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Title: The Influence of Plant Densities on Gene Action Estimates and Associations in Seven Winter Wheat Parents and Their F_2 Progeny

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The F_2 progeny from a diallel cross involving seven winter wheat parents along with the parents were grown at the Hyslop Agronomy Farm near Corvallis, Oregon to determine the influence of three plant densities on gene action estimates for yield and its primary components. The plant densities were designed to provide different levels of competitions involving solid, six and 12 inch spacing within the rows with one foot spacing between the rows. Gene action estimates were obtained by the combining ability analysis as well as narrow sense heritability estimates. In addition, path-coefficient analysis was utilized to investigate the direct and indirect associations of the primary components of yield under different stresses of competition resulting from the changes in population densities. The morphological characters measured were 1) total yield per plant, 2) kernel weight 3) number of kernels per spikelet,

4) number of spikelets per spike, 5) tiller number and 6) plant height.

A small additive gene action for yield was noted in the six inch spacing while additive gene action effects could not be detected in the 12 inch and solid plantings. Yield being a complex trait seems to be affected by the environmental changes resulting from different plant densities.

Consistent general combining ability estimates were observed for kernel weight and plant height in all the plant densities, indicating a small genotype-environment interaction.

In the spaced plantings additive gene action estimates were obtained for tiller number and spikelets per spike while there was no evidence of additive gene effects in the solid planting. No additive gene action was noted for kernels per spikelet in the 12 inch planting while six inch and solid plantings revealed considerable genetic variability. These results would suggest that the genotypes are susceptible to environmental fluctuations for the traits tiller number, spikelets per spike and kernels per spikelet.

The correlation coefficients reveal that in spaced plantings tiller number, spikelets per spike and kernels per spikelet are significantly and positively related to yield. In the solid seeding only spikelets per spike was significantly associated to yield.

When the four variables were considered in terms of their associations with yield it was observed in the F_2 that in spaced plantings all the four components of yield have direct positive influence on yield. In the solid seedings however, spikelets per spike and kernels per spikelet had high positive direct effects on yield while tiller number and kernel weight showed a negative direct influence on yield. The data revealed that spikelets per spike and kernels per spikelet are the most important traits contributing towards yield. However, the results obtained with correlation coefficients indicate that a negative association existed between these two traits as well as between kernels per spikelet and tiller number suggesting the possible existence of a biological limitation between these components of yield.

The results indicate that a breeding program with emphasis on the selection of plants in competitive conditions in the early generations may make the selection work more efficient. Moreover, increases in yield which considers each of the components separately or in combination of two or more would offer the most promise. By this procedure the breeder would take advantage of the large amount of additive genetic variances associated with each of the components and at the same time take into consideration any biological limitations which may exist.

The Influence of Plant Densities on Gene Action Estimates and Associations in Seven Winter Wheat Parents and Their F_2 Progeny

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INTRODUCTION

Scientific breeding and improvement of wheat has been carried on since the dawn of the present century. The development of high yielding varieties constitutes a land mark in wheat improvement. However, if further yield increases are to be realized, more refined techniques and a better understanding of the genetics and particularly the genotypic-environment interaction influencing the expression of gene action governing yield, will be needed.

Plant characters can be described with regard to the nature of their inheritance as being either qualitatively (simple) or quantitatively (complex) inherited. The method of studying the simply inherited traits is by determining the ratio of one contrasting character to another in the segregating generation following a cross. Because it is impossible to accurately determine the nature of inheritance of the complex traits, they are often evaluated by determining various estimates of gene actions governing their inheritance.

Grain yield of the wheat plant is a product of several morphological and quantitatively inherited traits. Therefore yielding ability per se, is also influenced by many genes. Quantitatively inherited characters are particularly susceptible to environmental influences and it is the manner of reaction under a particular condition that is inherited and not the character itself. Since the quantitative traits are susceptible to environmental fluctuations, it is important to understand the behavior of certain genotype under different environmental conditions.

Wheat is grown commercially in competitive conditions (solid planting). However, early generation selection of the desirable plants is usually conducted in non-competitive conditions (spaced plants), since it is easier to evaluate certain traits, such as lodging and disease on the basis of individual plants. In a normal breeding program a large number of progenies have to be tested and it is essential to devise a suitable technique for evaluating breeding material. The early generation selection, which is based on spaced plantings is free from interplant competitions and therefore the plant breeder has no idea as to how the selected plants will do under later generation testing (in solid plantings). Very little research has been done to show if the genetic estimates based on spaced plantings are accurate for solid seeding as well.

The main object of this study was to obtain estimates of gene action, of a diallel set of crosses involving seven divergent winter wheat varieties, for yield and the primary components of yield in solid, six and 12 inch spacings. A second purpose of this investigation was to study the association between yield and various morphological factors as well as to separate the coefficients of correlation into their direct and indirect influences; and to determine the influence of population densities on these associations.

LITERATURE REVIEW

For the purpose of this review, the pertinent literature has been grouped into sections for each of the major areas investigated. These studies are as follows: combining ability, heritability, correlations and path-coefficient analysis as well as genotype-environment interactions.

Combining Ability Analysis and Early Generation Testing

Some varieties are good parents, as judged by their ability to transmit high yield to their progeny in crosses whereas others are less desirable. The importance of combining ability has been known and utilized for many years in the breeding of hybrid corn. However, very little work has been done on the use of combining ability in self-pollinated crops.

The difference in the performance of hybrid combinations or combining ability, was separated in general combining ability (GCA) and specific combining ability (SCA) by Sprague and Tatum (1942). In corn general combining ability was defined as the average performance of a line in hybrid combination and interpreted primarily as a measure of additive gene effects. Specific combining ability determines the performance of those crosses in which certain combinations did better than others on the basis of the average performance of the parental lines involved. Specific combining ability is assumed to measure the non-genetic variance, which is made up of dominance and epistatic interaction.

According to Lush (1948), Schmidt in 1919 was the first to use diallel crossing system in which each of a group of males was crossed to each of a group of females. An analogous situation in plants is seen whereby crosses are made in all possible combinations within a group of parents.

Griffing (1956) developed four methods of diallel cross analysis. The type of analysis depended on the presence or absence of the parental inbreds or the reciprocal crosses. Kronstad and Foote (1963) using one method developed by Griffing (1956) estimated general and specific combining ability for grain yield and the components of grain yield involving parents and F_1 winter wheat crosses. No significant specific combining ability was found for any of the components but specific combining ability was found for grain yield and plant height. The variances associated with the general combining ability were found to be significant for yield, weight per kernel, kernels per spikelet, spikelets per spike, spikes, per plant, and plant height.

Harrington (1923) was one of the first to suggest that genetic analysis of characters in an F_2 population may be useful in predicting the value of a given cross, although it had distinct limitations with respect to quantitatively inherited characters like baking quality, which could not be studied in an F_2 generation because of limited number of seeds as well as the segregating nature of the F_2 population. Immer (1938) studied the extent of heterosis for number of heads per plant, seeds per head, weight per seed, and yield per plant between six crosses of barley. As an average of all crosses, the F_1 exceeded the average of the parents by 8.3 percent in number of heads per plant, 11.1 percent in number of seeds per head, 4.9 percent in weight per seed, and 27.3 percent in yield per plant. The average yield of six crosses in F_2 and F_3 exceeded the parents by 24 and 13 percents respectively. Based on these studies, it was suggested that the average yield performance of different crosses may be determined by means of yield trials in F_2 or F_3 generations and such yield trials may be used to discard those crosses which have not performed well.

Weiss, Weber and Kalton (1947) in soybeans studied whether or not heterosis as measured by yields of spaced plants in F_1 generations, could serve as a criterion of the recommendations potentialities of a cross, when the degree of heterosis as expressed in F_1, was compared with the mean yield of F_5 selections. They found no apparent relationship among crosses. Thus, in this study the degree of heterosis of spaced F_1 plants could not be used as a reliable criteria to predict the yield potentialities of segregates from a cross.

Kalton (1948) studied the bulk F_2, F_3 and F_4 populations of 25 soybean crosses grown in replicated trials in successive years and evaluated seed yield, date of maturity and plant height in comparison with three of the parental varieties. While the bulk population varied considerable from one generation to the next for yield differences, behavior was relatively consistent for height and maturity. It was concluded that elimination of the poorer crosses on the basis of single year test was not possible. Yield differences between parental varieties was not considered a good criterion of bulk population yield performance of crosses in early segregating generations. The results of this study appear to justify the conclusion that soybean varieties differ widely in combining ability for factors determining the agronomic characters studied in this investigation.

Heritability

Heritability estimates are of considerable importance to the plant breeder for partitioning the total variance into that caused by the environment and that due to genetic expression. It is a measure of the phenotypic variation in a population that is due to genetic causes.

Warner (1952) gives an excellent review of historical development of methods for estimating heritability in literature prior to 1952. These methods in general were reported to fall into three main categories.

1. Parent - offspring regression
2. Variance components of analysis of variance
3. Approximation of non-heritable variances from genetically uniform populations to estimate total genetic variance.

A significant reference to the term 'genetic' was made by Fisher (1918). The genetic variance was separated into three components: 1) that due to additive effect of the genes 2) that due to dominance deviation arising from interaction of alleles (intra-allelic interaction), and 3) an epistatic part associated with interactions of non-alleles (inter-allelic interaction or epistasis). Mather (1949) has described the techniques for partitioning phenotypic variance into these components.

Heritability has been defined by Robinson et al (1949) as an estimate of the additive variance in percent of total variance. Panse (1940) suggested the use of the ratio of additive genetic variance to the total variance as a measure of the degree of heritability.

Wright (1921) also referred to the type of hereditary variances described above, and the genetic variance reflected the degree to which the progeny resemble parents. Heritability in pure lines was taken to be additive genetic variance in percent to the total variance. According to Wright only additive effects contribute to permanent gain.

Lush (1949) stressed the utility of estimates of genetic components as the basis for predicting the response of quantitative characters to selection in breeding programs. Lush described heritability of quantitative characters in two ways: 1) in the broad sense, heritability refers to the functioning of the whole genotype as a unit and is used in contrast with the environmental effects; 2) in the narrow sense, heritability includes only the average effects of genes transmitted additively from parent to progeny or ratio of additive genetic variance to total variance.

In self pollinating crops such as wheat, narrow sense heritability which is a measure of additive gene action, is of primary interest to a plant breeder because it is this part of the heritable variation that can be fixed in the succeeding generations. This literature review will, therefore, be confined to the narrow sense heritability estimates in self pollinating crops.

Mahmud and Kramer (1951) in a study with 60 soybean crosses, compared heritability estimates which were calculated in several ways. One method utilized the variability among spaced F_2 plants in relation to the variability among spaced plant of the non-segregating parents. Regression of F_3 lines on F_2 plants and F_4 progeny on F_3 lines was also used. It was found that the heritability estimates ranged from 69 to 77 percent for yield and 74 to 91 percent for plant height.

In three soybean crosses, Bartley and Weber (1952) obtained heritability values in a narrow sense, by regression of progeny means on their parents in F_2 and F_3 generations, for seed yield as well as plant height, and the respective heritability estimated were 10 to 40 and 49 to 63 percent.

By using the F_2 variable method, Fiuzat and Atkins (1953) reported in two barley crosses that the heritability estimates were variable between the two crosses for plant height (74. 6 and 44. 4 percents), lower for tillers per plant (29. 6 and 23. 6 percents), as well as kernel weight (38. 5 and 21. 2 percents) and a moderate estimate for yield (50. 7 and 43. 9 percents).

Frey (1954) used the regression of F_5 lines on F_4 lines to obtain a narrow sense heritability of 30 percent for yield in barley crosses. While Jogi (1956) in two barley crosses obtained heritability percentages of 60 to 64 and 59 to 77 for yield and plant height respectively.

A 50 percent heritability value was reported in wheat by Weibel (1957), for plant height, 1. 3 percent for number of tillers and 7. 7 percent for yield. Nandpuri (1958) studying three wheat crosses obtained heritability values of 88.4 and 24.4 percents for plant height and number of tillers respectively. Heritability estimates for yield and yield components were studied by McNeal (1960). He observed that the regression of F_3 lines on F_2 was too low to be of any value in selection. Tillers per plant had the highest value of 35.6 percent. Kronstad and Foote (1963) by using parent-progeny regression of F_1 on parents reported in their studies with wheat crosses a high heritability estimate for plant height 82.9 percent), followed by spikelets per spike (60.7 percent). Kernels per spikelet,weight per kernel and spikes per plant had somewhat lower estimate of 47.8, 47.2 and 40.1 percents respectively. Carleton and Foote (1965) in barley crosses obtained a low heritability for yield, 26 and 52 percents by parent-offspring regression and variance components respectively.

Correlations

Correlation studies enable the breeder to measure the association between two or more factors. The correlation of characters in relation to yielding ability of a plant infers the relative importance of certain characters and their influence on yielding ability.

Arny and Garber (1919) were among the early investigators to work in this area. They observed the increase in yield was closely accompanied by an increase in number of kernels and number of culms in wheat. Significant positive correlation between yield and height of plant was reported by Clark (1924) in crosses between Kota and Hard Federation. Engledow and Shelton (1922) stressed the importance of earliness of tillering and tillering capacity to be important indices of yielding ability of wheat varieties growing under highly fertile conditions. They also laid stress on number of grains per head for yielding ability.

Engledow (1925) suggested that for selection purposes number of grains per head is useful index of yield per plant in wheat. The Punjab Cerealist annual report (1930) indicated that the correlation between number of ears and grain weight per plant in wheat was positively significant.

Keeping leaf rust, stem rust and heading date constant, Martin (1931) found significant positive correlations between yield and plant height. Similar results for yield and plant height were reported by Bridgeford and Hayes (1931) in hard red spring wheats.

Number of grains per ear was found by Waldron (1932) to be positively correlated with yield. Waldron also suggested that for the development of new varieties careful attention must be paid to the number of grains per head.

Aamodt (1935) observed that there was highly significant positive correlation between tillering survival and grain yield in wheat. A high correlation between yield and tiller number was observed by Simlote (1947). Tan (1949) in his studies in wheat reported a significant positive correlation of yield with kernel number and plant height. Weibel (1957) obtained a high correlation of grain yield with plant height and the number of spikes in wheat, while a small correlation for these traits was reported by Poehlman (1949).

Quinsenberry (1926) used path coefficient analysis to measure the direct influence of one variable (independent) upon another (dependent) and separated the correlation coefficients into direct and indirect effects. He contended that the number of spikes per unit area was one of the most important factors in determining yield, closely followed by the number of kernels per spike or size of spike. He did not consider weight of 1000 kernels to be as important in determining yield as the other two factors mentioned. Kronstad and Foote (1963) found that path-coefficient analysis indicated the number of kernels per spikelet had the greatest direct effect on yield. They also reported that weight per kernel, number of kernels per spikelet and the number of spikelets per spike have mainly direct effect on yield. The number of spikes per plant had little direct effect, but an indirect effect on yield was contributed through the other variables.

Influence of Spacing on Gene Action Estimates

Literature on the influence of plant spacing on gene action estimates is meager, however, several investigations have indicated interactions do exist between the expression of the genotypes and plant spacings.

Tysdal and Kieselback (1944) in alfalfa found an interaction for yield between genotype and plant spacing. The spacing consisted of spaced rows and solid seeding. It was found that under competitive conditions, higher yielding plants have benefited through competition with less vigorous and lower yielding plants. Large interaction of genotypes and spacing were reported by Pearson and Elling (1961) and Theurer and Elling (1964) suggesting that space planted trials in alfalfa were invalid for yield determination in solid seedings. Rumbaugh (1963) observed in two varieties of alfalfa grown at different plant densities (spacings) that the relationship of crown width, length of longest stem and stem number with dry matter yield per plant altered with increasing population densities. It was concluded that selection indices based upon yield components data obtained in spaced nurseries may not accurately portray the forage yield potential of genotypes in solid seeding. Similar results were also indicated by Davies and Reusch (1964) wherein widely spaced plants were reported to give a misleading impression of some varieties in drill (solid seeding) plots as to their herbage yield in alfalfa. Evans, Davies and Nyquist (1966) in two inch spaced plants, simulating solid seeding, found no significant interaction between genotype and spacing, suggesting that the breeding lines can be evaluated in non-competitive plantings for alfalfa yield.

MATERIALS AND METHODS

The experimental material for this study consisted of two populations. The first involved five high yielding winter wheat varieties and two experimental selections, which included Panter, Druchamp, Nord Desprez, Heines VII, Redmond Pullman Selection 1 and Corvallis Selection 55-1744. The second population represented 21 F_2's resulting from a diallel cross involving the seven enteries from population I used as parents. A description of these parental lines and their pedigrees are given in the appendix Table 1.

The 21 F_2 crosses and the seven parents were grown in a randomized block trial during the 1965-66 crop year at the Hyslop Agronomy Farm, near Corvallis, Oregon. Parental lines and F_2 plants were grown under three plant spacings with four replications. The between row spacings were 12 inches while the within row plantings were solid, six and 12 inches apart between plants. The rows were 20 feet long in each replication, thereby the number of plants in the 12 and six inches spacings were 20 and 40 respectively. The solid plantings were sown at the rate of 100 lbs. per acre. After the seedlings emerged, 50 plants in each solid seeding plot were counted and tagged so that all subsequent observations and measurements were taken on these 50 plants in each replication.

Single plant observations in the spaced plantings as well as for the 50 solid seeded plants for both the parental lines and F_2 progeny were taken and the following information recorded.

1. number of spikes per plant
2. average number of spikelets per spike
3. average number of kernels per spikelet
4. average weight of a kernel in milligrams
5. plant height from ground level to the tip of the tallest spike in centimeters
6. total weight of kernels per plant in grams

In solid planted plots all 50 plants in each row were harvested at maturity and the above mentioned measurements were taken on all the spikes obtained therein. Plant height was taken by measuring the tallest culm from 50 random samples within the row. These random samples were each considered representative of individual plants.

Analysis of variance, for each of the characters was conducted on the data obtained from the parents and F_2 crosses.

General and specific combining ability estimates were obtained by the technique proposed by Griffing (1956) where one set of F_2's are included in a matrix and neither parents nor reciprocal F_2's were used.

The variance components of the general combining ability effects were interpreted as being due primarily to additive effects of genes, whereas specific combining ability was considered to be the deviation from the additive scheme (Sprague and Tatum). The method for computing the analysis of variance for combining ability is presented in Table 1.

General and specific combining ability for each parental estimates were obtained by the following procedure.

General combining ability of the ith (jth) parent

$$g_i = \frac{1}{p\,(p-2)} \quad pX_{i.} - 2\,x_{..}$$

Specific combining ability of ith and jth parent such that

$S_{ij} = S_{ji}$

$$S_{ij} = x_{ij} - \frac{1}{p-2} \quad (X_{i.} + X_{j.}) + \frac{2}{(p-1)(p-2)} \quad X_{..}$$

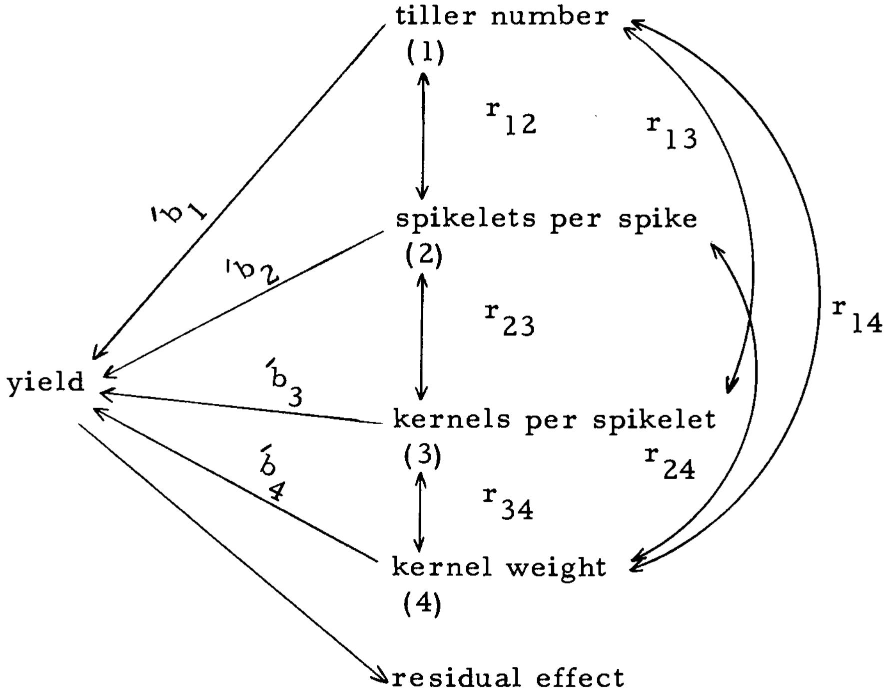
Heritability studies provided a second measure of estimating the nature of gene action controlling a given character. Narrow sense heritability as obtained from the portion of the additive variance to the total variance, was obtained separately for the different plant spacings in the F_2 crosses. The additive variance was obtained from the component of variance due to general combining ability effects.

Table 1. Analysis of variance and the error mean square for a diallel analysis.

Source of Variation	d. f.	Sum of Square	Mean Square	Expected Mean Square
Replication	N-1	$2\ \frac{\Sigma X..K^2}{P\ (P+1)} - \frac{2X..^2}{NP\ (P+1)}$	M_1	
G. C. A.	P-1	$\frac{1}{P-2i}\ \Sigma Xi.^2 - \frac{4}{P(P-2)}\ X..^2$	M_2	$\sigma^2 + \sigma s^2 + (P-2)\,\sigma g^2$
S. C. A.	$\frac{P(P-1)}{2}$	$\underset{i>j}{\Sigma\Sigma} Xij^2 - \frac{1}{P-2}\ \Sigma Xi.^2 + \frac{2}{(P-1)(P-2)}$	M_3	$\sigma^2 + \sigma s^2$
Replication X Genotype	$\left[\frac{P(P+1)}{2} - 1\right]$ $[N-1]$	$\Sigma XijK^2 - 2\frac{\Sigma X..K^2}{P(P+1)} - \frac{\Sigma Xij.^2}{N} + \frac{2X..^2}{NP(P+1)}$	M_4	σ^2

Phenotypic and genetic correlation coefficients were computed in all possible combinations for the five measured traits. Plant height was omitted since this was not regarded as an important component of yield. The associations were determined for the three plant spacings involving the seven parents and the 21 F_2 crosses separately. The phenotypic correlations for the parents as well as the crosses were obtained from the variances and covariances by substracting replication effects from the total variances. The genetic correlations in the parents were estimated from the parental variances and covariances as obtained in the respective analysis of variance and covariance. This was done on the assumption that differences between parents were due to genetic effects only. The genetic correlations in the F_2 population were obtained from the component effects of general combining ability which is interpreted as measuring additive gene action.

Path coefficients, measured in terms of standardized partial regression coefficients, were also studied for the five variables. These five variables representing the 'casual' system in the analysis are represented diagramatically below



In the path-way diagram the double arrowed lines indicate the mutual associations as measured by correlation coefficients r_{ij} and the single arrowed lines represent the direct influence as measured by the standardized partial regression coefficients $'b_{ij}$. The path coefficients were determined by the simultaneous solution of the following equations

$$r_{1y} = {'b_{1y}} + r_{12} \cdot {'b_{2y}} + r_{13} \cdot {'b_{3y}} + r_{14} \cdot {'b_{4y}}$$

$$r_{2y} = r_{12} \cdot {'b_{1y}} + {'b_{2y}} + r_{23} \cdot {'b_{3y}} + r_{24} \cdot {'b_{4y}}$$

$$r_{3y} \pm r_{13} \cdot {'b_{1y}} + r_{23} \cdot {'b_{2y}} + {'b_{3y}} + r_{34} \cdot {'b_{4y}}$$

$$r_{4y} = r_{14} \cdot {'b_{1y}} + r_{24} \cdot {'b_{2y}} + r_{34} \cdot {'b_{3y}} + {'b_{4y}}$$

EXPERIMENTAL RESULTS

Analysis of Variance

The mean squares, for the six characters measured, involving the parental and F_2 populations in solid, six and 12 inch spacing are presented in Tables 2 and 3. A separate analysis of variance is provided for the parents and the F_2 crosses. Highly significant differences among the phenotypes were observed in the parents and F_2 populations for all traits in the three plant densities.

Since in the analysis of variance highly significant F ratios were obtained for all characters, an analysis of variance for combining ability was computed using Griffing's method (1956, p. 464) and the results are presented in Table 4. The variances associated with general combining ability were found to be significant for kernel weight, kernels per spikelet and plant height in all the three plant spacings. Significant differences were also obtained for tiller number and spikelets per spike in the six and 12 inch plantings. For yield, significant differences for the variances associated with general combining ability were revealed in six inch spacings only.

Direct comparisons of the general combining ability performances of individual varieties and selections along with corresponding standard errors for each character presented in Table 5 revealed that no significant general combining ability effects were observed

Table 2. Observed mean squares from randomized block analysis of variance for all characters measured involving the seven parents in solid, six and 12 inch plant spacings.

Source of Variation	D. F.	Yield	Kernel Weight	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Plant Height
<u>Solid</u>							
Blocks	3	.047	.824	.017	1.254	.052	2.656
Parents	6	4.198**	68.885**	.597**	-2.784**	.245**	89.801**
Error	18	.044	2.476	.031	.599	.023	1.131
<u>6 Inch</u>							
Blocks	3	.091	.882	.009	.120	.008	3.834
Parents	6	.646**	135.800**	.158**	7.635**	.310**	81.853**
Error	18	.041	1.769	.006	.209	.019	5.135
<u>12 Inch</u>							
Blocks	3	.082	1.729	.011	.317	.009	.116
Parents	6	.966**	57.435**	.134**	10.992**	.332**	34.282**
Error	18	.052	1.736	.009	.312	.031	1.902

*Significant at the five percent level

**Significant at the one percent level

Table 3. Observed mean squares from randomized block analysis of variance for all characters measured involving the 21 F_2 crosses in solid, six and 12 inch plant spacings.

Source of Variation	D. F.	Yield	Kernel Weight	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Plant Height
Solid							
Blocks	3	.089	3.809	.057	.301	.007	11.786**
Treatment	20	1.078**	24.880**	.446**	4.055**	.143**	22.887**
Error	60	.099	2.969	.052	.749	.019	2.539
6 Inch							
Blocks	3	15.696**	4.454	1.705	.186	.032	16.026**
Treatment	20	33.277**	46.451**	6.527**	2.427**	.141**	31.178**
Error	60	7.661	3.556	1.433	.315	.024	3.682
12 Inch							
Blocks	3	39.421**	19.567**	4.420	1.419**	.008	1.863
Treatment	20	53.700**	35.008**	9.000**	4.129**	.115**	14.485**
Error	60	11.356	3.202	2.826	.497	.084	2.072

*Significant at the five percent level

**Significant at the one percent level

Table 4. Observed mean squares from general and specific combining ability analysis for all characters measured involving the 21 F_2 crosses in solid, six and 12 inch plant spacings.

Source of Variation	D. F.	Yield	Kernel Weight	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Plant Height
Solid							
Blocks	3	.089	3.809	.057	.301	.007**	11.786**
G. C. A.	6	1.304	68.042**	.575	7.425	.334**	42.754**
S. C. A.	14	.982**	6.382	.389*	2.610**	.059**	14.372**
Error	60	.099	2.969	.052	.749	.019	2.539
6 Inch							
Blocks	3	15.696	4.454	1.705	.186	.032	16.026**
G. C. A.	6	78.597**	135.372**	19.106**	5.788**	.349**	87.781**
S. C. A.	14	13.854	8.343*	1.136	.987*	.052	6.921
Error	60	7.661	3.556	1.433	.315	.024	3.682
12 Inch							
Blocks	3	39.421	19.567**	4.420	1.419	.008	1.863
G. C. A.	6	79.175	99.396**	24.400**	10.547**	.226*	38.462**
S. C. A.	14	42.818**	7.415*	2.400	1.378**	.067	4.208*
Error	60	11.356	3.202	2.816	.497	.084	2.072

*Significant at the five percent level
**Significant at the one percent level

Table 5. Estimates of general combining ability effects for all characters measured from all possible F_2 crosses involving the seven parents in solid, six and 12 inch plant spacings.

Crosses Involving Parents	Yield X_1	Kernel Weight X_2	Tiller Number X_3	Spikelets/ Spike X_4	Kernels/ Spikelet X_5	Plant Height X_6
Solid						
Nord Desprez	.2611	3.0614*	.0588	.1351	-.0849	-.0751
Heines VII	.0631	.8414	.0388	.5751	-.1851*	.5769
Pullman Selection 1	-.2548	-2.3786*	-.0351	-1.0608	.1817*	-.9591
Druchamp	.2011	-.2426	.2709	.7691	-.2941*	.4209
Panter	-.1068	-2.0086	-.1491	-.2988	.1983*	1.7209
Redmond	.2231	.7614	.0728	-.2388	.2125	1.0409
Selection 55-1744	-.2868	-.0346	-.2571	.1191	-.0283	-2.7251
S. E.	.1987	1.0887	.1439	.5475	.0884	1.0078
6 Inch						
Nord Desprez	-2.0157*	2.8654*	-1.0577	-.2245	-.1501	.8306
Heines VII	.6863	1.7694	-.2017	.0894	-.0369	1.2506
Pullman Selection 1	1.3983*	-3.8505*	1.8523*	-.5006	.1391	-1.4354
Druchamp	-.3997	.7614	.2763	-.7385*	-.0649	-1.2694
Panter	-.9957	-2.0125	-.2777	.3934	.0225	2.6245*
Redmond	-2.0357*	2.4353*	-.9337	.1374	-.1219	1.3985
Selection 55-1744	3.4323*	-1.9686	.3422	.8434*	.2101*	-3.3994*
S. E.	.5536	1.1927	.7571	.3551	.0981	1.2136

Table 5. (Cont.)

Crosses Involving Parents	Yield X_1	Kernel Weight X_2	Tiller Number X_3	Spikelets/ Spike X_4	Kernels/ Spikelet X_5	Plant Height X_6
12 Inch						
Nord Desprez	-1.7209	2.3011*	-1.2697	-.1406	-.0651	.0951
Heines VII	1.7791	1.8011	.2583	.3614	-.0331	.3271
Pullman Selection 1	1.1591	-3.4888*	2.1063	-.9666*	.1391	-.3808
Druchamp	-1.3139	1.3351	.4262	-.8105	-.1309	-.8428
Panter	-1.2309	-1.2448	-.8397	.7354	-.0095	1.9751*
Redmond	-1.8009	1.3111	-.5477	-.1165	-.1499	1.1431
Selection 55-1744	3.1271	-2.0148	-.1337	.9374*	.2494	-2.3168*
S.E.	2.1313	1.1317	1.0632	.4458	.1830	.9103

for yield in the 12 inch and solid planting. In the six inch spacing however, Pullman Selection 1 and Selection 55-1744 had significantly positive effects, while Nord Desprez and Redmond showed significantly negative effects.

The general combining ability effect for kernel weight in all plant densities was significant and positve for Nord Desprez, while Pullman Selection 1 revealed a significant negative estimate for the general combining ability effects. Redmond also exhibited good general combining ability in the six inch spacing.

In the case of tiller numer significantly greater positive general combining ability effect was obtained for Pullman Selection 1 in the six and 12 inch planting while in the solid seeding tiller number did not show any significant effects.

Spikelets per spike also revealed significant positive general combining ability effects for Selection 55-1744 in the spaced plantings while significantly negative effects were obtained in six and 12 inch spaced plants for Druchamp and Pullman Selection 1 respectively. Spikelets per spike in the solid planting did not show any significant differences.

When kernels per spikelet are considered none of the 12 inch spaced varieties revealed significant differences whereas Selection 55-1744 had significantly positive value in the six inch planting. In the solid seedings Pullman Selection 1, Panter and Redmond had significantly positive effects, while significantly negative values were obtained for Heines VII and Druchamp. Significant negative general combining ability effects were also revealed for plant height with Selection 55-1744 in all the plant densities. The spaced plants also had significantly positive effect for Panter.

Significant differences were detected for the variances associated with specific combining ability for all the variables measured in solid planting as can be noted in Table 4. In six inch spacing kernel weight and spikelets per spike had significant effects while in 12 inch planting yield, plant height, kernel weight and spikelets per spike showed significant specific combining ability effects. Estimation of effects of specific combining ability involving each F_2 mean along with standard error for each character are found in Tables 6, 7 and 8. Even though in the six and 12 inch spacing the analysis of variance had shown significant effects for specific combining ability, performances of the individual varieties and selections revealed no significant differences. In the solid seeding Pullman Selection 1 combined well with Redmond for kernels per spikelet and with Nord Desprez for yield; but not as well with Selection 55-1744 for plant height. In the case of kernels per spikelet the combination of Panter and Selection 55-1744 had significant positive effects.

Table 6. Estimates of specific combining ability effects for all characters measured from all possible F_2 crosses involving seven parents in solid seeding.

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_1	X_1	-.146	-.596	-.436	-.054	.892*	.344
	X_2	-.754	.800	.100	1.034	-1.430	.378
	X_3	-.200	-.310	-.268	-.068	.468	.374
	X_4	1.127	-.435	-.625	-.723	1.187	.529
	X_5	-.090	-.028	-.049	.254	-.046	-.058
	X_6	1.282	-1.464	.936	-.294	.736	-.200
P_2	X_1	.142	-.138	-.488	.134	.010	
	X_2	.046	-1.150	.490	.704	-.340	
	X_3	.140	-.110	-.348	.072	-.132	
	X_4	.917	-.522	-.385	-.087	-.333	
	X_5	-.158	-.018	-.098	.139	.076	
	X_6	1.380	.164	-1.996	-.916	1.564	
P_3	X_1	-.688	.500	-.270	-.440		
	X_2	2.286	1.870	-1.610	-.776		
	X_3	-.256	-.046	.376	-.414		
	X_4	-1.527	.461	.441	-.227		
	X_5	-.151	.489*	-.186	-.183		
	X_6	-4.514*	-1.450	1.190	2.470		
P_4	X_1	.124	.654	-.166			
	X_2	-1.370	-.266	.674			
	X_3	-.062	.348	.120			
	X_4	-.077	.401	.541			
	X_5	-.046	-.037	-.128			
	X_6	.206	.190	-1.660			
P_5	X_1	.282	.020				
	X_2	.696	-.350				
	X_3	.188	-.072				
	X_4	-.639	-.101				
	X_5	.605*	-.146				
	X_6	.806	1.720				

Table 6. (Cont.)

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_6	X_1	.332					
	X_2	-.904					
	X_3	.186					
	X_4	.201					
	X_5	-.161					
	X_6	.836					

S.E.	X_1	X_2	X_3	X_4	X_5	X_6
	.3975	2.1797	.2879	1.0951	.177	2.0158

P_1 = Nord Desprez
P_2 = Heines VII
P_3 = Pullman Selection 1
P_4 = Druchamp
P_5 = Panter
P_6 = Redmond
P_7 = Selection 55-1744

X_1 = grain yield
X_2 = kernel weight
X_3 = tiller number
X_4 = spikelets per spike
X_5 = kernels per spikelet
X_6 = plant height

Table 7. Estimates of specific combining ability effects for all characters measured from all possible F_2 crosses involving seven parents in six inch plant spacings.

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_1	X_1	.144	1.642	-1.498	-2.444	-.872	3.200
	X_2	2.672	.518	-1.254	-1.778	-1.496	1.334
	X_3	-.276	.350	-.056	-.830	.594	.298
	X_4	-.403	.103	-.303	.029	.241	-.669
	X_5	-.032	.119	-.142	.016	-.146	.181
	X_6	-.288	.984	.708	-.668	1.398	-2.138
P_2	X_1	.572	-.510	-3.150	-.446	.506	
	X_2	.518	-.436	-.588	-.812	-.020	
	X_3	-.302	-.056	-.282	.284	.138	
	X_4	.763	-.281	-.937	.115	.007	
	X_5	-.044	.056	-.116	-.049	-.031	
	X_6	2.092	1.194	-1.112	-.338	.298	
P_3	X_1	-.620	-1.172	2.458	-.308		
	X_2	-1.512	.584	.482	1.958		
	X_3	.564	-.416	-.016	-.890		
	X_4	-.547	.009	-.097	.385		
	X_5	.001	-.024	.229	-.031		
	X_6	-1.172	-1.100	-.746	1.318		
P_4	X_1	-.022	1.826	1.386			
	X_2	.106	-.778	1.300			
	X_3	.340	.766	.310			
	X_4	-.459	-.233	.161			
	X_5	.030	-.014	.045			
	X_6	.332	-1.336	.688			
P_5	X_1	1.254	-.458				
	X_2	-.920	.976				
	X_3	.174	-.150				
	X_4	.709	.465				
	X_5	.083	-.100				
	X_6	-.382	.840				

Table 7. (Cont.)

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_6	X_1	1.336					
	X_2	-.868					
	X_3	-.520					
	X_4	-.065					
	X_5	-.040					
	X_6	-.586					

S. E.	X_1	X_2	X_3	X_4	X_5	X_6
	3.501	2.3855	1.5142	.7101	.197	2.4273

P_1 = Nord Desprez
P_2 = Heines VII
P_3 = Pullman Selection 1
P_4 = Druchamp
P_5 = Panter
P_6 = Redmond
P_7 = Selection 55-1744

X_1 = grain yield
X_2 = kernel weight
X_3 = tiller number
X_4 = spikelets per spike
X_5 = kernels per spikelet
X_6 = plant height

Table 8. Estimates of specific combining ability effects for all characters measured from all possible F_2 crosses involving seven parents in 12 inch plant spacings.

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_1	X_1	-.096	-.038	-.122	-.139	-.346	.747
	X_2	.320	-2.326	-.050	.150	-.106	.166
	X_3	-.330	1.020	.030	-1.060	.790	1.130
	X_4	-.012	-.738	-.390	.056	.512	.564
	X_5	.002	-.021	-.040	.037	-.180	.198
	X_6	.242	.112	.130	-1.202	1.436	-.722
P_2	X_1	-.038	.015	-2.450	.058	-5.310	
	X_2	-.180	.874	-1.600	-.230	-.876	
	X_3	-.510	-.460	-.450	.730	-.450	
	X_4	.686	.010	-.162	-.296	-.810	
	X_5	-.073	.151	-.075	.006	-.211	
	X_6	1.610	-.250	.068	-.014	-.696	
P_3	X_1	.116	1.970	0.860	4.850		
	X_2	.740	.714	-1.410	.910		
	X_3	-.270	.140	.430	.940		
	X_4	-.866	.738	-.264	.682		
	X_5	.151	-.023	.178	.081		
	X_6	-1.802	.158	-.724	1.744		
P_4	X_1	-1.670	-2.010	-0.310			
	X_2	-2.214	-.090	1.446			
	X_3	.710	-.580	-.740			
	X_4	-.342	-.318	.210			
	X_5	-.056	-.040	-.032			
	X_6	-.220	-.430	.118			
P_5	X_1	.238	.081				
	X_2	1.046	.540				
	X_3	.620	.110				
	X_4	.412	.186				
	X_5	.005	-.039				
	X_6	.142	.382				

Table 8. (Cont.)

Parents	Variables	P_7	P_6	P_5	P_4	P_3	P_2
P_6	X_1	-.048					
	X_2	.260					
	X_3	-.220					
	X_4	.114					
	X_5	-.032					
	X_6	.042					

S. E.	X_1	X_2	X_3	X_4	X_5	X_6
	4.2625	2.2632	2.1264	.8916	.366	1.8207

P_1 = Nord Desprez
P_2 = Heines VII
P_3 = Pullman Selection 1
P_4 = Druchamp
P_5 = Panter
P_6 = Redmond
P_7 = Selection 55-1744

X_1 = grain yield
X_2 = kernel weight
X_3 = tiller number
X_4 = spikelets per spike
X_5 = kernels per spikelet
X_6 = plant height

Heritability

Narrow sense heritability estimates presented in Table 9 indicated that for yield a heritability percent of 4.8 was obtained in the solid planting while in 12 inch spacing the value was 8.1 percent. These estimates were low, especially, in comparison to the heritability estimate of 22.9 percent in six inch planting.

Table 9. Heritability estimates for yield and yield components in the solid, six and 12 inch spacings.

	Solid	6 Inch	12 Inch
Yield	.048	.229	.081
Kernel	.372	.456	.401
Tiller Number	.061	.336	.251
Spikelets/Spike	.158	.293	.326
Plant Height	.182	.376	.339
Kernels/Spikelet	.281	.284	.089

Heritability values of 37.2, 45.6 and 40.1 percents were obtained for kernel weight in solid, six and 12 inch spacing respectively.

In the case of tiller number a low value of 6.1 percent was observed for solid seeding while the spaced plantings had higher estimates of 33.6 and 25.1 percents. Spikelets per spike and plant height exhibited heritability percents of 15.8 and 18.2 respectively for the solid seeding which were about one-half of the estimates obtained in spaced plantings.

Kernels per spikelet revealed a different trend. The 12 inch planting had a value of 8.9 percent while the solid and six inch spacings showed estimates of 28 percent. Lower heritability estimates were observed for the solid seeded plants.

Correlations

The correlations coefficients for the F_2 phenotypic relationships given in Table 10, reveal that in 12 inch spacing, yield was positive and significantly associated with tiller number, spikelets per spike and kernels per spikelet. No association was noted for the correlations of kernel weight with yield as well as kernels per spikelet. A similar lack of association was also seen for kernels per spikelet with spikelets per spike and tiller number. Spikelets per spike had a positive correlation with kernel weight while tiller number showed a significant negative association with spikelets per spike and kernel weight.

Table 10. Phenotypic correlation coefficients among four character and yield involving the 21 F_2 crosses. (Solid, six and 12 inch spacings presented in the respective order in each cell.)

	Yield	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight
Yield	---	.0892 .6830** .5274**	.4154** .3266** .3595**	.0078 .5525** .5666**	.1244 -.2121 .0063
Tiller Number		---	.4463** -.1186 -.3134**	-.2688* .3001** .0015	.0211 -.4736** -.3153**
Spikelet/Spike			---	-.8272** .0876 .2027	.4825** .0106 .2437*
Kernels/Spikelet				---	-.3262** -.7530** -.0039

*Significant at 5 percent level.
**Significant at 1 percent level.

In the six inch spacing significant and positive associations, as seen in the 12 inch plantings, were also obtained for yield with tiller number, spikelets per spike and kernels per spikelet; while a significant negative relationship was found between kernel weight and tiller number. Tiller number was significantly related to kernels per spikelet and non-significant relationships were obtained for the association of spikelets per spike with tiller numbers and between kernels per spikelet and kernel weight.

The solid seedings reveal a lack of relationship for yield with tiller number and kernels per spikelet which was in contrast to the significant correlation coefficients obtained for the corresponding spaced plantings. The significant positive association of the spaced plants for yield with spikelets per spike and lack of any such relationship for the kernel weight and yield were also retained for the solid planting. In contrast to the negative association of kernel weight and tiller number in the spaced plantings, the solid seedings showed a non-significant relationship. Spikelets per spike had significant positive associations with tiller number and kernel weight. Significant negative correlations were revealed for kernels per spikelet with spikelets per spike, kernel weight and tiller number.

A comparison can be made between the phenotypic correlation coefficients presented in Table 10 with the corresponding genetic associations presented in Table 11. It was observed that in the spaced plantings most of the phenotypic associations were maintained in the genetic associations as well. Exception to this can be noted for the relationships of yield with kernel weight and of kernels per spikelet with spikelets per spike whereby the non-significant phenotypic association of the former changed to a negative value in the genetic correlations and the non-significant relationship of the latter showed a relatively higher magnitude of relationship. In the solid plantings the non-significant phenotypic association of kernel weight with yield and tiller number increased to a higher magnitude in genetic relationships. Similar changes were seen for the association of kernels per spikelet with yield whereby the non-significant phenotypic correlations changed to high negative relationship. The rest of the associations maintained their respective degrees of relationship.

Table 11. Genetic correlation coefficient values among four characters and yield involving the 21 F_2 crosses. (Solid, six and 12 inch spacing presented in the respective order in each cell.)

	Yield	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight
Yield	---	.0501 .7090 .4843	.5899 .3534 .3522	-.6778 .9745 1.0274	1.5803 -.7855 -.7932
Tiller Number		---	.1569 -.2979 -.6582	-.9900 .8119 .0214	.7379 -.8694 -.6314
Spikelets/Spike			---	-.9269 .4598 .4875	.8086 -.1894 -.1003
Kernels/Spikelet				---	-.3587 -.9860 -.9198

The parental phenotypic correlation coefficients in Table 12 reveal that in the 12 inch spacing only the association of kernels per spikelet with yield and the correlation of spikelets per spike with tiller number were related significantly, positive and negative respectively. In the case of six inch planting yield was significantly correlated to tiller number and kernels per spikelet. A significant negative association was noted for the correlation of tiller number with spikelets per spike and kernel weight as well as for the association of kernel weight with kernels per spikelet. For the solid seeding it was found that apart from the lack of association between kernels per spikelet with yield and tiller number, all the correlation coefficients between yield and its components as well as among the components themselves were significant and positive.

A comparison of the parental correlation coefficients presented in Table 12, with the corresponding genetic associations in Table 13 showed that the degree and nature of the phenotypic associations in the 12 inch planting have been maintained in the genetic relationships. A similar observation can be made for six inch planting where the phenotypic correlation coefficients have been retained in the genetic associations as well. In the solid seeding however, the relative magnitudes of the phenotypic and genetic correlations revealed some differences. The significant positive relationships of kernels per spikelet with spikelets per spike and kernel weight changed to significant negative association in the former and lack of relationship in the latter. The rest of the phenotypic and genetic associations maintain their relative magnitudes.

Table 12. Phenotypic correlation coefficient values among four characters and yield involving the seven parents. (Solid, six and 12 inch spacing presented in the respective order in each cell.)

	Yield	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight
Yield	---	.8831** .5575** .3246	.5782** .0113 .2385	.2226 .3985* .6938**	.7435** .1620 .3694
Tiller Number			.5183** -.6185** -.6160**	.1276 .3570 .2227	.5043** -.3986* -.3159
Spikelets/Spike			---	.6029** -.0857 .0636	.5283** .2713 -.0372
Kernels/Spikelet				---	.5699** -.8269** .2795

*Significant at 5 percent level.
**Significant at 1 percent level.

A comparison of the F_2 phenotypic correlation coefficients with the corresponding parental association reveal the following. The significant positive association of yield with tiller number and kernel weight in the solid seeding of the parents was not revealed in the F_2 correlations. Similarly significant positive relationship of kernel weight with tiller number was not observed in the F_2 progeny. However, lack of association obtained in the parents for the correlation of kernels per spikelet and tiller number changed to a significant negative association in the F_2 population. The other associations of the parents maintained their degree of relationship in the F_2.

Table 13. Genetic correlation coefficient values among four characters and yield involving the seven parents. (Solid, six and 12 inch spacing presented in the respective order in each cell.)

	Yield	Tiller Number	Spikelets/ Spike	Kernels/ Spikelet	Kernel Weight
Yield	---	.9109 .5805 .3188	.6069 -.0145 .2507	.2579 .4193 .8278	.8059 .1603 .3394
Tiller number		---	.5477 -.6876 -.7273	.2218 .4220 .3673	.6065 -.4253 -.3441
Spikelets/Spike			---	-.5870 -.0610 .1274	.6576 .2795 .2998
Kernels/Spikelet				---	-.0102 -.6858 -.0225

It was observed in the 12 inch planting that non-significant associations of yield with spikelets per spike and tiller number increased to significant positive values in the F_2. Similar change from non-significant to significant relationship in F_2 was noted for the correlation of kernel weight with tiller number and spikelets per spike. The association of kernel weight and tiller number changed from a non-significant correlation to a significant negative relationship. In the case of six inch spacing it can be noted that the lack of association exhibited for the parents between yield and spikelets per spike as well as the relationship of kernels per spikelet with tiller number changed to significant positive association in the F_2. However, the significant negative correlation coefficient of spikelets per spike and tiller number changed to non-significant relationship in the F_2.

Path - Coefficient Analysis

The path - coefficients for the F_2 phenotypic correlations given in Table 14 showed that in the 12 inch spacing, the significant correlation between yield and tiller number appear to be due to the direct effects while some negative influence was also exerted through spikelets per spike. Spikelets per spike also had considerable direct effect on yield and through tiller number a negative influence was noted. The positive significant association of yield with spikelets per spike was the direct influence of spikelets per spike on yield. The direct effect of kernel weight was low and so were the indirect influences via the other components.

In the six inch spacing the direct effect of the tiller number on grain yield was high, as was the case in 12 inch plantings. A positive influence was also exerted through kernels per spikelet while kernel weight had a negative effect. The significant value of the correlation coefficient between yield and spikelets per spike was mainly attributed to direct effects. Kernels per spikelet had a high direct influence on yield however, an indirect positive effect through tiller number and a negative influence through kernel weight was observed. The direct effect of kernel weight on yield was counter balanced by negative influence through tiller number and kernels per spikelet.

Table 14. Direct and indirect inter-relationships of factors influencing total yield of F_2 phenotypic correlations in solid, six and 12 inch spacings.

		Solid	6 Inch	12 Inch
Yield vs tiller number	-r	.0892	.6830	.5274
Direct effect	-b	-.3590	.8695	.7075
Indirect, via spikelets per spike		.8040	-.0400	-.1429
Indirect, via kernels per spikelet		-.3492	.2840	.0007
Indirect, via kernel weight		.0066	-.4305	-.0379
Yield vs spikelets per spike	-r	.4154	.3266	.3595
Direct effect	-b	1.8015	.3371	.4560
Indirect, via tiller number		-.1602	-.1031	-.2217
Indirect, via kernels per spikelet		-1.0747	.0829	.0959
Indirect, via kernel weight		-.1512	.0095	.0293
Yield vs kernels per spikelet	-r	.0078	.5525	.5666
Direct effect	-b	1.2992	.9465	.4736
Indirect, via tiller number		.0964	.2609	.0011
Indirect, via spikelets per spike		-1.4902	.0295	.0924
Indirect, via kernel weight		.1022	-.6844	-.0005
Yield vs kernel weight	-r	.1244	.2121	.0063
Direct effect	-b	-.3134	.9090	.1201
Indirect, via tiller number		-.0076	-.4118	-.2231
Indirect, via spikelets per spike		.8692	.0035	.1111
Indirect, via kernels per spikelet		-.4238	-.7127	-.0018
Residual effect		.3125	-.0341	.1939

The solid plantings revealed that the lack of any association between yield and tiller number was due to negative direct effect as well as indirect influence via kernels per spikelet to counter balance the positive influence through spikelets per spike. The significant association of yield with spikelets per spike was attributable to high direct positive effect while the indirect influences of spikelets per spike involving the other components were negative. The lack of association between yield and kernels per spikelet was due to the negation of the direct effect of kernels per spikelet by the indirect negative influence of spikelets per spike. The direct effect of kernel weight on yield was negative and the indirect influence through kernels per spikelet was also negative while through spikelets per spike a positive effect was revealed.

From these results it would appear that all the direct effects of the spaced plantings were positive while in the solid seeding tiller number and kernel weight had a negative influence on yield. Furthermore,it can be seen that the indirect influence of the components was small in the 12 inch spacing. In six inch planting kernels per spikelet had some indirect influence for the association of tillers with yield. However, a negative influence via kernels per spikelet was obtained for the association of kernel weight and yield. Indirect effects of kernel weight was high and negative for the relationship of yield with tiller number and kernels per spikelet. In the solid seeding spikelets per spike as well as kernels per spike exerted indirect influences for all the associations, while kernel weight did not carry any pronounced indirect effect.

In contrast to the phenotypic associations the genotypic effects (Table 15) in 12 inch spacing showed that the direct effects were negative for tiller number, kernels per spikelet and kernel weight; while spikelets per spike also had little direct influence. In the six inch planting all the direct effects remained positive, whereas in solid seeding the negative effects of tiller number and kernel weight in the phenotypic association were positive. The lack of any indirect effect in the 12 inch spacing was maintained in the genetic associations as well. Tiller number and kernels per spikelet showed some indirect influences in comparison to phenotypic relationships, while kernel weight did have an indirect effect on yield. In the six inch spacing almost all the components exhibited indirect effect which was not evident in the phenotypic relationships where spikelets per spike did not have indirect influence on yield. Solid seeding revealed that kernel weight carried no indirect effect on yield while other components exerted considerable influence.

For the parents it was observed that in the phenotypic correlations (Table 16) the direct effects of all the components on yield was positive for six and 12 inch spacing. In solid seeding the direct effects were relatively lower in magnitude to the

Table 15. Direct and indirect inter-relationships of factors influencing total yield of F_2 genetic correlations in solid, six and 12 inch spacings.

		Solid	6 Inch	12 Inch
Yield vs tiller number	-r	.0501	.7090	.4843
Direct effect	-b	.9701	2.1734	-.6840
Indirect, via spikelets per spike		1.0819	-.2988	-.0795
Indirect, via kernels per spikelet		-2.0529	.7227	-.0184
Indirect, via kernel weight		.0517	-1.8883	1.2666
Yield vs spikelets per spike	-r	.5899	.3534	.3522
Direct effect	-b	1.9011	1.0031	.1208
Indirect, via tiller number		.5521	-.6475	.4502
Indirect, via kernels per spikelet		-1.9199	.4093	-.4202
Indirect, via kernel weight		.0565	-.4114	.2012
Yield vs kernels per spikelet	-r	-.6778	.9745	1.0274
Direct effect	-b	2.0714	.8903	-.8621
Indirect, via tiller number		-.9615	1.7646	-.0146
Indirect, via spikelets per spike		-1.7621	.4612	.0588
Indirect, via kernel weight		.0251	-2.1416	1.8453
Yield vs kernel weight	-r	1.5803	-.7855	-.7932
Direct effect	-b	.0700	2.1720	-2.0062
Indirect, via tiller number		.7158	-1.8896	.4319
Indirect, via spikelets per spike		1.5339	-.1900	-.0121
Indirect, via kernels per spikelet		-.7430	-.8778	.7930
Residual effect		1.1190	-.0569	.4168

Table 16. Direct and indirect inter-relationships of factors influencing total yield of parental phenotypic correlations in solid, six and 12 inch spacings.

		Solid	6 Inch	12 Inch
Yield vs tiller number	-r	.8831	.5575	.3246
Direct effect	-b	.5852	.7932	1.0295
Indirect, via spikelets per spike		.0754	-.1057	-.5442
Indirect, via kernels per spikelet		-.0283	.5499	.0495
Indirect, via kernel weight		.2512	-.6800	-.2102
Yield vs spikelets per spike	-r	.5782	.0113	.2385
Direct effect	-b	.1456	.1710	.8834
Indirect, via tiller number		.3033	-.4905	-.6342
Indirect, via kernels per spikelet		-.1335	-.1320	.0141
Indirect, via kernel weight		.2631	.4628	-.0248
Yield vs kernels per spikelet	-r	.2226	.3985	.6938
Direct effect	-b	-.2214	1.5402	.2223
Indirect, via tiller number		.0747	.2832	.2293
Indirect, via spikelets per spike		.0878	-.0146	.0562
Indirect, via kernel weight		.2839	-1.4106	.1860
Yield vs kernel weight	-r	.7435	.1626	.3694
Direct effect	-b	.4982	1.7060	.6655
Indirect, via tiller number		.2951	-.3162	-.3252
Indirect, via spikelets per spike		.0768	.0464	-.0328
Indirect, via kernels per spikelet		.1262	-1.2736	.0621
Residual effect		.0779	-.3343	.0549

corresponding associations in spaced plantings. Moreoever, kernels per spikelet had a negative direct influence on yield. The indirect effect of spikelets per spike on all the associations had been small in almost all the plant densities except in one case in the 12 inch spacing where it had an indirect influence on yield for the relationship of tiller number with yield. The indirect effect of kernels per spikelet was insignificant in the 12 inch spacing while in six inch planting it had effects both in positive and negative directions. However, in solid seeding some positive effect is observed. In the 12 inch planting kernel weight had a small indirect influence, while a considerable effect is discernible in six inch spacing. Some influence is also seen in solid planting. The indirect effects through tiller number is the same for six and 12 inch spacing whereas in solid planting the influence via tiller number is revealed for the association of yield with spikelet per spike and kernel weight as presented in Table 17.

The parental genetic associations revealed that all the components have a direct positive effect on yield for all the spacings. The indirect effects through the spikelets per spike is more pronounced in the solid rather than in the spaced planting. Kernels per spikelet did not reveal any definite trend in any of the spacings, while kernel weight had an appreciable indirect influence in six inch planting. The indirect effects of the solid plantings was low in

Table 17. Direct and indirect inter-relationships of factors influencing total yield of parental genetic correlations in solid, six and 12 inch spacings.

		Solid	6 Inch	12 Inch
Yield vs tiller number	-r	.9109	.5815	.3188
Direct effect	-b	.3350	1.0261	.6466
Indirect, via spikelets per spike		.3258	-.3303	-.3824
Indirect, via kernels per spikelet		.1185	.2652	.1993
Indirect, via kernel weight		.1318	-.3800	-.1447
Yield vs spikelets per spike	-r	.6069	-.0145	.2507
Direct effect	-b	.5950	.4804	.5258
Indirect, via tiller number		.1835	-.7055	-.4703
Indirect, via kernels per spikelet		-.3138	-.0383	.0691
Indirect, via kernel weight		.1430	.2497	.1261
Yield vs kernels per spikelet	-r	.2579	.4193	.8278
Direct effect	-b	.5346	.6284	.5425
Indirect, via tiller number		.0743	.4330	.2375
Indirect, via spikelets per spike		-.3492	-.0293	.0670
Indirect, via kernel weight		-.0022	-.6128	-.0094
Yield vs kernel weight	-r	.8059	.1603	.3394
Direct effect	-b	.2174	.8937	.4205
Indirect, via tiller number		.2031	-.4364	-.2225
Indirect, via spikelets per spike		.3912	.1342	.1585
Indirect, via kernels per spikelet		-.0055	-.4310	-.1022
Residual effect		.0205	.0035	.0703

comparison to 12 inch spaced plants.

A comparison of the F_2 phenotypic association with the corresponding parental values revealed that the direct effect of all the components in six and 12 inch spacings did not change appreciably from the parents to the F_2 generation. In the solid planting however, direct effects of tiller number and kernel weight changed from positive value in the parental generation to negative value in the F_2. Furthermore low effects of spikelets per spike and negative effects kernels per spikelet, changed to high positive influence in the F_2 progeny.

DISCUSSION

If the breeder is to make progress, he must be vitally concerned with the amount of variability present for the various agronomic characters. For the success of selecting a superior genotype, the breeder must handle large enough populations which include the potentialities for all the desirable characters which influence yield. The genetic component of variability, quite distinct from the non-heritable environmental component, is of primary importance to the breeder. Thus in breeding for any complex inherited character like yield, which is highly susceptible to fluctuations due to environmental factors, it becomes necessary not only to determine its various components but also to measure the extent to which each of these components is heritable and to determine the predominate type of gene action involved.

Wheat is grown commercially in competitive conditions (solid planting), but most genetic studies and selections are conducted in non-competitive conditions (spaced plantings) in the early generations, where large numbers of progeny necessitate early selection. It is therefore, important to know if the information gained in the genetic studies is meaningful in predicting those progeny which will give maximum yield when grown under commercial production.

Yield is a complex character which is quantitatively inherited and influenced greatly by the environment. The expression of yield is further influenced by its component parts; 1) weight of kernel 2) number of kernels per spikelet 3) number of spikelets per spike, and 4) number of spikes per plant. The seven parents used in this study were chosen because they differed in terms of one or more of these components. Considering that these components influence yield, an increase in any one of the components would result in an increase in yield, provided there is no corresponding decrease in other components. Such a decrease could result if each of the components were predominately controlled by different types of gene action or if a negative association existed between any of the components because of some biological limitations. The biological limitations could be competition among the components of yield for the total amount of metabolic substrates produced by the plants, then conditions which favor the development of one component could have an adverse effect on the other component. It was the purpose of this study to determine the influence of the environment on gene action estimates in seven widely divergent varieties of winter wheat and their F_2 crosses. Another objective of this investigation was to measure the relationship between the yield and its components. Path coefficient analysis was also employed to obtain a better insight into the direct and indirect influences of the components of yield on yield.

The general combining ability for yield revealed that the phenotypic expression of the genetic component of the total variance changed under different plant densities. The plants in six inch spacing showed a higher value of the additive gene action estimates than the 12 inch and solid seeded plants. The heritability estimates were also higher for the plants in the six inch planting. Specific combining ability effect was not noted in spaced plants while there was evidence for specific combining ability in solid seeding in the cross of Nord Desprez and Pullman Selection 1. Evidently the general combining ability and specific combining ability as well as the heritability estimates in the three plant spacing showed that yield is interacting differently to the environmental fluctuations. It would appear that the genetic studies based on spaced plantings are not valid estimates for solid seeded plants. It is therefore important that the selection work of breeding material in the early generations should be done in the same conditions (solid seeding) in which they will be evaluated in the later generations.

Kernel weight and plant height were quite stable in their genetic expression in all the plant densities. The general combining ability estimates indicate a large portion of the genetic variance was made up of additive gene action, which behave quite consistently in different plant densities. Heritability estimates also revealed a large portion of additive effects in all the plant densities. These high additive gene action estimates obtained from general combining ability and heritability values conform with the findings of Kronstad and Foote (1964). It could be inferred from these observations that kernel weight and plant height were governed by additive gene effects, had moderate heritability estimates and were independent of interplant competition. These findings are further strengthened by the lack of any significant specific combining ability effects for kernel weight, while for plant height a negative value for specific combining was evident only in one cross involving Pullman Selection 1 and Selection 55-1744. Selection 55-1744 had consistently shown a negative effect for the general combining ability in all the plant spacings. Because of the increased interest in dwarf wheats, due to their being stiff strawed, these results are interesting. It would seem possible to select individual plants for short heights while maintaining the yielding potential. Similar significant general combining ability effects were evident for tiller number and spikelets per spike in the six and 12 inch plantings, while in solid seeding no significant general combining ability effect was evident for any of the parents. Though the space planted F_2 population agreed with the results of the spaced F_1 plants of Kronstad and Foote (1964), the estimates of solid seeded plants behaved differently. Heritability values were in line with the results obtained for general combining ability. It would appear that for the characters tiller number and spikelets per spike, the genetic studies based on spaced plants are invalid for predicting the effects in the solid plantings. This points out that due care must be taken to select the breeding material under proper competitive conditions for a successful breeding program.

Kernels per spikelet exhibited a considerable genotype-environment interaction. It was evident that with the increased density of the plants the estimates of the additive expression of the genes increased. As the heritability estimate were also low in the 12 inch spaced planting it may be safe to conclude that with the increased inter-plant competition the genotypic expression behaves differently because of the interaction of the genotype with the environment. So the estimates of solid seeded plants cannot be predicted from 12 inch spaced plants. Similar genotype-environment interactions were also evident for the specific combining ability.

The correlation coefficients also reveal a significant amount of interaction involving the genotypes with the environment. The correlated associations of yield with its component parts as well as among the components themselves in many cases behaved differently, with the increase in plant densities. It can be noted that the correlation coefficients in the spaced planting showed that tiller number, spikelets per spike, and kernels per spikelet are significantly and positively related to yield. Kernel weight seemed to have no effect on yield. However, in solid seeding only the spikelets per spike was significantly associated with yield. It would appear therefore, that the relationships among traits changed with the change in plant density. So it may be safe to say that the correlation coefficient studies based on spaced planting may not be sound for solid seeded plants.

A further comparison of these correlation coefficients into the direct and indirect influences reveal that correlation coefficients can be misleading as far as telling the true nature of the association existing between the various traits. In the solid planting, the direct influence of kernels per spikelet on yield was high, yet the correlation value was insignificant. Based on correlated associations it might have been concluded that kernels per spikelet had no effect on yield but the path coefficient analysis revealed that this lack of association was due to the negative relationship between kernels per spikelet and spikelets per spike. In both these traits the direct effect is high but because of indirect negative effects through each of these characters the degree of total relationship is reduced. In the solid plantings these two traits namely, kernels per spikelet and spikelets per spike seem to be important attributes for obtaining higher yielding genotypes. Even though these two components of yield were negatively correlated yet by reaching a compromise in the desired level of these two traits high yielding potential can be achieved. These two components accounted for 76 percent of the total variability. Tiller number and kernel weight, in solid seeding, did not show any significant contribution towards higher yielding ability. However, in space plantings, in addition to kernels per spikelet and spikelets per spike, tiller number also showed a significant relationship with yield while kernel weight was again negligible in its association with yield. This was in conformity with the findings reported by Quinsberry (1926). The effect of the genotype-environment interaction on the relationship of yield with the components of yield, per se, and the association among the components themselves was quite evident.

Another interesting point worthy of note was evident in the phenotypic and genetic correlation coefficients as well as in the path coefficients analysis of the F_2 population and the parents. There was much less conformity between the phenotypic and genetic effects of the F_2 population than in the parents. This would lead to the conclusion that the parental types, which have reached a high degree of stability in a limited environment were less prone to environmental influences than were the plants in the F_2 population which were mostly segregating progenies. The mean values were used for these populations in which case each F_2 individual might have behaved differently to the environment causing a lack of consistency in the results for phenotypic and genetic expressions.

Both the path-coefficient and combining ability analysis showed that kernel number was an important component of yield. Similar results were also reported by McNeal (1960) and Kronstad and Foote (1963). However, the path-coefficient analysis indicated that spikelets per spike was also a very important component of yield which agrees with the findings of Quinsberry (1926).

The results obtained indicate that separate breeding procedures may be useful for several components of yield with the final step being the synthesis of the desired levels of each component into one variety. The large amount of additive gene effects for the estimates of kernels per spikelet and grain weight in solid planting can be desirably used by the breeder. Negative correlation coefficients were obtained for kernels per spikelet with kernel weight, spikelets per spike and tiller number. If a biological limitation is present, this may be the reason why yield in solid planting did not show additive gene effects even though the grain weight, kernels per spikelet and plant height had considerable genetic variance. In such a case a synthesis of the desired level of each component will be helpful.

SUMMARY

The major objective of this study was to determine the influence of plant densities on the estimates of gene action for yield and its component parts; namely tiller number, spikelets per spike, kernels per spikelet, kernel weight and plant height. Another purpose of this investigation was to determine the nature of the relationship between the components of yield and yield in spaced plant culture and solid plantings.

To accomplish these objectives, seven widely divergent winter wheat varieties were crossed in all possible combinations. The 21 F_2 crosses as well as parents were space planted six and 12 inches and solid seeded in four replications. Estimates of gene action of yield and its component parts were obtained by combining ability analysis and heritability estimates. Correlation and path-coefficient analysis were employed to study the direct and indirect association of these characters.

From the results of this study, the following conclusions can be made:

1. Additive gene action could not be detected for yield in 12 inch planting and solid seeding, while some additive gene action was noted in the six inch spacing.
2. Kernel weight had significant additive gene action estimates

in all the plant densities.

3. Tiller number and spikelets per spike showed additive gene effects in spaced plantings, while there was no evidence of additive gene effects in the solid seeding.
4. Kernels per spikelet did not show additive gene effects in 12 inch spacing whereas in the six inch spacing and solid seeded plants additive effects were indicated.
5. General combining ability effects for plant height were low in solid seeding and higher in spaced plantings.
6. Low heritability estimates for yield in the solid and 12 inch planting was obtained. In the six inch spacing the heritability value was 22.9 percent.
7. Kernel weight had a high heritability estimate in all the plant densities.
8. Tiller number, spikelets per spike and plant height had heritability percentages of 25.1, 32.6 and 33.9 respectively in 12 inch planting while in six inch spacing the heritability estimates were 33.6, 29.3, 37.6 percents respectively. In solid seeding the estimates were approximately half of those in spaced plantings.
9. Kernels per spikelet had a low heritability estimate of 8.9 percent in the 12 inch spacing while in six inch spacing and solid plantings the estimates were 28.4 and 28.1 percent

respectively.

10. In the spaced plantings, tiller number, spikelets per spike, and kernels per spikelet were significant and positively correlated with yield. In the solid seeding only spikelets per spike was significantly related to yield.

11. Path-coefficient analysis revealed that kernels per spikelet and kernel number were the most important components of yield.

12. The genotype-environment interaction as noted from the fluctuating behavior of the genotypes under the three plant densities was evident for yield, number of tillers, spikelets per spike, and kernels per spikelet. Therefore, the genetic studies based on spaced plantings were not valid for predicting the performance of the above mentioned components in the solid seeded plants. Kernel weight and plant height however behaved alike in all the plant densities.

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APPENDIX

Appendix Table 1. Pedigrees and description of the seven parental winter wheat lines.

Parent	Pedigree	Grain	Straw	Yield	Origin
Nord Desprez	Vilmorin 27 x Joniquois	Red	Short, Stiff	High	Europe
Heines VII	Svalof Kronen x (Ble 205 x Vilmorin 27)	Red	Medium, Stiff	High	Europe
Selection 1	[(Norin 10 x Brevor) x (Orfed x Brevor) x Burt]	White	Short, Stiff	High	United States
Druchamp	Unknown	White	Medium, Stiff	High	Europe
Panter	Pantser III x Alther	Red	Medium, Stiff	High	Europe
Selection 55-1744	Norin 10 x Staring	Red	Short, Stiff	High	United States
Redmond	Unknown	Red	Medium, Moderate	Medium	Europe