no significant indirect effects (Bhatt, 1973). Path coefficient analysis indicated that each of the components of yield in winter wheat had large direct effects on grain yield but important indirect effects resulting from negative correlations among yield components (Fonseca and Patterson, 1968). In a study on selection for yield in wheat, total correlations were high for grain yield versus number of grains per ear, number of ears per plant and 250 kernel weight. The direct effects of 250 kernel weight and number of ears per plant were responsible for their significant association with yield, while the relationship between number of grains per ear and yield was mainly due to indirect effects via 250 kernel weight and ear length (Das, 1972). Kronstad (1963) found high positive correlations between yield per plant with kernels per spikelet and with spikelets per spike. There was also a negative correlation between spikes per plant and yield, which was a result of negative associations of spike number with spikelet number and kernel number. Plant height exerted a positive indirect effect by way of kernel number on plant grain yield.

Multivariate analysis has been recently used to study relationships among variables. Usually grain yield is used as the dependent variable and the components of yield and other agronomic traits as independent variables. The independent traits are assigned predictive values and their reliability is measured by regression analysis (Hsu and Walton, 1970; Syme, 1972). Bhatt (1973) compared four methods of selecting parents by hybridization in common bread wheat and reported that the most effective was multivariate analysis. Das (1972) used discriminant functions and observed that a maximum genetic gain of 7.44 percent was obtained when grain yield per plant, 250 kernel weight, number of ears per plant and ear length were included in the function. This suggested that discriminant function would be superior to straight selection in wheat.

The associations among agronomic traits under various stresses may help in determining the most profitable plant morphology. In winter wheat, Bingham (1971) favored cultivars with restricted tillering to make use of the source-sink relationship. Lupton (1972) suggested that as sink capacity is increased by breeding new cultivars, erect leaves with high post-anthesis longevity and awned ears are to be favored especially in dwarf and semi-dwarf wheat. Yield depends on the photosynthetic capacity of the crop after anthesis (Grundbacher, 1963; Evans et al. 1972) and the ability of the grain to store the potential supply of carbohydrates. Better wheat and rice cultivars have been selected for shorter plant height, high tillering capacity and more erect leaves. Yoshida (1972) believed that the short stature recently preferred for crop varieties is related to lodging and is not necessarily the optimum height.

Influence of Plant Competition

Wheat is commercially grown in competitive conditions. Early generation selection is usually conducted under non-competitive conditions. Early generation selection practiced under space-planted conditions may cause a loss of the most competitive genotypes and does not take into account any biological limitations that may exist. However, selections made during the early generations under solid seeded conditions may not accurately evaluate the yield potential of a genotype. Plant competition in this case does not allow for the full expression of the yield components and other associated characters. Khalifa and Qualset (1975) studied the intergenotypic competition between tall and dwarf wheats and found that shorter genotypes were eliminated after seven generations of bulk cropping. Directional and stabilizing selection affected both yield and plant height. Thus, the agronomically desirable short plants were naturally selected against. Fischer and Kestesz (1976) reported that in spring wheat as the degree of competition declined going from crop plots to spaced plants, genotypes which can more fully occupy the increased space available were favored; thus the performance of non-erect genotypes improved noticeably relative to erect ones. A significant genotype by plot type interaction was observed and assumed to result in poor correlation between yield in small and large plots. This was not found in oats (Frey, 1965).

Yield is the product of the yield components which are directly or indirectly related to other agronomic characters of the plant. These components are reported to be influenced by variety, location, date and rate of seeding, level of nutrients and other factors. Grain yield per unit area showed a peak value at intermediate plant densities (Puckridge and Donald, 1967). High plant densities (competition) result in poor root growth (Kirby, 1967), in early exhaustion of moisture supplies (Pelton, 1969), and in early leaf and tiller senescences (Puckridge and Donald, 1967). Tillering could be suppressed by heavy competition but it is directly related to the supply of nutrients (Aspinall, 1963; Puckridge, 1968). Donald (1968) questioned the importance of tillering and supported a "uniculum" plant concept. Kernel weight is generally suppressed by heavy seeding (Pelton, 1969; Puckridge and Donald, 1967). Higher seeding rates lead to more spikes per unit area and consequently smaller spikes with fewer seeds (Day and Thompson, 1970; Finlay, et al. 1971; Syme, 1972). Plant height increased under competitive conditions (Puckridge and Donald, 1967), was inconsistent (Finlay et al. 1971) or decreased (Pelton, 1969; Syme, 1972). Heavy seeding resulted in earlier heading and earlier maturity (Pendleton and Dungan, 1960; Finlay et al. 1971).

Rumbaugh (1963) observed in two varieties of alfalfa that selection indices based upon yield component data obtained in spaced nurseries may not accurately portray the forage yield potential of genotypes in solid seeding. Theurer and Elling (1964) reached similar conclusions but Evans et al. (1966) reported otherwise in the same crop. It is apparent that information regarding the effectiveness of early generation selection under space planted conditions in predicting the potentially highest yielding cultivars is missing.

MATERIALS AND METHODS

Four studies were conducted over two locations in Oregon for the two crop seasons from 1973 through 1975. Five soft white winter wheat cultivars (Triticum aestivum, L. em Thell), Hyslop, Paha, Sprague, Yamhill and Luke, and a hard red winter wheat, Kavkaz, were used in the above experiments. The soft wheat cultivars have been in commercial production in the Pacific Northwest of the United States. Kavkaz is a cultivar developed and grown in Eastern Europe. Detailed descriptions of the cultivars are presented in the Appendix (Table 1). These cultivars represent a wide genetic diversity for the components of grain yield and other characters associated with grain yield. In this investigation the yield components were considered to include tiller number, spikelet number, fertility and seed size. Major emphasis was placed on the response of these yield components on grain yield where grown at different locations and levels of competition.

Hyslop, Paha, Sprague, Yamhill, and Luke were crossed in a diallel fashion. Reciprocals were not utilized. Due to a combination of unfavorable genetic factors, progressive necrosis was observed for those crosses involving Luke. Therefore Luke was replaced by Kavkaz in subsequent experiments.

The experimental sites, Hyslop Agronomy Farm near Corvallis and Sherman Experiment Station, Moro, represent two widely different environments. These will be referred to as Hyslop and Moro locations, respectively.

The soil type at Hyslop is a Woodburn silt loam. Precipitation follows a winter rainfall pattern which provides a very wet environment throughout most of the growing season of winter cereals. Total rainfall amounted to 1718.0 mm during the 1973-1974 growing season and 951.3 mm in 1974-1975. Winter temperatures are mild and freezing rarely occurs over extended periods. The flowering to maturity period occurs during the spring and summer when the temperatures are also quite mild. Prior to seeding, 100 kg/ha of nitrogen was applied in the form of amonium nitrate. At the tillering stage additional nitrogen fertilizer was topdressed in the form of Urea (46 percent N) at the rate of 100 kg. nitrogen per hectar.

Moro is a dryland location with wide temperature extremes. The soil is a deep, well drained and medium textured Walla Walla silt loam. Insufficient winter precipitation requires summer fallowing which is a system of alternate season crops that makes use of soil moisture carried over from the rainfall of the previous season. Precipitation during the 1974-1975 crop season was 279.0 mm. At seedbed preparation, 50 kg/ha of amonium nitrate nitrogen were applied. No additional nitrogen was required at this site.

It is difficult to produce large quantities of hand pollinated F_1

seed. Therefore, to provide competitive conditions, a modification of the blend method of seeding (Peterson, 1970) was introduced. This method consists of using a filler cultivar to make up for seeding rates. Three rates of seeding were used, 30.5 cm spacing, 100 and 200 kg/ha at the Hyslop location and 30.5 cm spacing, 68 and 136 kg/ha at Moro. The medium seeding rate corresponded to that used by farmers in each location. A semi-dwarf, brown chaffed winter wheat (Selection 172--R-69-214) was used as a filler. Experimental seeds or transplants were overplanted on plots presown with the filler cultivar. The plants were also tagged so as to be easily identifiable at all stages of growth. Adequate borders around each plot were planted with the filler variety and each experiment was surrounded with two rows of barley to further eliminate any border effects.

A split-plot design was used with seeding rates as main plots and genotypes (Parents and F_1s or F_2s) as subplots which consisted of one row with 30.5 cm between rows. There were four replications in each experiment. Major differences between the experiments are summarized in the following section.

Study I. Hyslop 1973-74

A diallel cross using the four winter wheat cultivars, Hyslop, Paha, Sprague and Yamhill was used. Experimental material consisted of four parents and six F_1s. Seeds were germinated in the greenhouse and transplanted into the field. Eleven seedlings of each entry were planted 30.5 cm apart in the center of a 4.5 meter row at three seeding rates (spacing, 100 and 200 kg/ha). A tag was wrapped around each seedling at transplanting time to ease identification at early stages of growth.

Study II. Hyslop 1974-75

The five winter wheat cultivars, Hyslop, Paha, Sprague, Yamhill and Kavkaz were crossed in diallel fashion. This constituted a one way diallel with five parents and ten F_1s. Eight seeds of each genotype were planted 30.5 cm apart in the center of a 3.6 meter row at three seeding rates (spacing, 100 and 200 kg/ha). At planting time, seeds planted in the filler were tagged with a popsickle stick for ease of identification. Karmex herbicide was applied at the four leaf stage at the rate of 1.5 kg/ha to control rye grass. An application of the systemic fungicide BAS 317OF (2-iodobenzanilide) was made in the spring to control an epidemic of stripe rust.

Study III. Moro 1974-75

This experiment was a duplicate of Study II except for the following: seeds were treated with a fungicide-insecticide chemical (Guardsman Seed Guard Plus Insecticide) to control wire worms and seedborne fungi. Seeding rates were: spacing, 67 and 134 kg/ha. The second seeding rate corresponded to that used by farmers in that area.

Study IV. Hyslop 1974-75

This study consisted of a diallel cross using the four winter wheat cultivars, Hyslop, Paha, Sprague and Yamhill, their six F_1s and six F_2s. Eight seeds of each parent and F_1 were planted 30.5 cm apart in the center of a 3.6 meter row at two rates of seeding; spacing and 100 kg/ha. In the case of F_2s, eleven seeds were planted per row and ten rows were used for each plot. Cultural practices were the same as those of Study II.

Data were collected from individual plants for the following eight agronomic traits: grain yield, plant height, tillering, spikelets per spike, kernels per spikelet, kernel weight, harvest index and post anthesis duration.

Grain yield was measured from the clean grain weight for each plant. Plant height measurements were taken from the crown to the top of the tallest spike at maturity. Tillering was recorded by counting the number of head-bearing tillers after the plants were pulled. The number of spikelets per spike (head size) was determined by averaging two random spikes of each plant. Kernels per spikelet (fertility) was indirectly calculated from grain yield, kernel weight, tiller number and spikelets per spike. Kernel weight was determined by finding the weight of 300 kernels from large plants which were spaced or by finding the weight of 100 kernels from small plants grown under solid seeding or by counting all available seed when the seed number was low. Harvest index (HI) was calculated as the grain weight to the grain plus straw ratio in percent. Post anthesis duration was determined from the difference between days to maturity and days to heading. Each of these characters was analyzed on a plot mean basis.

The data obtained from parents, F_1s and F_2s were analyzed separately and together by the analysis of variance for the eight characters (Cochran and Cox, 1957; Comstock and Moll, 1961).

Estimates of general and specific combining ability were obtained by using Griffing's model I and method 4 (Griffing, 1956). In this method, one set of F_1s are included in a matrix, and neither parents nor reciprocal F_1s are used. The fixed model was used because parents constituted a selected set of cultivars. The method for computing the analysis of variance for combining ability is given in Table 2.

Using this technique, GCA is interpreted as the relative performance due primarily to the additive effects of polygenes, whereas, SCA reflects the relative performance due primarily to deviations from the additive scheme.

Broad and narrow sesen heritabilities were estimated from the analysis of variance according to Gardner (1963).

Heritability estimates in the narrow sense were also obtained from the regression of F_1 or F_2 means on mid-parent values as described by Falconer (1960).

Simple correlation coefficients were computed for the eight measured traits, under all seeding rates for single crosses and for parents and single crosses together. The correlation coefficients of yield and other characters from single crosses were further partitioned into direct and indirect effects by the path-coefficient analysis (Wright, 1953; Li, 1956; and Dewey and Lu, 1959). In this analysis, direct and indirect effects would equal unity if all variables were accounted for. Unknown variables contribute to the deviation from unity which is well known as a residual effect ($1-R^2$). The associations of yield with all measured characters are illustrated in Figure 1 (Appendix). Standardized partial regression coefficients were obtained by the simultaneous solution of the equations observed in Table 4 of the Appendix.

EXPERIMENTAL RESULTS

Genotype x Environment Interactions

Comparisons of parental cultivars with their respective F_1s when grown under three rates of seeding and in two different environments are presented in Tables 1, 2 and 3. The F_1s outyielded their parents in all experiments and under the three rates of seeding. A similar situation existed for the components of yield with the exception of the number of tillers, which was lower at Moro (Table 3) and only then under solid seeded conditions. Even though the increased performance of F_1s was not high for any of the individual yield components, superior performance of F_1s was observed in grain yield due to the multiplicative effects of these components.

Higher yield increases were observed under non-competitive conditions except for one experiment (Table 1) where the highest yield increases were observed under competitive conditions. This was the higher rainfall environment where transplanted material grew faster than the filler and received less than the intended competition.

Seeding rates depressed yield and yield components in parental as well as single cross genotypes. An apparent component compensation was observed for fertility in the higher rainfall environment of Hyslop (Table 1) where the number of kernels per spikelet increased

Table 1. Average of our parental cultivars in comparison with the average of their six F_1s under three rates of seeding for the components of yield, Hyslop 1974 (Study I).

Component	Seeding Rate (kg/ha)	Parents	Relative Performance %	F_1s	Relative Performance %	$\frac{F_1 s}{\text{Parents}}$ %
Number of Tillers	Spacing	25.73	100.00	26.33	100.00	102.33
	100	11.53	44.81	13.63	51.77	118.21
	200	8.53	33.15	11.32	42.99	132.71
Spikelets/Spike	Spacing	22.56	100.00	23.87	100.00	105.81
	100	21.47	95.17	22.49	94.21	109.41
	200	20.66	91.58	23.10	96.77	111.81
Fertility	Spacing	2.70	100.00	2.74	100.00	101.48
	100	2.67	98.89	2.92	106.57	109.36
	200	2.69	99.63	2.85	104.01	105.95
Seed Size	Spacing	43.60	100.00	47.53	100.00	109.01
	100	43.59	99.98	45.66	96.07	104.75
	200	42.58	97.20	45.20	95.10	106.65
Grain Yield (gm/plant)	Spacing	68.31	100.00	81.14	100.00	118.78
	100	30.32	44.31	42.34	52.18	139.64
	200	20.65	30.23	29.07	35.85	140.77

Table 2. Average of five parental cultivars in comparison with the average of their ten F_1s under three rates of seeding for the components of yield, Hyslop 1975 (Study II).

Component	Seeding Rate (kg/ha)	Parents	Relative Performance %	F_1s	Relative Performance %	$\frac{F_1s}{Parents}$ %
Number of Tillers	Spacing	13.18	100.00	14.83	100.00	112.52
	100	1.95	14.82	1.90	12.84	97.44
	200	1.65	12.56	1.60	10.80	96.74
Spilelets/Spike	Spacing	21.94	100.00	22.92	100.00	104.47
	100	18.26	83.23	17.90	28.1	98.03
	200	16.58	75.56	17.03	74.2	102.71
Fertility	Spacing	2.96	100.00	3.13	100.00	105.53
	100	2.79	94.20	2.88	90.51	103.18
	200	2.55	85.97	2.69	86.13	105.72
Seed Size (mg)	Spacing	43.98	100.00	48.09	100.00	109.34
	100	43.18	98.18	44.60	92.74	103.29
	200	42.10	95.72	43.28	90.00	102.80
Grain Yield (gm/plant)	Spacing	40.48	100.00	50.79	100.00	125.44
	100	4.38	10.83	4.431	8.72	101.07
	200	3.04	7.51	3.236	6.37	106.38

Table 3. Average of five parental cultivars in comparison with the average of their ten F_1s under three rates of seeding for the components of yield, Moro 1975 (Study III).

Component	Seeding Rate (kg/ha)	Parents	Relative Performance %	F_1s	Relative Performance %	$\frac{F_1 s}{\text{Parents}}$ %
Number of Tillers	Spacing	15.16	100.00	16.96	100.00	111.86
	68	3.09	18.91	2.96	17.46	95.70
	134	2.19	14.48	2.14	12.67	97.86
Spikelets/Spike	Spacing	18.26	100.00	18.73	100.00	102.57
	68	14.48	79.30	14.91	79.60	102.97
	134	13.88	76.01	14.01	74.80	100.94
Fertility	Spacing	2.64	100.00	2.64	100.00	100.11
	68	2.02	76.53	2.05	77.69	101.63
	134	1.90	72.22	1.93	73.00	101.20
Seed Size (mg)	Spacing	33.58	100.00	34.66	100.00	103.22
	68	27.00	80.40	28.69	82.77	106.26
	134	27.32	81.36	28.02	80.84	102.56
Grain Yield (gm/plant)	Spacing	23.63	100.00	28.67	100.00	121.31
	68	2.46	10.42	2.58	9.02	105.00
	134	1.56	6.63	1.60	5.60	102.49

with stress while all other yield components were depressed. Seed size and fertility were the components least sensitive to the stress of seeding rates. Spikelets per spike did not change drastically with imposed competition whereas tiller number suffered the sharpest decline as the seeding rate increased. This drop was almost proportional to the decrease observed in yield.

In addition to the previous comparisons, an analysis of variance was applied to test for possible interaction of genotypes by locations (Table 4) and genotypes by years (Table 5). Eight measured characters were examined, yield, the components of yield, heading maturity duration, plant height and harvest index were all found to be unstable under the effects of locations and seeding rates. Harvest index, seed size and fertility were the most stable in the tested locations. However, when the effects of years are measured even the harvest index consideration becomes critical since it had significant interaction with years. Only seed size and fertility continued to be relatively valid criteria for selection under various environments and in consecutive years. Significant first order interactions of genotypes with locations and years and the second order interactions with seeding rates were observed. Variation across locations was more pronounced than that encountered over years. Genotypes reacted differently in consecutive years for only those characters which appeared not to be involved directly in the expression of yield, namely

Table 4. Observed mean squares for combined analysis of Hyslop 1975 (study II) and Moro 1975 (Study III) experiments for eight measured characters.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
Location	1	3458.36	137.20	1041.42	81192.11	5670.01	55.15	18932.65	38.59
Replicates/Location Error (a)	6	3.97	2.95	5.87	27.31	9.02	82.01	11.11	0.14
Seeding Rates	2	759.07**	6921.44**	900.94**	88.26	46935.23**	510.02	934.06**	10.53**
Location x Seeding Rate	2	16.12**	18.12**	9.32	1148.30**	3475.05**	69.48	104.43**	1.18**
Error (b)	12	4.14	2.24	2.56	74.15	3.75	53.34	8.34	
Genotypes	14	8.29**	22.82**	58.95**	308.75**	204.43**	35.61**	368.25**	1.04**
Location x Genotypes	14	5.83**	5.18**	5.00**	48.36**	85.25**	11.51	6.97	0.03
Genotypes x Seeding Rates	28	4.19	15.37**	1.69**	32.47**	148.70**	12.05**	10.44**	0.14**
Location x Genotype Seeding Rate	28	4.33	3.43*	1.83**	20.83	67.53**	8.51	6.80*	0.09**
Error (c)	252	3.02	2.17	0.96	14.82	22.16	7.29	4.30	0.05
C.V. (a) %		5.29	22.80	9.16	10.68	13.50	16.51	7.73	16.74
C.V. (b) %		4.52	22.47	5.62	4.77	32.82	6.11	5.55	8.55

* Significant at 5 percent level

** Significant at 1 percent level

Table 5. Observed mean squares for combined analysis of Hyslop 1974 (Study I) and Hyslop 1975 (Study IV) experiments for eight measured characters.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
Years	1	53.68	2103.29	163.83	17174.81	18771.42	1272.95	220.90	1.48
Replicates/Years Error (a)	6	4.98	17.99	1.73	40.08	124.33	11.92	21.25	0.15
Seeding Rates	1	610.74**	11507.86**	144.59**	124.78**	98703.23**	12.49	53.82*	0.24
Years x Seeding Rates	1	2.16	547.11**	61.13**	295.66	5060.02**	5.44	0.81	0.02
Error (b)	6	11.80	23.40	1.60	242.85	61.24	23.88	4.13	0.06
Genotypes	9	20.41**	58.47**	48.64**	906.01**	1496.20**	23.82**	13.37**	1.36
Year x Genotype	9	5.59*	12.60	4.35	161.21**	109.93	20.99**	10.31	0.12
Genotype x Seeding Rate	9	3.18	17.82	1.93**	15.43	388.34**	12.04*	0.96	0.07
Year x Seeding Rate x Genotype	9	7.69**	z 14.81	2.67**	23.94	173.05	15.69**	10.01	0.09
Error (c)	108	2.72	10.51	0.75	21.30	99.22	5.86	6.05	0.07
C.V. (a) %		7.59	30.62	5.75	14.20	17.05	11.29	4.59	8.92
C.V. (b) %		3.64	20.52	3.96	4.21	21.70	5.59	5.56	9.32

* Significant at 5 percent level

** Significant at 1 percent level

harvest index, heading-maturity duration and plant height.

Genotype-Environmental Interactions and Combining Ability Analyses

The mean squares for the eight characters measured involving the parental and F_1 populations when grown at the Hyslop site for two years and at the Moro site for one year are presented in Tables 6, 7 and 8. There were significant differences among parents and among F_1s in the expression of all measured traits for all environments. Also, parents and their F_1s differed significantly in the average expression of all characters for the three seeding rates. Only heading-maturity duration and fertility were stable and showed less variation than other traits when parental cultivars were compared with their F_1s.

Throughout the various experiments, the average general combining ability mean squares were consistently higher than average specific combining ability values. This indicated the importance of the additive genetic effects in the expression of all eight characters. Another significant feature of the average combining ability estimates is the interaction with seeding rates. There were no significant SCA by seeding rate interactions in the expression of any of the measured traits except for fertility at Hyslop 1975 (Table 7). On the other hand more significant interactions of seeding rates with GCA were observed at both locations and years.

Table 6. Observed mean squares for eight characters of four winter wheat parents and their six F_1s grown at Hyslop 1974 (Study I) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
Replicates	3	67.68	11.75	0.99	11.87	93.40	16.36	23.82	0.28
Seeding Rates	2	135.58	3117.82**	15.10**	92.99**	27527.82*	32.76*	35.42*	0.10
Error (a)	6	52.78	12.38	1.34	1.13	31.60	3.23	5.93	0.06
Genotypes	9	69.36	52.24	48.96	1213.14	1140.93	15.69	190.16	1.02
Parents	3	61.61**	46.19**	73.83**	1230.87**	1514.32**	18.11**	312.14**	1.46**
F_1s	5	86.83	56.39**	22.68**	1118.43**	425.14**	15.54**	103.14**	0.85
G.C.A.	3	100.37	89.69	37.04*	1836.00*	679.91	21.15	157.66	1.35
S.C.A.	2	66.50	6.46**	1.13	42.15**	42.99**	7.12**	21.36**	0.09
Parents vs. F_1s		5.23	49.65**	105.80	1633.52**	3599.69*	9.18*	259.32*	0.56**
Seeding Rate x Genotype	18	26.26	7.10	1.15	12.79**	72.56	3.34**	1.98	0.03
Seeding Rate x Parents	6	13.00	11.47**	1.14	14.44**	71.06	2.91	1.15	0.03
Seeding Rate x F_1	10	36.53	4.67	0.75	10.30**	77.59	2.46	1.47	0.02
Seeding Rate x G.C.A.	6	1.79	5.45	0.42	14.68**	104.43	3.13	1.23	0.02
Seeding Rate x S.C.A.	4	6.36	3.51	1.24	3.72	37.20	1.37	1.83	0.03
Seeding Rate x Parents vs. F_1s	2	14.71	25.79*	3.19**	20.30**	51.88	9.07**	7.05*	0.05
Error (b)	81	30.38	5.27	0.62	4.14	57.01	1.54	1.62	0.02
C.V. (a) %		15.19	21.91	5.11	0.89	12.11	4.50	5.40	9.30
C.V. (b) %		11.50	14.29	3.50	1.70	16.30	3.10	2.80	5.70

* Significant at 5 percent level

** Significant at 1 percent level

Table 7. Observed mean squares for eight characters of five winter wheat parents and their ten F_1s grown at Hyslop 1975 (Study II) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
Replicates	3	4.12	3.99	7.60	18.63	11.21	10.18	14.91	0.24
Seeding Rates	2	278.00	3133.31**	546.18**	369.07	37975.03	101.85	229.75**	2.75**
Error (a)	6	0.77	1.99	4.44	132.72	2.08	82.15	11.09	0.17
Genotype	14	27.46	27.50	37.39	222.54	251.28	24.77	220.88	0.61
Parents	4	8.35*	21.92**	71.13**	272.70**	503.78**	17.02	277.49**	0.45**
F_1	9	14.25	7.40**	25.97**	90.16**	112.09**	27.08**	198.19**	0.68**
G.C.A.	4	18.51	14.92*	56.97**	144.33**	172.79**	51.24*	438.85**	1.25*
S.C.A.	5	10.84	1.40	1.18	46.81**	63.53**	7.75**	5.68**	0.22
Parents vs. F_1	1	3.09	10.65*	5.11	1213.30**	493.97**	34.96*	198.61**	0.69**
Seeding Rate x Genotype	28	7.05*	7.56**	3.00	41.05**	185.38**	9.02	9.32*	0.11*
Seeding Rate x Parents	8	7.32	10.92**	1.30	37.32*	345.85**	12.70	10.64	0.05
Seeding Rate x F_1	18	6.79	5.48**	3.41	30.58*	83.45**	6.74	5.82	0.16
Seeding Rate x G.C.A.	8	5.83	10.14**	2.56	46.06**	112.49**	11.24	6.73	0.19**
Seeding Rate x S.C.A.	10	7.56	1.75	4.09	18.20	60.22	3.13	5.10	0.31*
Seeding Rate x Parents vs. F_1	2	8.33	12.89**	6.10	150.20**	460.84**	14.89	35.55**	0.02
Error (b)	126	4.46	2.14	2.21	17.48	37.69	7.83	5.69	0.06
C.V. (a) %		2.11	23.70	11.01	12.00	7.81	20.31	7.40	14.72
C.V. (b) %		5.00	24.61	7.72	4.41	33.50	6.32	5.41	8.90

* Significant at 5 percent level

** Significant at 1 percent level

Table 8. Observed mean squares for eight characters of five winter wheat parents and their ten F_1s grown at Moro 1975 (Study III) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
Replicates	3	3.81	1.90	4.13	35.99	6.82	153.84	7.31	0.04
Seeding Rates	2	497.18**	3806.24**	364.08**	867.48**	12435.24**	477.64**	808.73**	8.97
Error (a)	6	7.51	2.49	0.68	15.57	5.41	24.52	5.59	0.18
Genotypes	14	2.35	16.20	26.56	134.56	38.39	22.33	154.33	0.49
Parents	4	3.62	28.03**	48.36**	156.42**	34.92**	22.98**	236.89**	0.58
F_1	9	2.02	11.45**	19.29**	91.57**	30.85**	17.60	128.81**	0.51
G.C.A.	4	2.73	24.13**	42.80**	178.22**	53.59	31.08	280.87**	1.04
S.C.A.	5	1.45	1.31	0.49	22.25**	12.67**	6.81	7.15*	0.08
Parents vs. F_1s	1	0.25	11.66**	4.76**	434.06**	120.08**	62.33**	53.82**	0.01
Seeding Rates x Genotype	28	1.47	11.24**	0.51	12.25	30.84	11.53*	7.91**	0.11**
Seeding Rate x Parents	8	3.32*	17.02**	0.15	17.47	20.50**	14.63*	4.90	0.16**
Seeding Rate x F_1s	18	0.72	8.14**	0.50	8.93	26.73**	11.01	9.77	0.10
Seeding Rate x G.C.A.	8	0.73	17.58	0.55	11.82	46.12**	17.02*	13.92**	0.18**
Seeding Rate x S.C.A.	10	0.71	0.60	0.47	6.62	11.23	6.20	6.46	0.03
Parents vs. F_1	2	0.79	15.88**	0.44	45.26**	109.19**	3.75	3.23	0.00
Error (b)	126	1.58	2.02	0.50	12.16	6.63	6.74	2.91	0.02
C.V. (a) %		7.71	21.90	5.21	6.00	22.40	11.31	7.82	19.41
C.V. (b) %		3.52	19.80	4.52	5.30	24.81	5.92	5.61	7.72

* Significant at 5 percent level

** Significant at 1 percent level

Separate combining ability analyses for all traits, under three seeding rates and different environments are presented in Tables 9, 10 and 11. General combining ability effects were predominantly the most significant under non-competitive conditions. Additive gene action was involved in the expression of spike number per plant and fertility under all environments. Under competitive conditions of solid seeding, the non-additive type of gene action gained more importance in the expression of yield, plant height, fertility, and number of spikes as evidenced by the SCA significance in Studies I and II. SCA was also significant in the expression of seed size at Hyslop 1974 (Study I) and Moro 1975 (Study III).

Direct comparisons of the general combining ability performance of individual varieties along with corresponding standard errors for each character are presented in Tables 12, 13 and 14. No significant general combining ability effects were observed for yield except for the highest seeding rate at Moro where Kavkaz contributed positive and Sprague negative effects.

No cultivar contributed significant general combining ability effects for the trait heading-maturity duration under all seeding rates and environments. This was also true for number of spikes except for the high seeding rate at Hyslop 1975 where the varieties Sprague and Hyslop contributed significant GCA effects.

Spikelets per spike also revealed significant positive general

Table 9. Observed mean squares for General Combining Ability (GCA) and Specific Combining Ability (SCA) for eight characters in single crosses of four winter wheat cultivars grown at Hyslop 1974 (Study I) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spikes	Plant Height	Yield	Harvest Index	Seed Size	Fertility
30.5 cm Spacing									
Single Crosses	9	4.66	29.63**	8.21	501.28**	345.67*	9.09	33.75	0.35**
G.C.A.	4	5.93	42.89	11.87	827.66**	559.50*	14.46	33.99	0.59**
S.C.A.	5	1.76	2.24	2.73	11.70	24.91	1.05	3.40	0.00
Error	27	2.67	13.42	0.78	3.51	171.26	1.26	4.14	0.04
100 kg/ha									
Single Crosses	9	10.65	27.25**	7.25**	336.15**	170.46**	5.82	36.27**	0.29**
G.C.A.	4	9.91	42.93	12.03**	557.02**	280.61**	8.53	51.40	0.47**
S.C.A.	5	11.76	3.74	0.07	4.85	5.24	1.76	13.58**	0.02
Error	27	3.15	3.39	0.33	3.14	47.71	1.15	0.66	0.01
200 kg/ha									
Single Crosses	9	79.15	8.85*	8.71	301.61	64.20	5.54	36.10	0.25**
G.C.A.	4	88.12	9.76	13.98	480.66	48.82	4.53	54.70	0.33
S.C.A.	5	65.70	7.49*	0.81	33.05**	87.25*	7.06	8.06	0.13*
Error	27	80.37	1.78	0.57	4.15	20.18	2.34	0.60	0.02

* Significant at 5 percent level

** Significant at 1 percent level

Table 10. Observed mean squares for General Combining Ability (GCA) and Specific Combining Ability (SCA) for eight characters in single crosses of five winter wheat cultivars grown at Hyslop 1975 (Study II) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Spike	Fertility
<u>30.5 cms Spacing</u>									
Single Cross	9	14.39	17.66**	9.84**	34.28	271.51**	8.13*	85.25**	0.38**
G.C.A.	4	20.84	34.23	20.89**	39.95	388.85	16.07*	188.40**	0.71*
S.C.A.	5	9.23	4.41	1.00	29.73	177.64	1.77	2.72	0.12
Error	27	5.46	6.23	0.55	14.06	27.79	3.44	2.92	0.04
<u>100 kg/ha</u>									
Single Crosses	9	10.83	0.30	11.78**	68.34**	3.96	23.40**	63.12**	0.44
G.C.A.	4	6.93	0.64**	23.60**	116.53	6.25	45.02*	137.90**	0.81*
S.C.A.	5	13.95	0.03	2.32	29.80	2.13	6.10	3.30	0.14
Error	27	5.92	0.26	2.32	11.02	2.52	8.28	6.80	0.07
<u>200 kg/ha</u>									
Single Crosses	9	2.62	0.41*	11.18	48.69	3.52*	9.03	61.48**	0.17**
G.C.A.	4	2.40	0.35	17.60	79.96	2.67	12.63	126.00**	0.11
S.C.A.	5	2.78	0.45*	6.04	23.67	4.21**	6.15	9.87	0.21*
Error	27	2.89	0.13	3.74	25.65	1.05	6.98	5.83	0.06

* Significant at 5 percent level

** Significant at 1 percent level

Table 11. Observed mean squares for General Combining Ability (GCA) and Specific Combining Ability (SCA) for eight characters in single crosses of five winter wheat cultivars grown at Moro 1975 (Study III) under three rates of seeding.

Source of Variation	D.F.	Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
30.5 cm Spacing									
Single Crosses	9	1.25	27.12**	6.63**	39.32	43.69	18.27**	63.51**	0.52**
G.C.A.	4	1.16	58.53**	14.18**	58.09	145.23	39.20**	135.98**	1.09**
S.C.A.	5	1.32	2.00	0.59	24.31	34.47	1.52	5.53	0.07
Error	27	1.90	6.54	0.24	10.38	20.48	2.10	2.42	0.03
68 kg/ha									
Single Crosses	9	0.75	0.25	7.18**	24.66**	0.42	10.53	36.22**	0.09**
G.C.A.	4	1.05	0.36	15.67**	50.07**	0.39	14.91	65.06	0.21**
S.C.A.	5	0.51	0.15	0.39	4.32	0.45	7.03	13.15**	0.00
Error	27	0.27	0.29	0.57	9.39	0.38	3.22	3.52	0.02
136 kg/ha									
Single Crosses	9	1.46	0.37	6.49**	45.44**	0.20	10.81	48.62**	0.08
G.C.A.	4	1.99	0.39	14.04**	93.69**	0.20	11.00	107.66**	0.10
S.C.A.	5	1.04	0.35	0.44	6.84	0.21	10.65	1.39	0.06
Error	27	1.11	0.21	0.36	7.55	0.15	10.99	2.41	0.03

* Significant at 5 percent level

** Significant at 1 percent level

Table 12. Estimates of general combining ability effects for eight characters measured from all possible single crosses involving four winter wheat parents under three rates of seeding, Hyslop 1974 (Study I).

Parent	Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
30.5 cm Spacing								
Hyslop	0.37	1.99	0.52	14.37	4.04	1.77	0.10	0.00
Paha	-1.12	-1.40	1.52	2.58	7.94	-0.57	-1.60	0.33
Sprauge	0.87	2.14	-1.23	2.22	-11.41	0.17	-2.15	-0.33
Yamhill	-0.24	-2.73	0.23	9.58	- 0.56	-1.37	3.65	0.00
S.E.	2.67	13.42	0.78	3.51	171.26	1.26	4.14	0.04
100 kg/ha								
Hyslop	1.65	2.62	-0.67	-11.95	6.79	0.87	0.37	-0.01
Paha	-0.25	-0.83	1.42	1.85	3.10	-0.57	-1.32	0.23
Sprague	-0.70	0.82	-0.57	2.55	- 5.41	0.82	-2.32	-0.31
Yamhill	-0.70	-2.61	-0.17	2.55	- 4.48	-1.12	3.37	0.03
S.E.	3.15	3.39	0.33	3.14	47.71	1.15	0.66	0.03
200 kg/ha								
Hyslop	4.65	0.74	0.025	-10.97	1.54	0.27	0.77	-0.09
Paha	-3.75	-0.51	1.575	0.97	2.39	0.57	-0.97	0.26
Sprague	2.35	1.07	-1.625	2.72	- 3.08	0.22	-2.97	-0.21
Yamhill	-3.25	-1.30	0.025	7.27	- 0.85	-1.07	3.17	0.04
S.E.	80.32	1.78	0.573	4.15	20.18	2.34	0.60	0.02

Table 13. Estimates of general combining ability effects of eight characters measured from all possible single crosses involving five winter wheat parents under three rates of seeding, Hyslop 1975 (Study II).

Parent	Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
30.5 cm Spacing								
Hyslop	-0.09	2.01	0.97	- 1.83	- 5.88	-0.01	-0.62	-0.20
Paha	-1.46	-1.19	1.27	- 1.22	-10.19	1.46	3.62	0.33
Sprague	0.40	1.23	-1.89	1.84	- 0.83	0.72	-3.88	-0.26
Yamhill	-0.82	0.04	0.44	- 0.88	12.83	-0.77	3.31	0.01
Kavkaz	1.97	-2.10	-0.79	2.08	4.80	-1.40	4.81	0.12
S.E.	3.64	4.15	0.37	9.37	51.86	2.29	1.95	0.02
100 kg/ha								
Hyslop	-0.82	0.22	0.80	- 2.74	0.74	-1.44	0.16	-0.00
Paha	-0.45	-0.35	1.80	- 3.37	- 0.04	2.72	-4.33	4.16
Sprauge	0.84	0.04	-1.96	- 0.07	- 1.12	0.16	-2.36	-3.04
Yamhill	-0.32	-0.08	-0.33	2.26	- 0.09	-2.24	2.76	-0.77
Kavkaz	0.74	0.16	-0.30	3.92	0.51	0.79	3.76	-0.34
S.E.	3.94	0.17	1.55	7.34	1.68	5.52	4.52	0.05
200 kg/ha								
Hyslop	0.38	1.30	0.39	- 8.10	0.27	-1.47	1.06	-0.19
Paha	-0.48	0.04	1.29	- 7.80	0.15	1.43	-3.74	0.04
Sprauge	-0.44	1.17	-1.37	- 8.93	- 0.34	0.19	-3.07	-0.12
Yamhill	0.05	0.40	0.89	- 2.46	0.53	-0.14	2.02	0.34
S.E.	1.92	0.09	2.49	17.10	0.70	4.65	3.88	0.04

Table 14. Estimates of general combining ability effects for eight characters measured from all possible single crosses involving five winter wheat parents under three rates of seeding, Moro 1975 (Study III).

Parent	Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
30.5 cm Spacing								
Hyslop	-1.44	0.75	0.12	-0.18	-1.21	-1.91	-1.18	-0.18
Paha	0.25	0.62	0.96	-2.62	5.74	2.79	-2.98	0.53
Sprague	0.22	2.57	1.87	-0.52	-2.96	0.52	-2.78	-0.20
Yamhill	-0.51	-0.55	0.52	-0.15	0.62	-1.11	2.18	-0.10
Kavkaz	0.15	-3.40	0.26	3.48	-2.18	-0.30	4.75	-0.04
S.E.	1.26	4.36	0.16	6.93	13.65	1.40	1.61	0.02
68 kg/ha								
Hyslop	-0.38	0.06	-0.24	0.88	0.07	-1.28	0.98	-0.09
Paha	0.08	0.01	1.22	-3.58	0.23	1.52	-3.22	0.18
Sprague	0.38	0.26	-1.54	0.95	-0.24	-0.24	-1.62	-0.11
Yamhill	-0.18	-0.19	0.32	0.38	-0.13	0.68	1.68	-0.05
Kavkaz	0.08	-0.10	0.25	1.35	0.06	-0.68	2.18	-0.14
S.E.	0.18	0.19	0.38	6.26	0.25	2.14	2.35	0.01
136 kg/ha								
Hyslop	0.40	-0.04	-0.38	0.49	0.00	0.69	1.70	0.04
Paha	0.50	-0.03	1.35	-4.70	0.07	0.39	-3.49	0.14
Sprague	0.36	0.29	-1.54	0.12	-0.17	-1.40	-2.82	-0.07
Yamhill	-0.56	-0.19	0.15	1.56	-0.07	-0.54	1.30	-0.04
Kavkaz	-0.23	-0.01	0.42	2.52	0.16	0.86	3.30	-0.07
S.E.	0.74	0.14	0.24	5.03	0.10	7.33	1.61	0.02

combining ability effects were contributed by Paha under all seeding rates and environments. Sprague contributed negative effects when that trait was considered.

Plant height was not fully expressed under the dryland condition of Moro, thus no significant effects were detected for any of the varieties tested. Under highly competitive conditions of the Hyslop location, Kavkaz and Paha exhibited real or significant positive effects for height. The variety Hyslop contributed highest negative GCA effects which are highly desirable in breeding for short plant stature.

When harvest index is considered, no cultivar excelled in providing significant GCA values under all conditions. Only Paha showed significant GCA effects under spaced planting at Moro.

The cultivars Yamhill and Kavkaz, had the highest positive GCA effects for seed size under all conditions. The most significant effects for seed size were observed under the lowest seeding rate. The GCA effects involving spikelet fertility indicated Paha as the most fertile and Sprague as the least fertile among the group of cultivars utilized in these studies. Significant positive GCA values were observed for Paha while those of Sprague were negative for fertility.

Significant differences were detected for the variances associated with specific combining ability for most variables measured in solid planting as can be noted in Tables 9, 10 and 11. Under competitive conditions of the Hyslop location, yield, fertility, tiller number and plant height showed significant specific combining ability effects. Under the dryland site of Moro, only seed size had significant specific combining ability effects. Estimates of the effects of specific combining ability involving each F_1 mean along with standard error for each character for two rates of seeding and three environments are found in Tables 15, 16 and 17. Even though the analysis of variance had shown significant effects for specific combining ability in solid seeding, performance of the individual varieties revealed no significant differences for grain yield, seed size or plant height. Paha combinations with Hyslop, Kavkaz and Sprague gave significant positive effects for spikelet fertility under the high rainfall environment at Hyslop location. Hyslop and Paha combined well with Sprague and Yamhill for tillers per plant.

Heritability

Narrow sense heritability estimates were obtained by parent progeny regressions. These values along with heritability values in standard units obtained by simple correlations are presented in Tables 18 and 19. Under non-competitive conditions, significant heritability values were obtained for yield and all components of grain yield in all environments. Heritability values as high as 98.9 percent were observed for fertility. Low and inconsistent heritability

Table 15. Estimates of specific combining ability effects for eight characters measured from all possible single crosses involving four winter wheat parents under three rates of seeding, Hyslop 1974 (Study I).

		30.5 cm Spacing			100 kg/ha per Hectar			200 kg/ha per Hectar		
		P_4	P_3	P_2	P_4	P_3	P_2	P_4	P_3	P_2
	X_1	-0.10	0.50	-0.40	-1.22	1.18	0.03	2.03	5.07	-3.03
	X_2	0.62	-0.29	-0.31	-0.57	1.11	-0.54	0.71	0.39	-1.10
	X_3	-0.50	-0.15	0.65	0.43	-0.67	0.23	-0.33	0.32	0.02
	X_4	0.70	-1.40	-0.75	0.63	-0.87	0.23	1.72	-2.23	0.52
P_1	X_5	0.10	-2.06	1.06	0.22	0.68	-0.89	3.29	0.01	-3.30
	X_6	0.42	-0.03	-0.38	0.43	-0.52	0.08	1.08	-0.62	-0.47
	X_7	-0.15	0.75	-0.60	0.73	0.78	-1.52	0.57	0.62	-1.18
	X_8	0.01	0.00	-0.01	0.03	-0.06	0.04	0.12	-0.14	0.02
X	X_1	0.50	-0.10		1.18	-1.22		5.07	-2.03	
	X_2	-0.29	0.62		0.62	-0.08		0.39	1.83	
	X_3	-0.15	-0.50		0.23	-0.47		0.32	-0.33	
	X_4	-1.40	-0.65		-0.87	0.63		-2.23	1.72	
P_2	X_5	-2.04	1.07		0.67	-4.40		0.01	3.29	
	X_6	-0.03	0.42		-0.52	0.43		-0.62	1.08	
	X_7	0.75	-0.15		0.78	0.73		0.62	0.57	
	X_8	0.00	-0.01		-0.06	0.03		-0.14	0.12	
	X_1	-0.40			0.03			3.03		
	X_2	-0.31			-0.05			-1.10		
	X_3	0.65			-0.67			0.01		
	X_4	0.75			0.23			0.52		
	X_5	0.99			-0.89			-3.30		
	X_6	-0.38			0.08			-0.47		
	X_7	-0.66			-1.52			-1.18		
	X_8	-0.01			0.04			0.02		

Table 15. Continued.

		Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
S. E.	Seed Rate	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
	Spacing	2.68	13.43	0.78	3.51	171.26	1.26	4.14	0.04
	100 kg/ha	3.15	3.39	0.33	3.14	47.71	1.15	0.66	0.02
	200 kg/ha	80.37	1.78	0.57	4.15	20.18	2.34	0.60	0.02

P_1 = Hyslop

P_2 = Paha

P_3 = Sprague

P_4 = Yamhill

Table 16. Estimates of specific combining ability effects for eight characters measured from all possible single crosses involving five winter wheat parents under three rates of seeding, Hyslop 1975 (Study II).

		30.5 cm Spacing				100 kg/ha per Hectar				200 kg/ha per Hectar			
		P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2
P_1	X_1	1.20	0.00	0.57	-1.77	1.63	-1.90	-0.97	1.23	0.51	-0.75	0.35	-0.12
	X_2	-0.58	0.30	-0.18	0.44	-0.05	0.05	-0.08	0.07	0.50	1.87	2.80	-5.16
	X_3	0.10	-0.43	-0.10	0.43	-0.30	-0.17	-0.64	1.10	0.58	0.78	0.25	-1.62
	X_4	0.85	-0.08	-0.12	-0.65	-0.37	2.00	-2.86	1.23	-21.80	9.06	7.03	5.70
	X_5	7.43	13.87	7.18	26.53	-0.54	0.20	-0.60	0.94	0.12	1.05	0.29	-1.46
	X_6	-0.32	1.05	-0.25	-0.49	0.52	-0.28	-0.95	0.79	0.37	-0.33	-1.03	1.07
	X_7	0.22	0.52	-0.48	-0.25	-0.07	0.27	-1.10	0.97	0.23	0.33	-0.77	0.20
	X_8	-0.05	0.19	0.04	-0.18	-1.88	0.45	-0.98	2.42	0.04	0.04	0.01	-0.08
P_2	X_1	-0.84	1.86	0.73		-2.14	-0.17	1.06		-0.02	-0.39	0.51	
	X_2	0.13	-0.41	-1.23		-0.11	-0.04	0.07		1.17	1.84	1.57	
	X_3	-0.50	0.47	-0.40		-0.60	-0.57	0.06		-0.12	0.18	1.55	
	X_4	2.15	1.55	-2.65		-0.93	0.53	-0.93		-24.90	9.86	9.33	
	X_5	10.54	13.96	3.97		-0.30	-0.76	0.12		0.40	0.38	0.68	
	X_6	0.21	-0.22	0.48		-0.78	-1.18	1.32		-0.70	-1.36	0.97	
	X_7	0.12	0.62	-0.48		-0.43	-0.93	0.40		-2.07	0.13	-1.73	
	X_8	0.19	0.05	-0.04		0.55	-2.21	-0.75		0.25	-0.19	0.04	
P_3	X_1	0.10	-1.40			-0.84	0.73			-1.25	0.38		
	X_2	1.40	-0.01			0.08	-0.08			1.46	-2.90		
	X_3	0.47	0.03			0.36	0.20			-0.65	-1.15		
	X_4	0.78	2.35			3.87	-0.07			-25.17	8.80		
	X_5	-0.66	-10.52			0.38	0.10			-0.03	-0.95		
	X_6	0.35	-0.59			-0.78	0.52			-0.66	0.77		
	X_7	0.88	0.08			0.30	0.40			0.66	-1.64		
	X_8	0.05	-0.04			0.65	1.09			0.26	-0.30		

Table 16. Continued.

		30.5 cm Spacing				100 kg/ha per Hectar				200 kg/ha per Hectar			
		P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2
P_4	X_1	-0.47				1.33				0.75			
	X_2	-0.96				0.06				-0.80			
	X_3	-0.07				0.53				0.18			
	X_4	-3.78				-2.57				-22.74			
	X_5	-17.31				0.46				0.49			
	X_6	-0.25				1.12				0.97			
	X_7	-1.22				0.27				1.16			
	X_8	-0.19				0.69				-0.54			

		Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
S.E.	Seed Rate	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
	30.5 cm Spacing	7.38	8.31	0.74	18.75	103.72	4.59	3.90	0.06
	100 kg/ha	7.90	0.35	3.10	14.69	3.36	11.06	9.07	0.10
	200 kg/ha	3.85	0.18	4.99	34.21	1.40	9.32	12.90	0.09

P_1 = Hyslop

P_2 = Paha

P_3 = Sprauge

P_4 = Yamhill

P_5 = Kavkaz

Table 17. Estimates of specific combining ability effects for eight characters measured from all possible single crosses involving five winter wheat parents under three rates of seeding, Moro 1975 (Study III).

		30.5 cm Spacing				68 kg/ha per Hectar				136 kg/ha per Hectar			
		P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2
P_1	X_1	0.75	-0.18	-0.12	-0.45	-0.03	-0.50	0.33	0.13	-0.01	-0.38	0.69	-0.28
	X_2	-1.02	0.49	0.12	0.41	-0.19	0.17	0.11	-0.08	-0.27	-0.17	0.42	0.02
	X_3	-0.01	0.42	-0.48	0.09	-0.37	0.27	-0.07	0.17	0.05	-0.38	0.02	0.32
	X_4	-1.03	1.74	-2.33	1.69	0.60	0.70	-1.20	-0.17	-0.05	-0.89	-0.15	1.08
	X_5	-3.19	3.06	-0.32	0.45	-0.45	0.28	0.30	-0.14	-0.23	-0.08	0.24	0.14
	X_6	-0.47	0.73	0.20	-0.47	-0.50	0.00	1.76	-0.70	0.02	2.12	-1.72	-0.52
	X_7	-0.24	1.23	-0.90	-0.11	-1.15	-0.75	2.25	-0.35	0.67	-0.63	-0.10	0.07
	X_8	-0.16	0.05	0.13	-0.01	0.03	0.05	-0.12	0.04	-0.11	0.12	-0.05	0.05
P_2	X_1	-0.12	0.65	-0.08		-0.23	0.23	-0.13		0.15	0.59	-0.45	
	X_2	-0.01	2.75	-0.15		0.02	-0.09	0.14		0.17	-0.05	-0.20	
	X_3	-0.05	-0.01	-0.01		0.06	0.10	-0.33		-0.18	0.28	-0.42	
	X_4	1.10	-1.16	-1.60		0.57	-0.47	0.07		0.75	-0.29	-1.55	
	X_5	0.42	0.35	-1.22		0.03	0.12	-0.02		0.19	-0.12	-0.22	
	X_6	0.13	0.03	0.30		0.50	0.00	0.16		0.16	-1.68	-1.08	
	X_7	-0.84	-0.27	1.19		-0.35	0.35	0.35		-0.73	0.27	0.40	
	X_8	0.13	0.03	-0.14		0.11	0.05	-0.20		0.14	-0.13	-0.05	
P_3	X_1	0.02	0.18			-0.13	-0.06			-0.08	-0.15		
	X_2	0.64	-0.62			0.00	-0.24			-0.15	-0.07		
	X_3	0.49	0.02			0.00	-0.63			0.48	0.18		
	X_4	2.20	1.74			0.13	1.00			-0.09	1.81		
	X_5	3.85	-2.33			-0.13	-0.16			-0.09	0.07		
	X_6	0.30	-0.80			-0.64	-1.30			0.02	0.22		
	X_7	-0.86	-1.17			-0.75	-1.85			-0.30	0.00		
	X_8	0.07	-0.05			-0.19	-0.15			0.03	0.08		

Table 17. Continued.

		30.5 cm Spacing				68 kg/ha per Hectar				136 kg/ha per Hectare			
		P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2	P_5	P_4	P_3	P_2
P_4	X_1	-0.65				0.33				-0.05			
	X_2	0.39				0.16				-0.24			
	X_3	-0.41				0.26				1.88			
	X_4	2.26				-1.30				-0.62			
	X_5	-1.08				0.54				0.13			
	X_6	0.03				1.23				-0.65			
	X_7	0.09				2.25				0.37			
	X_8	-0.03				0.05				-0.05			

		Maturity Duration	Number of Spikes	Spikelets/ Spike	Plant Height	Yield	Harvest Index	Seed Size	Fertility
S.E.	Seed Rate	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
	30.5 cm Spacing	2.53	8.73	0.32	13.84	27.31	2.81	3.23	0.04
	68 kg/ha	0.37	0.39	0.76	12.53	0.51	4.29	4.70	0.03
	136 kg/ha	1.49	0.28	0.49	10.07	0.21	14.66	3.22	0.04

P_1 = Hyslop

P_2 = Paha

P_3 = Sprauge

P_4 = Yamhill

P_5 = Kavkaz

Table 18. Parent progeny regression (b) and correlation coefficients (r) by mean value of F_1 crosses and mean parental values for the three experiments at Moro and Hyslop. n = 10 for Moro 1975 and Hyslop 1975 and n = 6 for Hyslop 1974.

	30.5 cm Spacing		67 kg/ha		134 kg/ha	
Seeding Rate	b	r	b	r	b	r
			Moro 1975 (Study III)			
Yield	1.388*	0.750	0.488	0.586	0.285	0.329
Tiller Number	1.124**	0.964	0.225	0.260	0.205	0.217
Spikelet/Spike	1.139**	0.965	1.021**	0.979	1.018	0.928
Fertility	1.375**	0.850	1.219**	0.895	0.529	0.399
Seed Size	1.358**	0.970	1.030*	0.820	1.213	0.910
Harvest Index	0.696	0.454	0.664	0.386	0.470	0.349
Maturity Duration	0.147	0.106	0.405	0.519	0.404	0.436
Plant Height	0.661	0.557	0.071	0.069	0.456	0.217
			Hyslop 1975 (Study II)			
Yield	0.611*	0.736	0.595	0.501	0.535	0.405
Tiller Number	0.839*	0.747	-0.093	0.080	0.364	0.333
Spikelet/Spike	0.919**	0.892	1.130**	0.934	0.978*	0.761
Fertility	1.439	0.611	1.607*	0.753	0.295	0.106
Seed Size	1.172**	0.946	1.525**	0.914	1.572**	0.930
Harvest Index	1.102**	0.863	2.229	0.603	-0.323	-0.294
Maturity Duration	1.588	0.481	0.326	0.244	-0.031	-0.126
Plant Height	0.073	0.051	0.237	0.200	0.494	0.494
			Hyslop 1974 (Study I)			
Yield	0.985*	0.887	0.710	0.676	0.578	0.567
Tiller Number	1.539*	0.803	0.664	0.392	0.010	0.005
Spikelets/Spike	1.116*	0.884	0.890**	0.995	0.992**	0.961
Fertility	1.584**	0.989	1.213**	0.943	1.156*	0.882
Seed Size	1.033*	0.903	0.910*	0.881	0.954**	0.931
Harvest Index	1.358*	0.824	-0.331	-0.221	-0.709	-0.371
Maturity Duration	0.060	0.060	0.415	0.376	2.022	0.613
Plant Height	1.324	0.772	1.337	0.700	1.036	0.638

r = 0.576 and 0.708 for n = 10 at 5 and 1 percent level of significance, respectively.

r = 0.707 and 0.834 for n = 6 at 5 and 1 percent level of significance, respectively.

* Significance at 5 percent level

** Significance at 1 percent level

Table 19. Parent progeny regression (b) and correlation (r) coefficients by mean values of F_1 and F_2 on mid parental values, Study IV.

	30.5 cm Spacing				100 kg/ha			
	F_1		F_2		F_1		F_2	
	b	r	b	r	b	r	b	r
Yield	1.161	0.779	1.084*	0.955	0.822	0.593	1.775	0.932
Tiller Number	1.132	0.606	1.198*	0.826	-0.833	-0.583	1.043*	0.875
Spikelets/Spike	0.898*	0.880	0.937**	0.989	2.460**	0.961	1.590*	0.935
Fertility	1.387*	0.853	1.235*	0.866	1.699*	0.856	1.478*	0.889
Seed Size	1.351*	0.878	1.235*	0.879	0.833	0.635	0.701	0.735
Harvest Index	1.696	0.666	1.290*	0.864	-2.074	-0.417	0.851	0.184
Maturity Duration	1.145**	0.948	1.460	0.763	-0.595	-0.773	-0.092	-0.145
Plant Height	0.442	0.318	1.504*	0.785	0.693	0.332	1.165	0.773

r - 0.707 and 0.834 for n = 6 at 5 and 1 percent levels of significance, respectively.

estimates were observed for harvest index, maturity duration and plant height. The two methods of estimation, regression and correlation, agreed very closely in providing a suitable measure of the possible progress in selecting for higher yield potential.

Under competitive conditions of solid seeding, significant changes in the estimates of heritability were observed. Only seed size and spikelets per spike continued to possess high heritability values. The moderate stress representing farmers conditions revealed that spikelet fertility had high heritability estimates. The negative heritability value of harvest index for the F_1 indicated the influence of genes which behave non-additively.

Using the F_2 segregating populations to estimate heritability values did not appreciably change the relationships. The number of spikes showed higher heritabilities and seed size exhibited lower heritability values. Again, correlations and regressions provided close estimates of heritability.

Heritability values exceeding 100 percent were encountered when regression methodology was used. This revealed the existence of associations of non-genetic nature and justified the use of other techniques of estimating heritability especially when the estimates are needed for comparative purposes.

Association Among Agronomic Traits

The correlation coefficients for the single cross relationships and those including parents are provided in Tables 20 and 21. Inclusion of parents in the correlation matrix resulted in changes in the magnitude of the correlation coefficients but not in their sign. In a few cases the sign changed but the magnitude was originally not significant. Under non-competitive conditions yield correlated significantly with fertility and spikelets per spike. There was considerable lack of association between yield with tiller number and seed size under all environments and all imposed stresses. None of the measured variables, harvest index, heading-maturity duration or plant height was significantly related to grain yield. Predominantly negative associations were observed for number of spikes with spikelets per spike, fertility, seed size and plant height. Large spikes tended to be more fertile as indicated by the positive correlation between spikelets per spike and fertility where significant associations were noted under normal seeding rates. No evident direct relationship was noted for seed size or harvest index and spikelets per spike. The consistently negative relationship between maturity duration with spikelets per spike, though rarely significant, indicated some difficulty of selecting for large spikes having long maturity duration. Plant height did not bear any significant relationship to spike size.

Table 20. Correlation coefficients of eight measured characters in F_1 generation in three environments and three planting densities.

	Study I Hyslop 1974 n = 6			Study II Hyslop 1975 n = 10			Study III Moro 1975 n = 10		
	30.5 cm Spacing	180 kg/ha	200 kg/ha	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	68 kg/ha	136 kg/ha
Yield vs. # Spikes	-0.394	0.485	0.251	0.313	0.377	0.809	0.140	0.002	0.266
vs. Spikelets/Spike	0.756	0.395	0.523	0.693	0.674	0.801	0.669	0.728	0.512
vs. Fertility	0.929	0.518	0.563	0.284	0.519	0.511	0.863	0.437	0.335
vs. Seed Size	0.115	-0.040	0.369	0.377	0.471	-0.005	-0.249	0.333	0.261
vs. Harvest Index	0.043	0.228	0.612	-0.101	0.015	-0.350	0.643	0.678	0.203
vs. Maturity Duration	-0.794	0.671	-0.48	-0.233	-0.110	-0.174	-0.070	-0.162	0.045
vs. Height	-0.248	-0.825	-0.289	-0.206	0.091	0.433	-0.342	-0.542	0.089
# Spikes vs. Spikelets/Spike	0.741	-0.503	-0.495	0.028	-0.334	0.530	-0.510	-0.529	-0.442
vs. Fertility	-0.594	-0.466	-0.517	-0.653	-0.539	0.170	-0.008	-0.081	-0.150
vs. Seed Size	-0.614	-0.455	-0.385	-0.363	0.583	-0.328	-0.856	-0.215	-0.371
vs. Harvest Index	0.861	0.801	0.601	0.245	-0.431	-0.415	0.224	0.097	-0.579
vs. Maturity Duration	0.641	0.647	0.713	-0.199	0.179	-0.154	-0.028	0.279	0.658
vs. Height	-0.698	-0.840	-0.477	-0.074	0.352	0.032	-0.578	-0.018	-0.002
Spikelets/spike vs. fertility	0.879	0.951	0.733	0.387	0.907	0.322	0.560	0.622	0.438
vs. Seed Size	0.080	0.084	0.308	0.000	-0.199	-0.069	0.323	0.043	0.051
vs. Harvest Index	-0.535	-0.589	-0.010	0.142	0.395	0.074	0.106	0.478	0.325
vs. Maturity Duration	0.927	-0.102	-0.339	-0.508	-0.235	0.004	-0.154	-0.319	-0.323
vs. Height	0.294	0.186	-0.134	-0.607	-0.419	0.356	0.049	-0.625	-0.389

Table 20. Continued.

	Study I Hyslop 1974 n = 6			Study II Hyslop 1975 n = 10			Study III Moro 1975 n = 10		
	30.5 cm Spacing	180 kg/ha	200 kg/ha	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	68 kg/ha	136 kg/ha
Fertility vs. Seed Size	0.105	0.180	0.217	0.177	-0.307	-0.157	-0.302	-0.637	-0.416
vs. Harvest Index	-0.233	-0.516	0.318	0.179	0.557	0.043	0.820	0.709	0.491
vs. Maturity Duration	-0.878	0.003	-0.810	-0.129	-0.281	-0.636	0.198	0.057	-0.035
vs. Height	0.033	00.025	0.276	0.062	-0.350	0.448	-0.365	-0.937	-0.522
Seed Size vs. Harvest Index	-0.375	-0.546	-0.417	-0.873	-0.493	-0.370	-0.417	-0.165	0.311
vs. Maturity Duration	0.017	0.020	-0.099	0.421	0.148	0.559	-0.275	-0.176	-0.312
vs. Height	0.281	0.172	0.069	0.203	0.745	0.500	0.697	0.512	0.768
Harvest Index vs. Maturity Duration	0.448	0.137	-0.044	-0.448	0.373	-0.105	0.382	0.306	-0.421
Maturity Duration vs. Height	-0.301	-0.776	-0.672	0.441	0.193	0.155	-0.057	-0.234	-0.002

r = 0.632 and 0.765 for n = 10 at 5 and 1 percent levels of significance respectively.

r = 0.811 and 0.975 for n = 6 at 5 and 1 percent levels of significance respectively.

Table 21. Correlation coefficients of eight measured characters in parents and F_1s in three environments and three planting densities.

	Study I Hyslop 1974 n = 10			Study II Hyslop 1975 n = 15			Study III Moro 1975 n = 15		
	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	68 kg/ha	136 kg/ha
Yield vs. # Spikes	-0.237	0.668	0.578	0.670	0.579	0.853	0.216	0.407	0.354
vs. Spikelets/Spike	0.823	0.721	0.845	0.705	0.812	0.738	0.636	0.515	0.532
vs. Kernel/Spikelet	0.803	0.688	0.672	0.424	0.559	0.564	0.694	0.504	0.462
vs. Seed Size	0.661	0.548	0.720	0.417	0.263	0.019	-0.122	0.182	0.312
vs. Harvest Index	-0.021	0.617	0.734	0.058	0.017	0.268	0.665	0.065	0.351
vs. Maturity Duration	-0.041	0.085	0.001	-0.189	-0.115	-0.046	0.066	-0.684	0.215
vs. Height	0.063	-0.129	0.192	0.192	0.256	0.196	0.009	-0.107	0.169
# Spikes vs. Spikelets/Spike	-0.610	0.077	0.165	0.214	0.147	0.455	-0.512	-0.070	-0.436
vs. Kernel/Spikelet	-0.609	-0.084	-0.116	-0.207	-0.264	0.268	-0.208	0.311	0.482
vs. Seed Size	-0.349	0.163	0.262	-0.130	0.161	-0.267	-0.769	-0.445	-0.460
vs. Harvest Index	00.843	0.847	0.762	0.313	-0.260	0.275	0.389	-0.301	-0.544
vs. Maturity Duration	0.544	0.472	0.610	-0.196	-0.185	-0.023	0.027	-0.120	0.579
vs. Height	-0.666	-0.545	-0.297	0.105	0.069	-0.209	-0.298	-0.138	-0.205
Spikelet/spike vs. Kernel/ Spikelet	0.892	0.939	0.850	0.547	0.807	0.442	0.641	0.311	-0.148
vs. Seed Size	0.460	0.356	0.592	0.341	-0.809	-0.036	0.372	0.207	0.339
vs. Harvest Index	-0.475	0.074	0.377	0.011	0.285	0.324	0.044	0.144	0.517
vs. Maturity Duration	-0.230	-0.521	-0.249	-0.359	-0.067	-0.015	-0.036	-0.684	-0.041
vs. Height	0.440	0.461	0.382	0.113	0.050	0.444	0.194	-0.074	0.063
Kernel/Spikelet vs. Seed Size	0.357	0.444	0.404	0.281	-0.199	-0.111	-0.155	-0.627	-0.114
vs. Harvest Index	-0.284	0.021	0.293	0.229	0.417	0.334	0.573	0.429	0.556
vs. Maturity Duration	-0.264	-0.408	-0.670	-0.097	-0.076	-0.356	0.367	-0.110	-0.092
vs. Height	0.187	0.329	0.551	0.300	0.075	0.320	0.573	-0.598	-0.320

Table 21. Continued.

	Study I Hyslop 1974 n = 10			Study II Hyslop 1975 n = 15			Study III Moro 1975 n = 15		
	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	100 kg/ha	200 kg/ha	30.5 cm Spacing	68 kg/ha	136 kg/ha
Seed Size									
vs. Harvest Index	-0.241	-0.317	-0.361	-0.516	-0.409	-0.314	-0.344	-0.059	0.559
vs. Maturity Duration	-0.054	0.119	0.004	0.367	0.213	0.382	-0.378	-0.299	-0.362
vs. Height	0.288	0.050	0.083	0.341	0.655	0.545	0.519	0.488	0.736
Harvest Index									
vs. Maturity Duration	0.597	0.260	0.152	-0.068	0.279	0.076	0.458	0.372	-0.344
vs. Height	-0.938	-0.427	0.113	0.414	-0.167	-0.191	-0.189	-0.425	0.215
Maturity Duration									
vs. Height	-0.484	-0.800	-0.566	0.468	0.314	-0.057	-0.249	-0.143	-0.013

$r = 0.514$ and 0.641 for $n = 15$ at 5 and 1 percent levels of significance respectively.

$r = 0.632$ and 0.765 for $n = 10$ at 5 and 1 percent levels of significance respectively.

Maturity duration tended to associate negatively with fertility but no specific trends could be established for fertility relationships with seed size, harvest index or plant height. Seed size correlated positively with plant height but negatively with harvest index and had no apparent relationship with maturity duration. Harvest index decreased as plant height increased. Maturity duration had no significant association with plant height or harvest index.

When path-coefficient analysis (Table 22) was used to partition correlations into direct and indirect effects, compensatory effects among agronomic traits appeared responsible for the poor correlations. The low correlation between grain yield and number of spikes was a result of indirect negative influences exerted by spikelets per spike, fertility and seed size, although direct effects were very high. Harvest index, maturity duration and plant height had very small direct and indirect effects on yield, thus were not considered as components of yield. Direct effects of spikelets per spike on yield corresponded to the simple correlation coefficient. This was mainly the result of opposing indirect influences via tiller number and fertility. Other characters had less important effects. Fertility had high association with yield and had large direct influences. The compensating effect of spikelets per spike and seed size resulted in apparent stability of the fertility association and its direct effect on yield.

Partitioning the low correlation coefficient between seed size

Table 22. Path coefficient analysis of components of yield in single crosses under three rates of seeding.

	Study I Hyslop 1974			Study II Hyslop 1975			Study III Moro 1975		
Seeding Rates	Spaced	100 kg/ha	200 kg/ha	Spaced	100 kg/ha	200 kg/ha	Spaced	68 kg/ha	136 kg/ha
Yield vs. Tiller # r =	0.394	0.485	0.251	0.313	0.377	0.809	0.140	0.002	0.266
Direct effect b[1]	0.929	1.033	0.972	0.731	0.616	0.620	1.180	0.531	1.004
Indirect via Spikelets/ Spike	-0.487	0.069	-0.160	0.015	-0.115	0.216	-0.260	-0.299	-0.322
Indirect via Fertility	-0.503	-0.506	-0.373	-0.183	-0.371	0.045	-0.007	-0.056	-0.073
Indirect via Seed Size	-0.334	-0.112	-0.187	-0.366	0.231	-0.098	-0.731	-0.173	-0.214
Indirect via Harvest Index				0.120	0.032	0.013	-0.030	0.011	-0.058
Indirect via Maturity Duration				0.001	0.006	0.013	-0.004	-0.008	-0.063
Indirect via Plant Height				-0.016	-0.022	0.000	-0.006	-0.002	-0.004
Yield vs. Spikelets/Spike r =	0.756	0.395	0.523	0.693	0.674	0.801	0.669	0.728	0.512
Direct effect b[1]	0.657	-0.138	0.325	0.539	0.344	0.408	0.511	0.566	0.728
Indirect via Tiller #	-0.688	-0.519	-0.481	0.020	-0.206	0.328	-0.602	-0.280	-0.443
Indirect via Fertility	0.744	1.032	0.529	0.109	0.625	0.085	0.520	0.433	0.213
Indirect via Seed Size	0.043	0.021	0.149	0.000	-0.079	-0.021	0.276	0.034	0.029
Indirect via Harvest Index				0.069	-0.029	-0.002	-0.014	0.054	0.032
Indirect via Maturity Duration				0.003	-0.008	0.000	-0.022	0.009	0.031
Indirect via Height				-0.048	0.026	0.003	0.000	-0.088	-0.080
Yield vs. Fertility r =	0.929	0.518	0.563	0.284	0.519	0.511	0.863	0.437	0.355
Direct effect b[1]	0.847	1.086	0.722	0.487	0.281	0.689	0.929	0.697	0.487
Indirect va Tiller #	-0.551	-0.506	-0.502	-0.150	-0.478	-0.332	-0.009	-0.043	-0.150
Indirect via Spikelet/Spike	0.577	-0.131	0.238	0.319	0.208	0.312	0.286	0.352	0.319
Indirect via Seed Size	0.057	0.044	0.105	-0.240	0.178	-0.121	-0.258	-0.515	-0.240
Indirect via Harvest Index				0.049	0.086	-0.041	-0.109	0.080	0.049
Indirect via Maturity Duration				0.003	0.001	-0.010	0.028	-0.001	0.003

Table 22. Continued.

Seeding Rates	Study I Hyslop 1974 Spaced	Study I Hyslop 1974 100 kg/ha	Study I Hyslop 1974 200 kg/ha	Study II Hyslop 1975 Spaced	Study II Hyslop 1975 100 kg/ha	Study II Hyslop 1975 200 kg/ha	Study III Moro 1975 Spaced	Study III Moro 1975 68 kg/ha	Study III Moro 1975 136 kg/ha
Indirect via Height				-0.113	0.095	0.022	-0.004	-0.133	-0.113
Yield vs. Seed Size r =	0.115	-0.040	0.369	0.377	0.471	-0.005	-0.249	0.333	0.261
Direct effect b[1]	0.544	0.247	0.486	1.007	0.397	0.544	0.854	0.808	0.578
Indirect via Tiller #	-0.570	-0.470	-0.374	-0.265	0.359	-0.203	-1.010	-0.114	-0.372
Indirect via Spikelet/Spike	0.053	-0.012	0.100	0.000	-0.068	-0.028	0.165	0.024	0.037
Indirect via Fertility	0.089	0.195	0.156	0.050	-0.212	-0.042	-0.281	-0.443	-0.203
				-0.427	0.036	0.012	0.055	-0.019	0.031
				-0.003	0.005	-0.047	-0.040	0.005	0.003
				0.016	-0.046	0.005	0.008	0.061	0.158
Yield vs. Harvest Index r =				-0.101	0.015	0.350	0.643	0.678	0.203
Direct effect b[1]				0.489	-0.074	-0.032	-0.132	0.114	0.101
Indirect via Tiller #				0.179	-0.265	-0.257	0.264	0.051	-0.581
Indirect via Spikelets/spike				0.076	0.136	0.030	0.054	0.270	0.237
Indirect via Fertility				0.050	0.384	0.011	0.762	0.494	0.239
Indirect via Seed Size				-0.879	-0.196	-0.110	-0.356	-0.133	0.179
Indirect via Maturity Duration				0.003	0.013	0.008	0.055	-0.009	0.040
Indirect via Height				-0.020	0.017	-0.001	-0.004	-0.109	-0.015
Yield vs. Maturity Duration r =				-0.233	-0.110	-0.174	-0.070	-0.162	0.045
Direct Effect b[1]				-0.007	0.035	-0.084	0.144	-0.029	-0.096
Indirect via Tiller #				-0.146	-0.110	-0.095	-0.033	0.148	0.660
Indirect via Spikelet/Spike				-0.274	-0.081	0.002	-0.079	-0.180	-0.235
Indirect via Fertility				-0.036	-0.194	-0.168	0.184	0.039	-0.017
Indirect via Seed Size				0.424	0.059	0.167	-0.235	-0.142	-0.180
Indirect via Harvest Index				-0.219	-0.027	0.003	-0.051	0.035	-0.042

Table 22. Continued.

Seeding Rates	Study I Hyslop 1974			Study II Hyslop 1975			Study III Moro 1975		
	Spaced	100 kg/ha	200 kg/ha	Spaced	100 kg/ha	200 kg/ha	Spaced	68 kg/ha	136 kg/ha
Yield vs. Plant Height r =				-0.206	0.091	0.433	-0.342	-0.542	0.089
Direct Effect b[1]				0.080	-0.063	0.010	0.011	0.142	0.206
Indirect via Tiller #				-0.054	0.217	0.020	-0.682	-0.009	-0.022
Indirect via Spikelet/Spike				-0.327	-0.144	0.145	0.025	-0.353	-0.283
Indirect via Fertility				0.017	-0.241	0.118	-0.339	-0.653	-0.269
Indirect via Seed Size				0.204	0.296	0.149	0.595	0.413	0.444
Indirect via Harvest Index				-0.124	0.021	0.003	0.055	-0.087	-0.007
Indirect via Maturity Duration				-0.003	0.007	-0.013	-0.008	0.006	0.019
Residual $(1-R^2)$	0.021	0.001	0.001	0.003	0.002	0.008	0.002	0.008	0.002

and yield revealed a high direct effect of this component but it was offset by large, negative, indirect influence of the number of spikes and small negative effect through fertility. The apparent correlation of harvest index with yield at Moro was only a result of indirect influences of the components of yield. Maturity duration and plant height correlated poorly with yield and had no significant direct or indirect effects.

When cause and effect relationships were measured over consecutive generations (Table 23) F_1 and F_2 progeny showed similar reactions in response to the effects of the components of yield on grain yield. Direct effects were very high and low indirect effects were notable under competitive conditions. All indirect effects were positive when the F_2 generation was tested under solid seeded conditions. Under spaced plantings, as the number of tillers increased, a drop in fertility and seed size was observed in both F_1 and F_2 generations.

Table 23. Path coefficients of the components of yield in all possible single crosses and F_2 populations of four winter wheat varieties grown at Hyslop 1975 under two rates of seeding Study IV.

	30.5 cm Spacing		100 kg/ha	
	F_1	F_2	F_1	F_2
Yield vs. Spike # r =	0.391	-0.236	0.458	0.835
Direct effect b[1]	0.874	0.476	0.589	0.457
Indirect via Spikelet/Spike	0.116	-0.293	-0.144	0.217
via Fertility	-0.409	-0.237	0.009	0.077
via Seed Size	-0.189	-0.182	0.004	0.084
Yield vs. Spikelets/Spike r =	0.919	0.919	0.436	0.952
Direct effect b[1]	0.300	0.563	0.263	0.286
Indirect via Spike #	0.336	-0.248	-0.323	0.347
via Fertility	0.170	0.266	0.255	0.218
via Seed Size	0.113	0.338	0.240	0.101
Yield vs. Fertility r =	0.314	0.709	0.682	0.725
Direct effect b[1]	0.624	0.298	0.504	0.297
Indirect via Spike #	-0.573	-0.379	0.011	0.118
via Spikelet/Spike	0.082	0.503	-0.133	0.210
via Seed Size	0.181	0.287	0.033	0.100
Yield vs. Seed Size r =	0.407	0.870	0.613	0.710
Direct effect b[1]	0.448	0.432	0.414	0.185
Indirect via Spike #	-0.369	-0.200	0.005	0.208
via Spikelet/Spike	0.076	0.440	0.152	0.156
via Fertility	0.253	0.198	0.040	0.161
Residual	0.004	0.008	0.018	0.001

DISCUSSION

The breeder of self-pollinated crops is faced with the decision of identifying the most promising parents for hybridization and subsequently selecting the superior lines from the resulting segregating progeny. In the case of wheat there are many potential parents available for hybridizing. For simply inherited characters such as those controlled by major genes for resistance to diseases, selection of parents and desired progeny is obvious and straight forward. Quantitatively inherited traits such as grain yield are controlled by many genes and are frequently under a large environmental influence, thus the breeder must set guidelines or selection criteria when making parental choices and progeny selections.

Grain yield in wheat is the product of the genotype and the sum total of all environmental factors which have influenced the genotype during its development. To gain a better understanding of the inheritance of this complex trait, research workers have considered yield in terms of its primary components. Some workers have even suggested that yield is only an artifact and the end product of combined contributions of its components so there realistically are no genes for yield per se and consequently estimates of such genetic parameters as heritability and combining ability are meaningless. Thus in breeding for complex traits such as grain yield, the breeder should examine the components and the amount and nature of the genetic variability of these components including the possible associations between components. The components are regarded as spikes per plant (tillers), spikelets per spike (head size), kernels per spikelet (fertility) and weight per kernel (seed size). Like grain yield, the components have also been shown to be quantitatively inherited and influenced by environmental effects.

The possible existence of negative correlations or compensating effects among the components of yield would greatly influence progress toward allowing maximum yield by an overemphasis of one or more of the components during selection. This is particularly true since the various components are determined at different stages in the morphological development of the wheat plant. Thus environmental stresses at different stages of growth may actually influence the various components in both a direct and an indirect manner.

Associations and interrelationships among agronomic traits may therefore impose biological or developmental limitations which may be intensified by the inter and intra plant environment. If the wheat b reeder is to make effective progress in utilizing the component approach in developing superior cultivars then information regarding the compensating effects of the components must be understood and accounted for in the development of any selection index or values assigned to the components.

A further factor which must be considered is that wheat is grown commercially under solid seeded conditions, however, most genetic studies and selections in the early generations are conducted under non-competitive conditions (space planting). It is therefore necessary to know if the information gained from space planting is meaningful in predicting performance when selections are grown under commercial production. It was the purpose of this study to measure the effects of competition on the interrelationships and associations between yield, the components of yield and three associated characters, namely, harvest index, heading-maturity duration and plant height. Another objective was to determine the influence of the environment on genotypes and on gene action estimates in five widely divergent cultivars of winter wheat and their F_1 and F_2 crosses. Analysis of variance, diallel analysis, correlations, regression and path-coefficient analyses were employed to obtain parameters that could help in making comparisons and give better insight into yield potential that may be tailored to specific cultivars. Since the cultivars selected for this study are adapted to the growing conditions observed in the Pacific Northwest, information on how they achieved their respective yields in terms of the components was also obtained.

Compensating Effects

As previously noted during the life cycle of the plant, it is subjected to a chain of interrelated events which are gene regulated at times and highly influenced by non-genetic factors at other times. These events are not random but follow an integrated pattern that allows for the genetic expression as far as the prevailing environment permits. Yield of grain in wheat is an example of integrated pattern where the components of grain yield are sequentially interdependent in the course of their development. It is possible to trace the development of components in order of their sequence. Correlation and path-coefficient analyses measure the degree of interdependence between yield and the components of yield and within the components themselves. Correlation analyses for yield, components of yield and the agronomic characters, harvest index, heading-maturity duration and plant height obtained in this study revealed that the degree of correlation was dependent on the particular environment utilized. The poor correlation between number of spikes per plant, seed size, and yield reflected the importance of other yield components in the expression of the final product. The high positive correlations between spikelets per spike and fertility indicated that these components play significant roles in the numerical value of yield under all situations encountered in the present studies. These results indicated further that large spikes with high fertility could contribute to maximizing yield. Harvest index showed no consistent correlation with yield under any environment of this study. However, under dryland conditions it may be of value in the selection process owing that to the high correlation coefficient with grain yield. The data suggest the desirability of further investigation in this respect. The prevalence of negative correlations among grain yield with plant height and heading-maturity duration are of special significance. Short plant types which are quick maturing are thus favored under the environment of these studies. This contrasts with Grundbacher (1963) and Lupton (1972) who indicated the importance of post anthesis longevity and awned ears as contributors to higher yield under the conditions of their studies. The cultivars used in these studies were high yielding and adapted to the Pacific Northwest conditions thus possessing low variability in their maturity duration. Heading and maturity are also highly influenced by temperature and moisture conditions.

Negative associations between the components of yield indicated the compensatory behavior of these components. Plants have evolved with an inherent flexibility that enables them to take alternative pathways in attaining survival form or value. The components of yield utilize this flexibility to maintain some yield stability when in the course of development variation in a component is compensated for by one or more of the other components. For the plant, seed production is a means of survival especially under environmental stress. Component compensation becomes an expected feature of development and leads to negative correlations between most of the components of yield which are thought to result from the oscillatory nature of the yield components. In this sense, yield becomes a sort of buffer that neutralizes breeding efforts to develop varieties with exceptionally high yields. Thus, increasing the weakest component of a good variety may not lead to the expected gains in grain yield. High yielding cultivars achieve their high yields by emphasizing different components. They rarely excel in more than one or two components of grain yield. Genetic and environmental factors impose upper limits observed in grain yield. Higher yields may be expected from those genotypes with a balance in the composition of their yield components. Results from the present studies did not support the preconceived idea that correlations are near zero under non-competitive conditions (Adams, 1967) and become more negative as competition increases. This must be related to the presence of important stresses resulting from inadequate resources within individual plants even under the least competitive conditions. These stresses should have operated under all the present situations. The negative associations of plant height with number of tillers and harvest index are worth noting. If tall plants do not tiller as much and have lower harvest index and grain yields as shown by the negative correlations, then breeding methodology should concentrate on shorter plant types especially under irrigated and high rainfall conditions. The positive correlation between seed size and plant height indicated that it would be relatively hard to breed large grain into short statured wheat plants, even so, if it were possible, the negative associations of seed size and fertility would make yield superiority a more complicated task.

Compensating effects were observed to be more acute when viewed from another angle. Direct and indirect associations noted by the path-coefficient analysis revealed that each of the components of yield was directly responsible in contributing to the expression of yield. The low correlations were mainly caused by some indirect negative effects through one or more of the other yield components. Yield correlated poorly with tiller number as a result of the indirect influences of seed weight, fertility and spike size. Seed weight and yield correlated poorly due to the indirect effects of tiller number. High associations were mainly the result of direct effects and any indirect effects were nullified by the presence of opposing indirect influences. The indirect effects of fertility were offset by tiller number, spike size and seed weight. The path-coefficients also indicated that harvest index, maturity duration and plant height had very small direct and indirect influences on grain yield. They could not be considered components of yield and must properly be considered as associated characters. In the regression process, their total contribution to the coefficient of determination never exceeded a few percentage points. The variation in yield was almost totally accounted for by the variation in its components as evidenced by the R^2 values which ranged between .96 and .99. The very low residual values in the regression analyses showed that path-coefficient analysis, as applied to the components of yield, was very efficient in revealing the true nature of the interrelationships between yield and the components of yield in this study. Results from this analysis magnified the following basic relationships. As the number of tillers increased, head size and seed size decreased. Their proportions in compensation changed with spacing and location and the fertility was affected drastically at Hyslop. Tillers compensated for head size and seed size compensated for fertility. Space planted F_2s showed a similar reaction but under solid seeding no compensating effects were observed and the high correlations were made up of a sum total of direct and indirect small effects. This would not be unusual since F_2 data were collected from the mean of 400 plants each of which could have reacted differently to the environment and the non-competitive plants could have been overshadowed by the filler variety.

These data suggest that compensating effects of the components of yield are a major obstacle in breeding for higher yields. For immediate use in breeding projects, a compromise must be reached where selection for any one component is mild enough to create no serious compensatory reactions. A balance must be reached in the expression of the components of yield where their reaction could be multiplicatively complementing rather than negatively compensating. The components of grain yield should be considered all together when selecting new lines so that compensating effects may be minimized. It is suggested that simulation experiments be run on large enough data under spaced plantings and solid seeded conditions to determine the optimum yield component combinations that could result in maximum yields in major wheat producing areas.

Based on the previous observations from correlation and path-coefficient analyses a high yielding variety may be defined as that which produces enough tillers per unit of area to cover the field with large and fertile spikes of medium to large grain and semi-dwarf plant type. Such varieties would be most suitable for areas of high soil fertility and under abundant rainfall or irrigated conditions.

Gene Action

The vast number of wheat cultivars available for utilization as potential parents makes it necessary for the plant breeder to make correct choices based on the probability as to which combination will result in desirable progenies. Possible guidelines for selecting potential parents include such factors as their relative combining ability, the heritability of the traits to be selected for, the genotype x environment interaction and the possible associations between the desired traits.

Combining ability describes the breeding behavior of a particular character within a population of selected genotypes. Those characters that respond to additive gene action are reflected in terms of higher general combining ability estimates (GCA), whereas deviations from the additive scheme are noted by high specific combining ability estimates (SCA). Combining ability is also a means of identifying high and low general and specific combiners. Those cultivars which when crossed to broad based genetic testers provide a high GCA estimate are most useful in conventional breeding programs with self-pollinating species, while high specific combiners may contribute to hybrid wheat production. Estimates of non-additive genetic variance provide a measure of potential hybrid vigor and expose the contribution of hybrid vigor to yield increases.

Heritability estimates help in evaluating expected gains from planned crosses. In the narrow sense, heritability may be considered as an index of transmissibility or repeatability. It provides a guide to the effectiveness of selection when a particular trait is controlled largely by additive gene action.

Earlier workers, Kronstad and Foote (1962), Brown et al. (1966) and Bitzer et al. (1968) have reported that additive gene action estimates (general combining ability) made up a large portion of the total genetic variance involved in the expression of the yield components. Results from the current studies substantiated their findings (Tables 6, 7 and 8) under space planting conditions. Most studies of gene action estimates have been conducted under spaced or hill plantings. In the present studies, solid seeding was simulated so comparisons with space planting could be made. Under non-competitive conditions, additive gene action was most predominant and contributed more than the non-additive gene action (Tables 9, 10, and 11). As competition increased due to higher seeding rates, the effects of specific combining ability became more important in the expression of many of the characters studied, namely yield, number of spikes, spikelets per spike and plant height. The environment affected GCA and influenced the relationship with SCA in the expression of the total genetic variation. This conforms to reports of Saini (1968) and Peterson (1970) who used similar testing conditions. Space planting tended to mask the effects of specific combining ability. It is reasonable to conclude that results from spaced plants do not apply to solid seeding conditions.

Evidence of complementation between the varieties used in the current studies was suggested by the contribution each had to the general and specific combining ability effects. Each variety in these studies was chosen since it excelled in one or more of the components of yield. Paha contributed significant general combining ability effects in the expression of spikelets per spike and fertility. Its combinations with other varieties exhibited positive specific combining ability effects for the latter character. Kavkaz contributed large seed size to its progeny while Hyslop and Sprague contributed to tiller number. A note worth mentioning in this respect is the negative contribution of the semi-dwarf variety Hyslop to plant height. It would be possible to select short plant types from the progeny involving crosses where Hyslop was used as one of the parents. This has been a highly desirable characteristic in high yielding modern wheat and rice varieties. The results of these studies agree with what has been accomplished in selecting individual plants for short height while maintaining the potential for yield.

A similar situation was encountered when combining ability estimates were compared to heritability estimates. High narrow sense heritability estimates were observed for most of the measured characters when the plants were not under competitive stress regardless whether the progeny was an F_1 or F_2. Head size usually referred to as spikelets per spike and kernel weight were most consistent in showing high heritability estimates under high competitive stress. These results indicate that progress may be expected when seed size and head size are used as selection criteria under solid seeding conditions. The persistence of spikelet fertility in exhibiting high heritability and general combining ability estimates offered hope that this character be used as a selection index under solid seeding conditions. Heritability and combining ability estimates differed considerably in the measurement of grain yield. The high heritability estimates of yield contrast with the low general combining ability estimates. This indicated that genetic parameters concerning yield may not be reliable. Regression analyses revealed that yield variations were almost completely the result of variations of the yield components. These results support the observation that yield is only an end product of its components which are polygenically inherited and it is their interaction that gives rise to the artifact yield.

It was a purpose of this experiment to determine if any of the agronomic characters, harvest index, heading-maturity duration and plant height could be used as selection criteria. Results from combining ability and heritability analyses did not support this idea under all conditions of the experiments. Heritability and combining ability estimates were low and highly variable under the three seeding rates for two locations and over two years. Nevertheless, harvest index showed some promise as a selection criterion under non-competitive conditions due to its high heritability, and the high general combining ability involved in its expression and the possible direct involvement with yield.

Genotype-Environment Interactions

Genotype x environment interactions are important in the parental and progeny evaluation because they may influence the genetic expression for some traits and particularly those which are quantitatively inherited. Information about these interactions also help in deciding on the number of testing sites and under what conditions selection for certain characters must be practiced.

Examination of the performances of parental cultivars and their F_1 hybrids revealed that no large differences existed between parents and single crosses in the expression of the yield components under the conditions of these studies. Hybrids averaged significantly higher than their parents in grain yield (up to 40 8 percent) and demonstrated that component interaction in the expression of a complex trait yield is not at the level of some primary gene products controlling single traits, but at the developmental stages which are sequentially interdependent and genetically independent. This means that the ability to manipulate single traits at various stages of growth could lead to favorable interactions. The large estimate of heterosis observed for yield supports the findings of Grafius (1956, 1959) and williams and Gilbert (1960) that heterosis for complex traits could be a consequence of multiplicative relationships among the components of these traits. If this heterosis is potentially fixable in self-pollinated species as Duarte and Adams (1963) claim, then breeding methods should concentrate on the developmental stages of the wheat plant, where compensating effects of the yield components may play large roles in stabilizing yield levels.

Increasing competition from spaced to solid seeded plants resulted in lower values for grain yield and the yield components. However, genotypes reacted differently to various environmental conditions. Significant genotype by location and genotype by years as well as genotype by seeding rate interactions were observed in the expression of all characters studied. The genotype x year component is explained on the basis that one year was extremely wet and experimental plants were transplanted into the field so they received less competition from the filler variety. The large genotype x location and genotype x seeding rate interactions indicated that the genotypes behaved differently relative to each other at the two locations and under the three seeding rates. These results are in contrast with those reported by Rasmusson and Lambert (1961) who suggested that the number of testing sites for barley be reduced in Minnesota but agree with Frey and Horner (1957) who proposed division of the state of Iowa into testing areas for oat research. A great amount of environmental variability is observed in Oregon particularly in a west to east direction and the use of many testing sites is justified.

These results further suggest that significant interactions of genotype with environment do not justify the use of data from non-competitive conditions to assess performance under competitive conditions. Kernel weight and spikelets per spike were the most stable characters in that they had least significant interactions under the environmental fluctuations involved and may be the most useful as selection criteria.

Much work has been done on gene action estimates and the possibilities of advance in grain yield were very encouraging. Compensating effects of the components of grain yield have hindered advancement prospects. Early generations selected under space planting utilize the additive gene action that is expressed under non-competitive conditions. In later generations, the non-additive gene action effects are minimized by the increased homozygosity. Selection for a balance between the components of yield could be achieved under non-competitive conditions especially those components which showed consistent stability under all environments, namely seed weight and head size. Balanced components of yield lead to minimizing the effects of component compensation. In the course of this experiment it was noticed that plants that overtillered in the dryland site suffered a dieback of many secondary tillers and those that made it had fewer and smaller seeds. This effect was more pronounced under the competitive stress of solid seeding. Under the high rainfall conditions similar situations were encountered but fertility and seed size continued to be higher than those under dry-land conditions. It seems reasonable to state that compensating effects operate within the framework of available environmental resources with the plant providing adaptability mechanisms to insure its survival and reproducibility.

From the results of this experiment a breeding procedure utilizing component approach was developed. Selection in the early generations (F_2, F ...) may be practiced under space planted conditions with emphasis on avoiding extreme values in any of the components of yield. A balanced combination of the components of yield should be established before selections are tested under solid seeding conditions in the next generation. Testing under competitive conditions would reveal those selections which are good competitors and excel in grain yield. This procedure ensures that compensating effects are kept to a minimum and additive gene action is made use of as early as possible.

SUMMARY AND CONCLUSIONS

The objectives of this investigation were as follows: (1) to study the compensating effects of the components of grain yield and the possible influence of competition on the interrelationships and associations between yield, the components of yield and the three agronomic characters, harvest index, maturity-duration, and plant height; (2) to determine the influence of competition on gene action estimates in five widely divergent varieties of winter wheat and their F_1 progeny; (3) evaluate whether early generation selection would be more effective under competitive or non-competitive conditions; and (4) to see if any of the agronomic characters, harvest index, maturity-duration or plant height could be used as a selection index in the screening of early generation progeny.

Data were obtained from diallel crosses grown at Hyslop, Oregon, for two years and at Moro, Oregon for one year. The cultivars Hyslop, Paha, Sprague, Yamhill, Kavkaz and their diallel crosses were utilized in this study. Three rates of seeding were used at each location and a modified blend method provided simulated solid seeding conditions. The first four parents and their diallel F_1 and F_2 generations were also planted under two seeding rates at the Hyslop location, in the second year of study.

Morphological traits measured were heading-maturity duration, spikes per plant, spikelets per spike, plant height, grain yield, harvest index, kernel weight and kernels per skipelet. Griffing's combining ability analysis, analysis of variance, correlation, and regression analyses were used to analyze the data.

Based on the results of this experiment, the following conclusions were made:

1. Grain yield correlated significantly with head size and fertility but not with tiller number or kernel weight. Negative correlations between the components of yield were observed under all environments of study.

2. All components of yield had high direct effects in the expression of grain yield. Component compensation resulted in low correlation coefficients between yield, tiller number and seed size.

3. Harvest index, maturity-duration and plant height had very low direct or indirect influences on yield, so they could not be used as selection criteria in the population investigated.

4. A high yielding variety was described as a plant type which produces enough tillers to cover a particular unit of land area with large, fertile spikes, having medium to large kernels and semi-dwarf stature.

5. Hybrids averaged significantly higher than their parents in terms of grain yield though they were not much higher when single

yield components were considered. This resulted from the multiplicative relationship of the yield components.

6. High genotype-environment interactions justify increasing the number of testing sites in areas of wide variability. They do not justify extrapolation of findings from spaced plants to solid seeding conditions.

7. Additive gene action was predominantly involved in the expression of all characters studied under space planting conditions.

8. Non-additive genetic effects gained more influence as competition increased at high seeding rates. The characters most affected were yield, number of spikes, spikelets per spike and plant height.

9. The cultivars utilized in this study complimented each other in the expression of the components of yield and the three associated characters. Kavkaz contributed to large grain, Paha to high fertility, Hyslop to lower plant height and Sprague to higher tillering.

10. Narrow sense heritability estimates were very high for all components of yield and the three associated characters. The estimates were less significant at higher seeding rates indicating the negative influence of competition on the additive type of gene action.

11. A breeding procedure utilizing the component approach was developed. Selection in the early generations may be practiced under space-planted conditions with emphasis on avoiding extreme values in any of the components of yield. A balanced combination of the components of yield should be established before selections are tested under solid seeding conditions.

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APPENDIX

Appendix Table 1. Pedigree and description of cultivars.

Hyslop:	(Nord Desprez/sel 101^2). A semidwarf, bearded, high yielding soft white winter wheat cultivar released by Oregon State University. Resistant to leaf rust and smut. Good milling and baking quality. Medium earliness, large head size and medium kernel weight.
Paha:	(Suwon 92/4 Omar). Soft club winter wheat cultivar with medium height and resistance to shattering. Resistant to smut and tolerant to foot rot. Excellent milling and baking quality. Released by USDA, Washington State University. Highly fertile spikes, small kernels and late maturing.
Sprague:	(PI 181268/Gaines). A semidwarf weak strawed cultivar released by Washington State University for dryland areas with snow mold problems. Early, small head size, good tillering, low fertility and medium to small seed size.
Yamhill:	(Heines VII/Redmond (Alha)). A low tillering, medium height high yielding soft white winter wheat cultivar. Resistant to stripe rust and mildew. Good milling and baking qualities. Released by Oregon State University. Late, large fertile spikes and medium to large kernels.
Kavkaz:	Tall, beardless, hard red winter wheat cultivar. Released in Eastern Europe. Large spikes and kernels, poor tillering, good milling and baking qualities.

Appendix Table 2. Analysis of variance for method 4 giving expectations of mean squares for the assumptions of model I. *

Source of variation	d. f.	Sum of Squares	Mean Squares	Expectation of Mean Squares
General Combining ability	P-1	Sg	Mg	$\sigma^2 + (P-2)(_{P-1}) \Sigma_i g_i^2$
Specific Combining ability	P(P-3)/2	Ss	Ms	$\sigma^2 + {}_{P(P-3)} \sum_{i>j} \sum Sij^2$
Error	m	Se	Me	σ^2

*Griffing, 1956, p. 477, P = number of parents

General combining ability effects (GCA) for i^{th} (j^{th}) parent were estimated by:

$$gi = \frac{1}{P(P-2)} (PXi. - 2X..)$$

Specific combining ability (SCA) of i^{th} and j_{th} parent such that Sij = Sij was estimated by:

$$Sij = Xij - \frac{1}{P-2}(Xi. + Xj.) + \frac{2}{(P-1(P-2)} X..$$

Standard error between two gi means was measured by: $\frac{2}{P-2} \sigma^2$

and between two Si means by: $\frac{2(P-3)}{P-2} \sigma^2$ on mean basis.

Appendix Table 3. Summary of climatic data for Hyslop and Moro locations during the growing seasons 1973-75.

Location and soil type	Month	Precipitation (mm)	Temperature (c)		
			Max.	Min.	Mean
Hyslop 1973-1974	October	35.8	20.1	2.8	11.5
	November	17408	11.9	3.6	7.8
	December	207.0	9.5	2.8	6.2
	January	118.4	8.9	2.7	5.8
	February	139.2	8.9	1.1	5.0
	March	117.8	11.1	2.1	6.1
	April	61.0	12.5	1.7	7.2
	May	52.6	18.6	5.7	12.2
	June	29.0	22.0	8.1	15.1
	July	15.7	26.6	10.6	18.6
	Total	951.35			
Hyslop 1974-1975	October	68.6	16.7	5.6	11.2
	November	464.4	9.6	3.5	6.6
	December	315.0	9.4	8.0	8.7
	January	294.4	6.4	-1.2	2.6
	February	191.0	8.5	1.7	5.1
	March	225.3	12.2	2.3	7.2
	April	60.7	14.2	4.8	9.5
	May	37.1	17.5	5.8	11.6
	June	15.5	23.7	9.1	16.4
	July	46.0	25.3	9.7	17.5
	Total	1718.0			
Moro 1974-1975	October	9.4	18.0	2.0	10.0
	November	25.9	9.3	0.4	4.8
	December	35.3	6.2	-1.3	2.5
	January	51.1	4.1	-3.5	0.3
	February	37.3	3.9	-3.7	0.1
	March	31.8	8.1	-0.2	3.9
	April	11.7	11.1	0.7	5.9
	May	13.5	17.9	4.7	11.3
	June	2.1	21.8	8.0	14.9
	July	10.2	29.0	14.1	21.5
	Total	219.12			

Appendix Table 4. Path-coefficient equations.

$$r_{2\,1} = P_{2\,1} + r_{2\,3}P_{3\,1} + r_{2\,4}P_{4\,1} + r_{2\,5}P_{5\,1} + r_{2\,6}P_{6\,1} + r_{2\,7}P_{7\,1} + r_{2\,8}P_{8\,1}$$

$$r_{3\,1} = P_{3\,1} + r_{2\,3}P_{2\,1} + r_{3\,4}P_{4\,1} + r_{3\,5}P_{5\,1} + r_{3\,6}P_{6\,1} + r_{3\,7}P_{7\,1} + r_{3\,8}P_{8\,1}$$

$$r_{4\,1} = P_{4\,1} + r_{2\,4}P_{2\,1} + r_{3\,4}P_{3\,1} + r_{3\,5}P_{5\,1} + r_{3\,6}P_{6\,1} + r_{3\,7}P_{7\,1} + r_{3\,8}P_{8\,1}$$

$$r_{5\,1} = P_{5\,1} + r_{2\,5}P_{2\,1} + r_{3\,5}P_{3\,1} + r_{4\,5}P_{4\,1} + r_{6\,5}P_{6\,1} + r_{7\,5}P_{7\,1} + r_{8\,5}P_{8\,1}$$

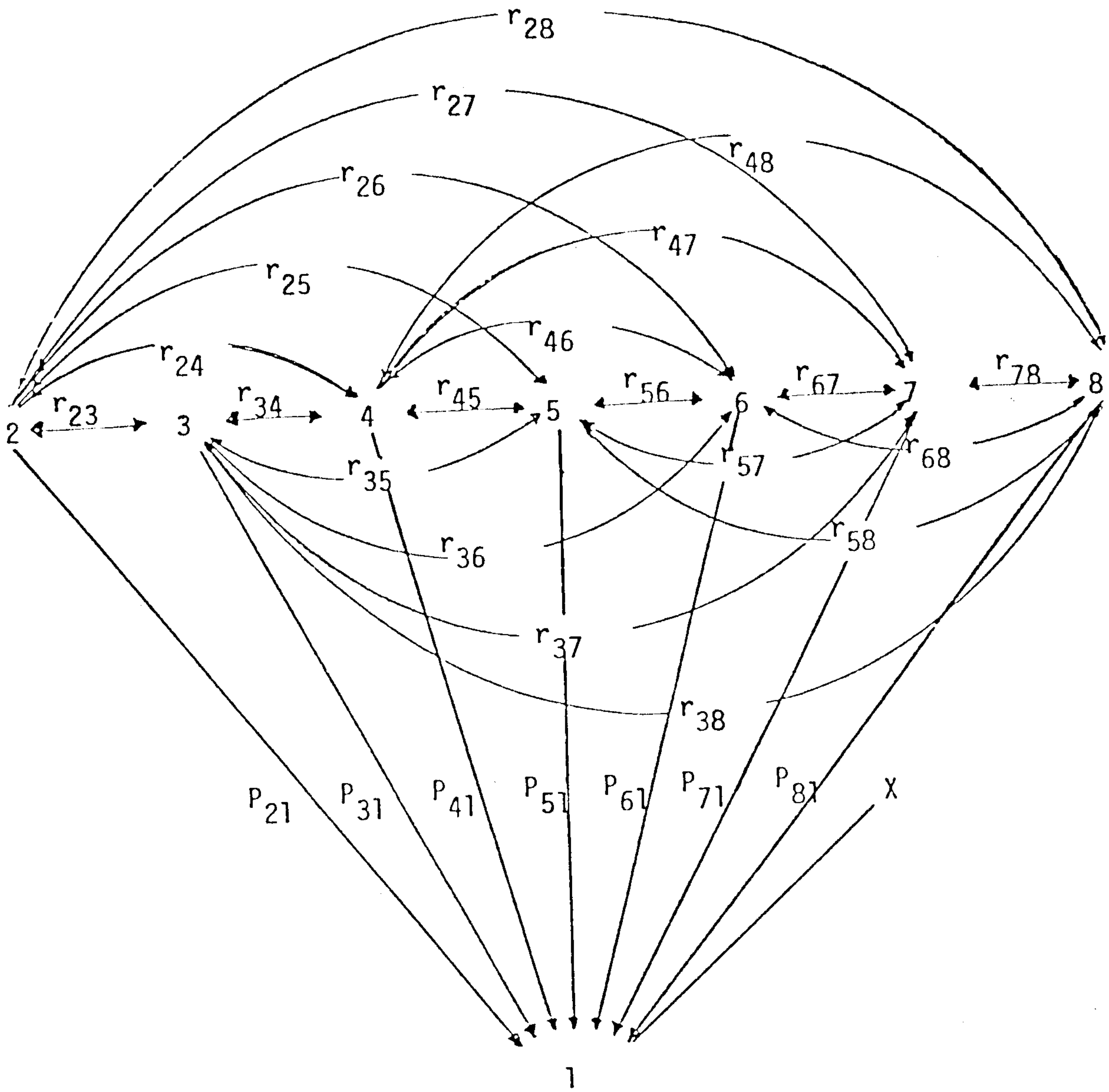
$$r_{6\,1} = P_{6\,1} + r_{2\,6}P_{2\,1} + r_{3\,5}P_{3\,1} + r_{4\,6}P_{4\,1} + r_{5\,6}P_{5\,1} + r_{7\,6}P_{7\,1} + r_{8\,6}P_{8\,1}$$

$$r_{7\,1} = P_{7\,1} + r_{2\,7}P_{2\,1} + r_{3\,7}P_{3\,1} + r_{4\,7}P_{4\,1} + r_{5\,7}P_{5\,1} + r_{6\,7}P_{6\,1} + r_{7\,8}P_{8\,1}$$

$$r_{8\,1} = P_{8\,1} + r_{2\,8}P_{2\,1} + r_{3\,8}P_{3\,1} + r_{4\,8}P_{4\,1} + r_{5\,8}P_{5\,1} + r_{6\,8}P_{6\,1} + r_{7\,8}P_{7\,1}$$

The variation in yield accounted for by the above associations was calculated by the formula:

$$R^2 = P_{21}r_{21} + P_{31}r_{31} + P_{41}r_{41} + P_{51}r_{51} + P_{61}r_{61} + P_{71}r_{71} + P_{81}r_{81}$$



1=yield per plant
2=tiller number
3=spikelets per spike
4=kernels per spikelet
5=seed weight
6=harvest index
7=heading maturity duration
8=plant height
P=path coefficient
X=residual factors

r=correlation coefficient between any two of the independent variables 2-8.

Figure 1. Path diagram and association of all measured traits.