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Title: COMBINING ABILITY AND ASSOCIATION OF AGRONOMIC TRAITS INVOLVING THREE SOURCES OF DWARFISM IN WHEAT (TRITICUM AESTIVUM, L. EM THELL.)

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Three genetically different dwarf cultivars of spring wheat were evaluated as potential sources of short stature to use in a wheat improvement program. The study involved a five parent diallel cross which included a semidwarf, a standard height and three dwarf cultivars. The genetic sources of dwarfism included a Norin 10 derivative named Vicam 71, a derived line from Tom Thumb called Tordo, and Olesen dwarf. Experimental material consisted of parental lines, F_1, F_2, and both backcrosses to the parents space planted in a randomized block design. The agronomic characters measured on an individual plant basis were: (1) plant height, (2) days to heading, (3) number of tillers, (4) number of spikelets per spike, (5) head length, (6) days to maturity, (7) grain yield, (8) harvest index, (9) kernel weight, (10) number of kernels per spikelet, (11) rachis internode length, (12) grain filling period and, (13) head grain weight.

Estimates of gene action were determined by heterosis, heterobeltiosis, broad and narrow sense heritabilities and combining ability analyses. Associations among traits were estimated by phenotypic, environmental, and genotypic correlations as well as path-coefficient analysis for grain yield and eight of the variables.

There were significant differences among the parental lines, their crosses, and generations for all traits measured. Either partial dominance for tallness or no dominance was manifested for those crosses involving the dwarf cultivars Vicam 71 and Olesen. Tordo, when crossed to taller wheats showed dominance for short stature. All three genetic sources of dwarfism and their resulting progenies manifested desirable agronomic characteristics. Vicam 71 was a good parent in terms of grain yield and number of tillers per plant. Tordo was the best source for increasing the number of spikelets per spike, kernel weight and head grain weight. Olesen was a good progenitor for increasing number of kernels per spikelet. All three dwarf cultivars displayed some advantage(s) over the other two and all could be used to breed short statured wheats with a possibility of success. Plant height did not appear to have a direct effect on plant grain yield in any of the 10 crosses.

With the exception of number of tillers per plant and grain yield, a major proportion of the phenotypic variability observed for all characters studied was due to genetic factors. A large portion of the total genetic variability associated with days to heading, maturity, height, rachis internode, spikelet number, kernels per spikelet, kernel weight, and harvest index was mainly a result of additive gene action. Both additive and non-additive genetic effects were involved in the expression of grain filling period and head weight. The non-additive portion of the genetic variance associated with tiller number and grain yield per plant was relatively large when compared with the additive portion. Therefore, selection for increased expression of tillers and yield should be delayed until the F_4 or later generations where a large degree of homozygosity has been obtained.

The genetic correlations for individual crosses indicated that only a few of the traits studied were associated in the same manner in most or all the 10 hybridizations. High positive genetic correlations were found between plant grain yield vs tiller number and kernels per spikelet, tiller number vs days to maturity, kernels per spikelet vs head grain weight, plant height vs head weight, and head length vs rachis internode length. High negative genetic correlations were found between kernel weight vs days to maturity, plant height vs harvest index, and days to heading vs grain filling period. Most correlations among agronomic traits were different in value and/or sign from one cross to another suggesting different gene associations in the parental cultivars. Genetic correlations between components of yield showed this type of inconsistency. Therefore, grain yield could be increased by a combined increase of more than one component of yield without compensatory oscillation among them because tiller number, spikelet number, kernels per spikelet and kernel weight were often not correlated between one another and sometimes were positively correlated. Path-coefficients analysis indicated that number of tiller per plant had a high direct effect on grain yield in all crosses. With the exception of two crosses, indirect effects of this trait were negligible. In the latter two crosses tiller number had a high negative indirect effect on plant grain yield via head grain weight. Kernels per spikelet and kernel weight had no direct effects on grain yield but their indirect effects via head weight were positive and significant.

Large amounts of additive gene action were observed in the expression of plant height. This trait was also highly negatively correlated with harvest index; therefore, phenotypic selection for restricted plant height would be useful in obtaining lines with high grain to straw ratios.

In general, crosses that showed high specific combining ability effects involved parents with low general combining ability. However, there were some exceptions to this rule. Crosses of high x high and high x low general combiners presented high specific combining ability effects, suggesting that some additive gene action may be involved in the superior performance of these combinations. Also the

F_2 generation did not differ from the F_1 in assessing general combining ability.

A wheat breeder should be aware of those genetic associations between agronomic traits that could be used to select superior cultivars. However, the genetic correlations in this study suggested that each cross represented a different set of gene associations depending upon the parents involved. If some progress is to be made in using the genetic variability available in the crop, the breeder should not try to select exactly the same type of plant from every cross. Every hybridization is potentially a source of better lines if they are well planned and the reasons they were made are remembered during selection. It is very important to realize what are the contributions of each parental line in a cross and what are the most important trait associations present in each parent. Superior genotypes could be selected on this basis while preserving the natural genetic variability existing in the crop.

Combining Ability and Associations of Agronomic Traits Involving Three Sources of Dwarfism in Wheat (*Triticum aestivum*, L. em Thell)

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WITH LOVE TO:

Raquel, my wife
Francisco, my son
Emilio and Leonila, my parents
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INTRODUCTION

Plant height is one of the most important agronomic traits in wheat. The impact of the semidwarf growth habit to wheat production is one of the major accomplishments in agriculture this century. Just recently even shorter wheats, the so called "triple dwarfs," have been released as commercial varieties in Mexico, India, and Pakistan. These wheats may allow better utilization of nitrogen fertilizer and more efficient moisture management than the semidwarf varieties first released to the farmer just a decade ago. Short statured wheats have spread rather rapidly in irrigated and high rainfall areas in developed and lesser developed countries. By 1970, in India alone, more than 10 million ha of wheat were planted with semidwarf varieties, most of them sister selections of one cross made in Mexico called 8156. Large areas of Bezostaya in the Soviet Union and Eastern Europe, Scout in the central plains of the United States, Blueboy in the southereastern part of the United States, Gaines in the Pacific Northwest, plus a few other varieties in other wheat producing countries of the world account for several additional million ha of short straw wheats. All these varieties are Norin 10 derivaties. The widespread acceptance and use of semidwarf wheats are both encouraging and dangerous. Their growth habit and required management practices make them a target for foliar diseases. Because large areas are planted to one variety or a few varieties all having a common genetic background, the genetic vulnerability of the crop is greatly increased. The semidwarf habit of growth is here to stay, but alternative genetic sources will have to be developed in order to broaden the genetic basis of the wheat crop. Most of the information on new sources of short statured wheats has been limited to genetic studies on number of genes involved in the expression of plant height and very often only one genetic source of dwarfism was used. Genetic studies are a source of valuable information, but the wheat breeder is also selecting for several other agronomic traits at one time. Therefore, an understanding of the type of gene action involved in the expression of the different agronomic traits under consideration at selection time is very important. It is also essential to know the genetic associations existing among these traits for a successful utilization of the short stature growth habit from each of the alternate genetic sources.

The objectives of the present study were: 1) to evaluate three genetically different dwarf cultivars as potential sources of short straw when crossed with a semidwarf and a tall standard variety; 2) to compare their dominant effects in the F_1 and F_2 generations; 3) to evaluate the type of gene action involved in the expression of plant height and several other agronomic traits in the parental cultivar and in the crosses from a five parent diallel; 4) to study genetic and phenotypic correlations between several agronomic traits in each of the three genetic sources for dwarfism; and 5) to assess the advantages and disadvantages, if any, of the different sources of dwarfism for a more efficient utilization in a wheat improvement program.

LITERATURE REVIEW

Semidwarf Wheats

The term semidwarf wheat has been used to refer to the growth habit of wheats derived from the Japanese variety Norin 10. These wheat cultivars then become distinguishable from the grass dwarf types reported in the literature as abnormal genotypes (Farrel, 1898; Ficks and Qualset, 1973a). Norin 10, a Japanese variety, was released in 1935 from a selection of the cross Turkey Red x Fultz-Daruma. Other sources of dwarfing wheats have been used but their success has not been as dramatic as with Norin 10. Dwarf cultivars available are: Seu Seun 27 and Suwon 92 from Korea (Reitz and Salmon, 1968); several Italian varieties of the Strampelli series which were derived from crosses between European varieties and unknown Japanese cultivars with short culms (Borojevic, 1971); Tom Thumb, a very short stiff-strawed wheat originally from Tibet; and Olesen dwarf, a complex cross between Pitic "sib" with a dwarf cultivar of unknown origin found in Rhodesia and with an additional cross to a Mara derivative (CIMMYT, 1966-67 report).

The need for short strawed varieties which do not lodge under high nitrogen fertilization and high soil moisture was stressed nearly two decades ago (Vogel et al., 1956; Borlaug, 1958). Vogel and co-workers mentioned selections of Norin 10 x Brevor crosses which were 60 to 80 cm tall and under experimental conditions yielded better than Brevor, a relatively short strawed variety of about 120 cm tall. They concluded that semidwarf growth habit represented an excellent opportunity for the breeding of wheats better suited to highly productive soils (Vogel et al., 1956).

The first semidwarf variety, a soft white winter wheat named after the late Professor Gaines of Washington State University, was released in 1961. This variety revolutionized wheat production in the Western Region of the United States (Frey, 1970). Other breeding programs were also interested in the potential of semidwarf wheats, and as a result other commercial semidwarf wheat cultivars were commercially released. In 1962 Pitic 62 and Penjamo 62, both Norin 10 derivatives, were released in Mexico and subsequently cultivated in many parts of the world. By 1968 there were about 6 to 7.5 million ha of several Norin 10 derivatives seeded as commercial varieties around the world (Borlaug, 1968; Reitz and Salmon, 1968).

The initial success of the semidwarf varieties stimulated breeders all over the world to incorporate this habit of growth into their breeding programs. Several new semidwarf wheat varieties were released as a consequence and one of the most outstanding was the Russian variety Bezostaya. To date Bezostaya is the widest grown winter wheat variety in the world. The genetic source of the short stature trait in this variety was the Japanese cultivar

Yakogomugi (Lukyanenko, 1966). There were also reports that short wheat cultivars outyielded the standard check varieties under irrigation and under high rainfall conditions, but under dryland conditions they produced less than or equalled the check varieties (Porter _et al._, 1964).

The association of other agronomic characteristics became apparent with the incorporation of short culms into the new wheats. These characteristics have been the subject of study by several workers in order to establish criteria for selection. The most efficient selection in terms of yield were combinations of high tillering capacity, early spring recovery for fall planted wheat, high lodging and shattering resistance, medium semidwarf plant height, medium culm diameter and head size, and small to medium length and width of leaf (Vogel _et al._, 1963).

Superiority of yield in semidwarf varieties when compared with tall standard varieties is due to more kernels per spikelet and more spikelets per spike (Johnson _et al._, 1966). Some semidwarf varieties have a test weight as high as the tall varieties (McNeal _et al._, 1960).

Synchronization of tillering in semidwarf wheat varieties may account for the lower rate of mortality in later formed tillers. In the tall spring wheat variety NP 798, mortality in later formed tillers was twice as great as in the semidwarf cultivar Sonora 63 (Singh _et al._, 1972).

In general, tall wheat varieties spend large amounts of nutrients in stem development, while short varieties achieve a more efficient distribution of assimilates between the grain and the straw (Borojevic, 1971). As a result of this, short varieties produce more spikes per plant, more kernels per spike, and more spikelets per spike, and also have longer heads (Virk and Khera, 1972).

The genetics involving the inheritance of the short straw characteristic in semidwarf wheats has received considerable attention. The number of genetic factors governing the expression of plant height in the Japanese variety Norin 10 is believed to be two major independent genes (Allan et al., 1968; Briggle and Vogel, 1968; Bhatt, 1972), which behave as partially dominant for tallness (Romero and Frey, 1973). The possibility of three factors being involved in the inheritance of plant height in Norin 10 has also been proposed. Two of this alleles have twice as much penetrance as the third allele, and all three genes involved have a cumulative effect (Romero and Frey, 1973).

Other genetic studies have shown that major genes for short culm in Norin 10 derivatives are the same for those found in the Korean varieties Suwon 92 and Seu Seun 27; the two genes have been identified as Sd_1 and Sd_2. These two genes produce very similar effects on the culm length phenotype when occurring singly. They are positively associated with agronomic traits such as high kernel weight, seedling vigor and yield; however, Sd_1 seems to be better adapted to a wide range of environmental conditions whereas Sd_2 is adapted to specific environmental or management conditions (Allan and Pritchett, 1973).

There are some indications that with Olesen dwarf, the mechanism of inheritance of short stem is different from Norin 10; in addition to the two major recessive genes contained in Norin 10, Olesen dwarf also carries a partially dominant gene for shorter culm length (Ficks and Qualset, 1973b). However, there is evidence that two major genes, each partially dominant for short stem, are also involved in the inheritance of plant height in the Olesen dwarf wheat cultivar (Hoff et al., 1973). Another hypothesis is that Olesen carries two partially dominant genes for short straw length with one of the genes exerting a greater effect in reducing plant height. The two genes together have a cumulative effect (Anand and Aulakh, 1971).

In Tom Thumb, another dwarfing source, the genetic mechanism may also be dominant in nature. The F_1's resulting of crosses made between Tom Thumb and several Norin 10 derivatives have been reported to be closer to the shorter parent in height, indicating partial dominance (Plech, 1968). Using crosses between the aneuploid series of two standard winter wheat varieties and Tom Thumb the chromosome bearing the genetic mechanism for short culm length has been identified as chromosome 4A. The gene present in Tom

Thumb showed the same expression for height in the heterozygous or hemizygous condition which indicated that the genetic mechanism of plant height was controlled by a single partially dominant height-reducing gene (Morris et al., 1972).

The suggested genetic mechanism involved in the inheritance of the semidwarf growth habit coming from Norin 10 and its derivatives is not consistent with respect to the number of genes involved. Four main theories have been proposed to explain the inheritance of plant height in semidwarf wheats: 1) one major gene and several minor genes (Powel and Schlehuber, 1967_; 2) two major genes (Allan and Vogel, 1963; 1964) with the possibility that minor modifying culm length genes can affect the height of short selections (Allan et al., 1968); 3) three or more genes (Johnson, Schmidt and Mekasha, 1966); and 4) three major genes with additive effects, one with a smaller effect and the possibility of several minor genes (Romero and Frey, 1972).

Reduced plant height has been of tremendous importance in increasing wheat yields. In short strawed varieties the problem of lodging has been reduced, thus making possible the application of high levels of nitrogen fertilizer (Athwal, 1971). In addition, semidwarf wheats also have more fertile florets than the tall standard varieties and as a consequence higher grain to straw ratios are obtained; another reason for the high harvest index in semidwarf varieties is a large number of kernels per head and more kernels per spikelet (Donald, 1968). The larger number of kernels per head and per spikelet may be attributed to the reduced competition by the stems for carbohydrates during the ear primordia development (Wareing, 1970).

Association Among Agronomic Traits

The amount of variability for a given trait in segregating populations is not often completely available because the breeder is often selecting for several important characteristics at one time. Therefore, an understanding of interrelationships among various traits is very important. Through the study of these relationships significant associations may be found between highly heritable traits and economically important ones that are of a complex nature, thus allowing the breeder to practice indirect selection (Ghandi et al., 1964). Another reason for studying relationships between different traits is to facilitate the interpretation of genetic analysis. It is desirable to know the degree of association between different traits and if possible to work with characters which are independent of each other at both the environmental and genetic level (Whitehouse et al., 1958).

Due to the independent development of yield components, they are used very often to explain the structure of economic grain yield in wheat. Each component, i. e. number of spikes per plant, number of kernels per spike, and kernel weight, or all of them together may give an indication of grain yield potential which is a very complex character (Baier and Robertson, 1967).

Simple correlations between several agronomic traits have been calculated. Five out of fifteen possible simple correlations were found to be significant: 1) kernels per spike were significantly correlated with yield and negatively correlated with number of spikes; 2) number of spikes was negatively correlated with earliness of flowering; and 3) kernels per spike had a positive correlation with height and earliness (Fonseca and Patterson, 1968). Culm length and kernel weight were reported to be highly positively correlated in two wheat crosses derived from Norin 10 (Reddi et al., 1969). However, correlations between tiller number and kernel weight were low and between tiller number and head length inconsistent.

The contributions of the area and duration of the different parts of the wheat plant to the grain yield of wheat have also been studied. The green area duration of the flag leaf and the peduncle gave a significant correlation with grain yield (Spiertz et al., 1971).

Phenotypic and genotypic correlations have been used to refine the estimation of the associations between different traits. In general, phenotypic and genotypic correlations have the same sign but differ in magnitude, hence allowing the identification of more precise levels of significance (Singh et al., 1969; Khadr, 1971).

When causal relationships among a set of interrelated variables are known, path coefficient analysis provides a means of detecting direct and indirect effects of one variable upon another. The correlation coefficient is broken down into components of direct and indirect causal relationships (Li, 1956). Path coefficient analysis, in a study on selection for yield in wheat, was a means of separating the direct and indirect effects of several traits and their complex correlations with yield. Total correlations were high for grain yield vs 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).

Direct and indirect effects of kernel weight, kernels per spikelet, number of spikelets per spike, spikes per plant, and plant height on total plant yield for forty five F_1 crosses between ten soft white winter wheats were studied. Negative association between kernel weight and number of kernels per spikelet canceled out large direct effects of kernel weight on plant yield. High positive correlations were found between yield per plant with kernels per spikelet and with spikelets per spike; both associations were determined almost completely by direct effects, and only small positive or negative effects were exerted indirectly. There was also a negative correlation between spikes per plant and yield, which was a result of negative associations of spike number with kernel number and spikelet number. Plant height exerted a positive indirect effect by way of kernel number on plant grain yield (Kronstad, 1963).

A similar study involving forty genotypes of spring wheat from diverse origins revealed that kernel weight had the greatest direct and indirect effects upon grain yield per plant. Head number had a significant direct effect on seed yield but the indirect effects via this trait were insignificant (Bhatt, 1973).

Recently multiple regression analysis utilizing different plant characters has been used to study relationships among variables. The percentage of the variability in the dependent variable which is accounted for by changes in the independent variables can be assessed. This percentage is used in determining which one(s) of the variable(s) can better predict the dependent variable's performance. Usually grain yield is used as the dependent variable and the components of yield, i.e. spike number, kernel number, and kernel weight, and other agronomic traits are assigned predicting values (Hsu and Walton, 1970; Walton, 1971a; Syme, 1972).

Generally association which show the most consistency are those between components of yield with grain yield. The most consistent is number of tiller per plant or per unit area with yield.

Associations between kernel weight and kernel number per head with yield are less consistent. The assumption that components of yield 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).

Heritability

In practice the plant breeder deals more often with plant traits which are not simply inherited, i. e. quantitatively inherited characters such as grain yield. Because of the nature of these complex traits biometrical procedures are used to estimate the relative degree of transmissability of the trait in question. The key to understanding these estimates of gene action is to realize that the differences between individuals or populations do not depend that much on the magnitude of the effect of individual genes. Their differences are mainly due to the total gene effects and the relative importance of heredity and the environment in producing the final phenotype (Allard, 1960).

One of the statistics used for estimating transmissability of a trait is the heritability estimate (H). The heritability concept is based on the assumption that the genotype and environment have contributed jointly to the final expression of the phenotype and this can be expressed by the formula:

$$P = G + E$$

where P represents the phenotype, G the genetic make up of the individual and E the environmental effects on the genotype (Wright, 1921). Heritability can be defined as that portion of the total variability which is due to genetic causes (Allard, 1960). More specifically heritability can be defined as the ratio of the additive genetic variance to phenotypic variance (Falconer, 1960). Heritability can also be referred as to the degree to which the characteristics of a plant are repeated in its offspring (Briggs and Knowles, 1967).

The ratio between total genetic variance to phenotypic variance has been termed broad sense heritability. The genotypic variance can be subdivided into additive and non-additive genetic variance. The ratio of the additive genetic variance to the phenotypic variance is called narrow sense heritability (Dudley and Moll, 1969).

Heritability estimates apply to a particular characteristic within a particular population. Because a heritability estimate is a ratio, its value can change either as the numerator or denominator changes. If a character is strongly influenced by the environment, its heritability estimate will be low when grown under widely fluctuating environments. But if the population were grown in an environment with low variation, the same character would show high heritability (Lush, 1945). There have been estimations of heritability for different traits in wheat but the most studied has been grain yield and its components.

Kernel weight was studied in a cross between a large kerneled spring wheat and a small kerneled cultivar. Narrow sense heritability for kernel weight was estimated using various methods and the values ranged from 37 to 69 percent with the latter value the most probable (Sharma and Knott, 1964).

A cross between two winter wheat cultivars differing in plant height was studied in the F_1, backcross, and F_2 generations. The heritability values of six plant and seed traits were estimated using narrow and broad sense heritability estimates. Number of heads per plant had a very low narrow sense heritability estimate. All the other components of yield, i. e. kernels per spikelet, spikelet number, and kernel weight, had relatively high values of transmissability. Their percentages were high enough to permit successful selection in the F_2 generation; the opposite was true for tiller number and grain yield. Broad sense heritability estimates were always higher than narrow sense heritability estimates (Johnson et al., 1966). In a similar study involving two semidwarf and two tall spring wheats, large grain number per ear was found to be dominant over small grain number. However, the major variance component controlling this character was additive, with heritability values ranging from high to low depending on the degree of environmental influence (Singh and Anand, 1971a). The same workers studied the other two components of yield and concluded that the effect of the environmental variations on the number of spikes per plant was quite significant and as a result of this, heritability values were low. Kernel weight had relatively high narrow sense heritability estimates even when the environment played a large role (Singh and Anand, 1971b; 1972).

Components of the analysis of variance were used to estimate heritability values in spring wheat. Randomly chosen F_5 lines of three spring wheat crosses were planted in a randomized block design over several years. The genetic variance was calculated from the mean square estimate of the differences among lines. The phenotypic variance was determined from the years times lines interaction mean square. The heritability value for grain yield was significantly higher for one of the crosses (Bush et al., 1971).

Components of yield have also been studied in durum wheats. A diallel analysis of crosses between six cultivars from five different countries indicated that the phenotypic expression of number of ears per plant and number of grains per spikelet was independent of the other characters. Phenotypic expression of spikelets per head and kernel weight was influenced by characters developed earlier in the developmental sequence. Therefore, heads per plant and kernels per spikelet had high narrow sense heritability values, i. e. 70 and 65 percent, respectively, while spikelets per head and kernel weight had low narrow sense heritability estimates, i. e. 30 and 19 percent, respectively (Lee and Kaltisikes, 1972).

Heritability estimates for and among various agronomic traits in wheat show some inconsistency due to: 1) the method used in calculating the heritability estimate (Johnson et al., 1966); 2) the genetic background of the parental lines (Schmalz, 1972); and 3) the intensity of the environmental variations. Estimations of broad sense heritability are usually higher than narrow sense heritabilities (Anwar and Chowdry, 1969). The heritability estimates of the components of yield are usually higher than estimates of grain yield heritabilities per se (Fonseca and Patterson, 1968) suggesting that selection for spike number, spikelet number, kernels per spikelet, and kernel weight in early generations has a better chance to be successful than direct selection for yield. Of the components of yield, kernel weight generally has a higher heritability value than the other yield components (Bhatt, 1972). The range in heritability estimates may also depend on how different the parental means are, i. e. wide crosses usually give high heritability values whereas crosses between closely related cultivars give low values for heritability (Sun et al., 1972). However, number of grains per spike, kernels per spikelet and spikelets per spike are traits which could also respond well to selection in early generations provided that the proper combinations are made (Virk et al., 1971).

Combining Ability

Combining ability is a relative measure of the power of a parental cultivar to transmit characteristics to its offspring. It may be thought of as two types: 1) general combining ability which refers to the average performance of a line in hybrid combinations, and 2) specific combining ability which designates those cases in which certain cross combinations do better or worse than expected on the basis of the average general combining ability of the two parental lines involved in the cross (Sprague and Tatum, 1942).

If selection is to be positive in segregating populations the breeder must be able to identify superior genotypes which when hybridized will transmit their desirable characteristics to future generations. The breeder of self-pollinated crops can base his selection utilizing that segment of the total genetic variability due to additive gene action and those gene interactions which follow the additive scheme, since this is the only type of gene action that can be retained after inbreeding (Kronstad, 1963).

General and specific combining ability effects were estimated from a diallel set of crosses in winter wheat. The combining ability analysis was done only for the F_1's excluding reciprocals, and a large part of the total genetic variation for yield and yield components was associated with a significant general combining ability effect. Specific combining ability effects were significant for plant yield and height but not for the components of yield (Kronstad and Foote, 1964; Walton, 1969).

Parental lines may differ in their combining ability and one of the problems of the plant breeder is to identify those lines which are going to produce high yielding progenies. It has been reported that crosses of wheat which were better than the parental means either in earliness or in plant height in the F_1 and F_2 generations (Borojevic, 1963).

However, in the case of yield, the differences in combining ability between the parental cultivars was not directly related to their own yielding capacity. Generally good combiners for yield were good combiners for some of the components of yield, but good combiners for the yield components were not necessarily good combiners for grain yield (Singh and Gupta, 1969).

There are several methods to estimate the type of gene action. The graphical analysis proposed by Jinks and Hayman (1953) and Griffing's combining ability analysis (1956) were compared by using data obtained from the F_1, F_2, and F_3 generations of a diallel set of crosses between five varieties of wheat. The combining ability analysis was found to be more reliable in predicting the prepotency of the parental lines. This was especially true in later generations when the expression of dominance effects was reduced and the contribution of non-allelic effects was greater (Tandon _et al._, 1970).

A partial diallel set of crosses has also been used to estimate general combining ability effects for several agronomic traits in wheat. The results were in agreement with those found with the complete diallel set of crosses in that genetic variation for yield and yield components was associated with significant general combining ability effects (Somayajulu _et al._, 1970).

The F_1 and F_2 generations of a diallel set of crosses between six wheat varieties were compared for their combining ability estimates. Correlations between F_1 and F_2 general combining ability effects during two years were significant not only for the components of yield but for plant grain yield also. This was not true for the specific combining ability effects of all the characters studied (Paroda and Joshi, 1970).

General combining ability effects were the major components of genetic variation in crosses involving soft red winter wheats, where heterosis levels exceeded 25 percent for grain yield. In this same experiment parents with high general combining ability were superior parents for wheat hybrids. However, there was a big loss of heterosis in the F_2 generation, suggesting that both dominance and epistatic type of gene action could be involved in the expression of heterosis in the F_1 hybrids of wheat (Blitzer and Fu, 1972).

A combining ability study involving ten varieties of durum wheat from diverse origin showed that number of tillers per plant, kernels per spike, and kernel weight had significant general combining ability effects. Kernel weight was the only character studied where significant specific combining ability effects were noted (Widner and Lebsock, 1973).

The study of combining ability may be useful in selecting parental cultivars that could produce more desirable progenies. There are indications that both additive and dominance components as well as epistatic components of genetic variance influence the expression of yield in wheat, because highly significant general and specific combining ability effects have been found. However, additive genetic variance is preponderant in the expression of the components of yield (Kronstad and Foote, 1964; Brown et al., 1966; Walton, 1971b; Gyawali et al., 1968). Those parental lines with high general combining ability effects seem to be good parents for F_1 hybrid combinations in wheat; specific combining ability would not make a significant contribution in the improvement of self-pollinated crops unless the commercial exploitation of heterosis becomes possible (Blitzer and Fu, 1972).

MATERIALS AND METHODS

Five parental cultivars of spring wheat were chosen from the genetic stock at the International Maize and Wheat Improvement Center in Mexico (CIMMYT). Crosses were made in 1970 at CIANO Experimental Station in Ciudad Obregon, Mexico, in a diallel fashion, excluding reciprocals. The F_1's were grown at the same station the following season, and the F_2 seed for each cross was harvested in bulk. During this season additional F_1 single crosses were made and the backcrosses to both parents were also obtained.

The parental lines used included: Yaqui 50, Sonora 64, Vicam 71, Olesen and Tordo. The pedigree and description of each cultivar is given in the Appendix. The first three entries have been commercial varieties in Mexico at different periods from 1950 to present. Yaqui 50 is a tall standard variety, Sonora 64 is a two gene semidwarf and Vicam 71 is a triple dwarf variety, the latter two were derived from Norin 10. Tordo is a line which is shorter than Vicam 71; it is a derivative of Tom Thumb and was produced in the hybrid wheat program sponsored jointly by CIMMYT-INIA in Mexico. Olesen is the shortest of all cultivars used in this experiment; it has very thick culms and very stiff straw.

The parental lines, first filial generation (F_1), second filial generation (F_2), backcrosses to the shorter parent in the single cross

(BC_1), and backcrosses to the tall parent (BC_2) were sown in a completely randomized block design on December 6, 1972, at the experimental station in Ciudad Obregon, Mexico. There were 67 rows, 7.5 m. long with 30 cm spacing between rows, per replication, and a total of four replications. There was one row of each parental line along with the respective F_1 planted in each replication. With the exception of the F_1's, each row was planted with 24 seeds approximately 30 cm apart. In the case of the F_1's, only 10 seeds per row were planted.

There were 45 entries in the experiment which included five parents, and 10 F_1's, 10 F_2's, 10 BC_1's, and 10 BC_2's. For the latter three generations there were either one, two, or four rows sown of each in every replication, and the number was dependent on the difference in height between the two cultivars involved in the cross. Crosses between Yaqui 50 and the three dwarf cultivars were planted with two rows for the backcrosses and four rows for the F_2's in each replication; other crosses were planted with one row for the backcrosses and two rows for the F_2 in every replication.

Prior to planting, 150 kg/ha of nitrogen and 50 kg/ha of phosphorous were applied. The plots were irrigated seven times during the season, including one at sowing time and the last one was applied on April 9, 1973. Diathion was applied two times during the season at a rate of 60 cc per 10 L of water for aphid control. Weeds were controlled by hand cultivation.

Data were collected on and individual plant basis. A total of thirteen characteristics were scored in the following manner:

1. Days to ear emergence was recorded when approximately half the number of tillers of each individual plant had the whole spike extruded beyond the auricules of the flag leaf.

2. Plant height was obtained by measuring the length from the base of the crown to the tip of the ear of the main tiller excluding awns.

3. Number of tillers was recorded as the number of spike-bearing culms.

4. Number of spikelets was obtained by averaging the number of spikelets on the head of the main tiller and on another tiller selected at random from the first flush of tillers.

5. Head length was obtained by measuring the length of the ear on the tallest culm, excluding awns.

6. Days to maturity was scored when approximately half of the tillers of the plant had reached physiological maturity.

7. Grain yield per plant was the weight of the grain in grams.

8. Harvest index, expressed in percent, was the ratio of grain yield per plant to the weight of the whole plant excluding roots (this character was recorded for only half of the plants harvested.

9. Kernel weight was calculated by weighing 500 kernel samples per plant and dividing by 500 to obtain the average weight of a kernel (when there was less than 500 kernels, the total number of kernels was used to calculate kernel weight).

10. Number of kernels per spikelet was calculated indirectly from grain yield per plant, 500 kernel weight, number of effective tillers, and number of spikelets per spike, using the following formula:

$$\text{kernels/spikelet} = \frac{\dfrac{(\text{Grain yield per plant/} \; \text{500 kernel weight) 500}}{\text{Number of tillers per plant}}}{\text{Number of spikelets per spike}}$$

11. Rachis internode length was calculated by dividing the head length by the number of spikelets per spike.

12. The grain filling period was calculated from the difference between number of days to maturity minus number of days to ear emergence.

13. Head weight was calculated from the ratio of grain yield per plant to number of effective tillers.

All the characters under study were subjected to analysis of variance and the F test was utilized to determine significant differences (Snedecor and Cochran, 1967). Plot per generation means were used for the analysis. The generations effects in the analysis of variance were divided into components' effects to detect differences between and within generations. In the case of the character harvest index, only the parents and F_1 generations were included in the analysis of variance.

Variances for each of the traits across replications were calculated to determine broad sense heritability (Hbs) and narrow sense heritability (Hns). The formula used to estimate heritability in the broad sense (Allard, 1960) was:

$$\text{Hbs} = \frac{VF_2 - (VF_1 + VP_1 + VP_2)/3}{VF_2}$$

and the formula to estimate narrow senseheritability (Warner, 1952) was:

$$\text{Hns} = \frac{2VF_2 - (VBC_1 + VBC_2)}{VF_2}$$

where: VF_1 = variance of the first filial generation, VF_2 = variance of the second filial generation, VBC_1 = variance of the backcross to the short parent, VBC_2 = variance of the backcross to the tall parent, VP_1 = variance of the short parent, and VP_2 = variance of the tall parent.

Degree of dominance displayed for plant height in the F_1 and F_2 was calculated using the following formula:

$$D = \overline{TP} - (\overline{P_1} + \overline{P_2})/2$$

$$d1 = \frac{\overline{F_1} - (\overline{P_1} + \overline{P_2})/2}{D}$$

$$d2 = \frac{\overline{F_2} - (\overline{P_1} + \overline{P_2})/2}{D}$$

where D = differential, d = degree of dominance, $\overline{TP}$ = tall parent mean, dl = degree of dominance for F_1, d2 = degree of dominance for F_2, $\overline{P_1}$ = tall parent mean, $\overline{P_2}$ = short parent mean, $\overline{F_1}$ = first filial generation mean. Heterosis was calculated for each trait in each cross as the percentage increase of the F_1 or F_2 above the mean of the parental lines. The formula used was that described by Matzinger _et al._ (1962):

$$\text{Heterosis} = \frac{\overline{F_1} - \overline{MP}}{\overline{MP}} \times 100$$

where $\overline{MP}$ is the mid parent value and $\overline{F_1}$ is the mean of the first filial generation. If the value resulting from this formula was negative, heterosis was considered negative in sign. Possible superiority of the F_1 in respect to the better parent was estimated by using the formula proposed by Fonseca and Patterson (1968a):

$$\text{Heterobeltiosis} = \frac{\overline{F_1} - \overline{HP}}{\overline{HP}} \times 100$$

where $\overline{HP}$ is the mean value of the better parent and $\overline{F_1}$ is the mean of the generation following the cross; as heterosis, negative heterobeltiosis values were considered.

Phenotypic, environmental and genotypic correlations were used to estimate degree of association between the agronomic traits studied for each of the 10 crosses. As suggested by Falconer (1960), the F_1 correlations were considered as environmental correlations, the F_2 correlations were considered as phenotypic correlations and the genetic correlations were calculated from the formula:

$$rPh = \sqrt{Hx}\,\sqrt{Hy}\;\; rG + \sqrt{Ex}\,\sqrt{Ey}\;\; rE$$

where: rPh = phenotypic correlation between x and y, rG = genetic correlation between x and y, rE = environmental correlation between x and y, H = heritability, with subscript x or y, according to the trait,

$E = 1-H$, also with subscripts according to the trait.

Path-coefficient analysis, as suggested by Wright (1921, 1922), and discussed by Dewey and Lu (1959) and Li (1948) was used to provide a means of studying the direct and indirect contributions of various characters in building up a complex correlation. By this method the relationships between yield and yield components from the replication means of the F_1, F_2, BC_1, and BC_2, for each cross were studied.

Estimates of general and specific combining ability were obtained for 10 of the traits studied, excluding rachis internode, days to heading and harvest index, by the method proposed by Griffing (1956) where the parents and one set of F_1's were included, reciprocals excluded. Because the parents were selected on the basis of plant height and represented a specific population, a fixed model was used. This combining ability analysis has been termed by Griffing as Experimental Method 2, Model I. The diallel crossing system gives rise to $p(p + 1)/2$ different genotypes, where p = number of parental lines in the diallel. Contributions of the parents due to general combining ability (G.C.A.) and specific combining ability (S.C.A.) effects were also computed for 10 of the traits studied (Griffing, 1956). Components of variance due to G. C. A. and S. C. A. were partitioned according to the same Griffings model. Ratios between G.C.A. effects and S.C.A. effects were calculated to compare the relative magnitude of these variances in the F_1 and the F_2 generations. The following F ratios were used to test for G.C.A. and S.C.A. effects:

$F, p-1, m = Mg/Me'$ to test for differences among G.C.A. effects

$F, p(p-1)/2, m = Ms/Me'$ to test for differences among S.C.A. effects.

where Mg = mean square for G.C.A., Ms = mean square for S.C.A. Me' = error mean square from the combining ability analysis, p = number of parental lines, and m = degrees of freedom for the error term in the combining ability analysis.

The analysis of combining ability was determined only for the F_1 and F_2 generations.

RESULTS AND DISCUSSION

Analysis of variance - The five parental cultivars used in this study represented a wide range in genetic diversity for plant height. These parental cultivars were also very diverse for the expression of other agronomic traits which may be of interest to the breeder when developing new semidwarf wheats. To test the significance of this genetic variability, an analysis of variance was used to detect differences among genotypes as well as between and within generations for all thirteen characters measured (Tables 1 and 2). Significant differences ($p = 0.01$) were observed among genotypes for all characters studied; among generations for all characters except days to maturity; and for all characters within generations.

To justify the combining ability analysis for the parental lines and the F_1 and F_2 generations, differences existing within each of the generations were tested for significance. Significant differences ($p = 0.01$) were detected within each of the generations for most of the traits studied. Yield per plant between F_1 crosses, number of tillers per plant between the parental lines, days to maturity between the F_1's, and head grain weight between the parents, were significantly different at a lower probability level ($p = 0.05$).

The within generations results from the analysis of variance, in general, confirm the assumption that genetic diversity existed

Table 1. Observed mean squares for twelve agronomic characteristics for parents, F1's, F2's, BC1's and BC2's, **of a five spring wheats diallel cross.**

Source of Variation	Degrees of Freedom	Yield per Plant	Number of Tillers	Number of Spikelets	Kernels per Spikelet	Kernel Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Inter-node	Head Grain Weight
Reps	3	341.57**	103.52**	5.90**	.039	49.10**	156.90**	36.55**	7.16	6.02	1.05**	.106*	.092*
Genotypes	44	304.17**	68.73**	4.98**	.103**	21.52**	2114.91**	48.01**	16.22**	22.82**	6.09**	.631**	.142**
Between Generations	4	977.02**	227.56**	1.24**	.150**	32.20**	2181.58**	74.45**	3.23	96.92**	.83*	.139**	.546**
Within Generations	40	236.88**	52.88**	5.36**	.098**	20.45**	2108.24**	45.37**	17.52**	15.41**	6.62**	.680**	.102**
Parents	4	317.94	131.42*	9.89**	.225**	41.22**	4933.62**	160.30**	49.30**	52.07**	14.83**	1.482**	.121*
F1's	9	522.54*	66.80	4.61**	.100**	17.57**	1729.71**	16.29**	14.89*	4.83	6.51**	.669**	.208**
F2's	9	106.47	34.73**	2.73**	.043**	20.97**	1669.58**	35.27**	11.58**	12.57**	3.92**	.455**	.068**
BC1's	9	78.13	26.51**	4.33**	.067**	18.06**	720.93**	15.89**	7.29**	7.36**	6.05**	.703**	.070**
BC2's	9	204.38**	48.58**	7.75**	.127	15.99**	3057.01**	62.95**	22.18**	20.57**	6.35**	.538**	.052
Genotypes x Reps(1	132	90.48	17.39	.27	.030	3.19	7.73	3.03	2.98	3.15	.26	.030	.032
Parents x Reps(2	12	118.59	36.96	.36	.017	2.29	3.56	4.67	1.50	9.11	.19	.021	.032
F1's x Reps(3	27	175.94	31.07	.41	.023	2.90	5.26	3.47	6.14	3.49	.30	.039	.056
F2's x Reps(4	27	49.34	10.46	.26	.012	2.22	10.76	1.95	2.52	1.69	.24	.033	.015
BC1's x Reps(5	27	41.91	8.00	.16	.020	3.09	5.01	2.24	1.83	1.63	.22	.039	.021
BC2's x Reps(6	27	64.68	9.16	.22	.063	3.01	10.59	2.09	2.32	2.57	.33	.019	.035
Between Gens x Reps	12	130.00	22.35	.24	.039	7.53	10.26	6.79	2.44	4.40	.22	.022	.039
TOTAL	179												
Coefficient of Variation		17.76	18.59	2.18	6.97	4.44	3.59	1.79	1.22	4.00	4.37	3.54	7.54

* significant differences at the 5% probability level
** significant differences at the 1% probability level

1) Error term for Reps, Genotypes, Between Generations, and Within Generations
2) Error term for Parents
3) Error term for F1's
4) Error term for F2's
5) Error term for BC1's
6) Error term for BC2's

Table 2. Observed mean squares for harvest index for F_1's and parents.

	Degrees of Freedom	Harvest Index
Reps	3	1.35
Genotypes	14	74.33**
Between Generations	1	66.16**
Within Generations	13	75.39**
Parents	4	203.95**
F_1's	9	18.26**
Genotypes x Reps[1]	42	2.09
Parents x Reps[2]	12	2.99
F_1's x Reps[3]	27	1.71
Between Generations x Reps	3	1.86
TOTAL	59	
Coefficient of Variation		3.39

**Significant differences at the 1% probability level

[1] Error term for Reps, Genotypes, Between Generations, and Within Generations

[2] Error term for Parents

[3] Error term for F_1's

among the parental lines. However, there were no statistical differences for yield per plant within the parental lines, within the F_2 generation, and within the BC_1, as well as for number of tillers per plant among the F_1's, kernels per spikelet among the BC_2, and grain filling period among the F_1's.

For most traits studied the coefficients of variation (C. V.) were below 8, but in the case of tillers per plant and yield they were 18.59 and 17.76 percent, respectively (Table 1). These are relatively high C. V. values (Snedecor and Cochran, 1967). Examining the means for number of tillers and yield per plant of the parental lines (Table 10), there were differences of 33 and 28 percent respectively between the line with the highest value and that with the lowest one. These differences appeared large enough to be significant. However, the expression of tiller number and plant yield may have been influenced to a greater extent by the environment, thus increasing the value of the error term and making differences more difficult to detect. Similar results of high C. V. for tillers per plant have been reported by Kronstad (1963) and Daaloul (1973). In both studies significant differences were difficult to detect among crosses otherwise proven to be genetically diverse. Because grain yield depended so much on tillering capacity in the present study, this could account for the difficulty in detecting yield differences.

From the results of the analysis of variance, there was enough evidence to assume genetic diversity among the parental cultivars and their crosses for all the traits measured, and to justify an analysis of the type of gene action involved in their genetic expression.

Degree of dominance for plant height and heterosis - The semi-dwarf trait could be better utilized in a breeding program if the type of gene action involved in the inheritance of this trait for each of the different genetic sources was better understood. One of the simplest ways to calculate gene action is to estimate the degree of dominance (d) using mean values. For calculating d the following assumptions were made: 1) if no dominance existed or any kind of epistatic effects, all the gene action was assumed to be additive if the F_1 value approached the mid parent value; 2) if only one gene was present, dominance would refer to that particular locus, and if more than one gene was involved dominance would be an average value.

Estimations of degree of dominance for plant height in each of the 10 crosses was calculated to determine if differences existed among the dwarf cultivars in this study (Table 3). In most of the crosses the value of d was positive, indicating dominance for tallness. The degree of dominance varied but, in general, it was about 10 percent higher than the midparent. However, in most of those crosses involving the cultivar Tordo dominance values were negative. In the cross Tordo/Olesen, in which Tordo was the tall parent, d was

Table 3. Means, Variances (Var.), Coefficients of Variation (C.V.), Broad Sense Heritabilities (Hbs), Narrow Sense Heritabilities (Hns), number of observations (n), and degree of dominance (d) for plant height, in the ten crosses studied and their parents.

Cross or Parental	Mean	Var.	C.V.	Hbs	Hns	n	d
Yaqui 50	135.78	12.73	2.63			55	
Sonora 64	82.57	17.80	5.11			68	
Sonora 64/Yaqui 50				87.9	86.0		
F_1	112.15	39.94	6.90			33	.11
F_2	110.00	193.80	12.66			101	.03
Backcross 1	92.40	121.94	11.95			53	
Backcross 2	121.82	99.00	8.17			69	
Sonora 64/Olesen				87.7	83.4		
F_1	67.10	22.64	7.09			30	.14
F_2	67.79	125.69	16.54			137	.18
Backcross 1	55.65	65.79	14.58			84	
Backcross 2	74.05	80.70	12.13			81	
Sonora 64/Tordo				96.0	85.6		
F_1	62.00	15.40	6.33			31	-.56
F_2	72.01	366.70	26.59			138	.20
Backcross 1	59.64	118.26	18.23			86	
Backcross 2	71.70	301.68	24.22			88	
Yaqui 50/Olesen				90.6	81.3		
F_1	91.34	22.23	5.16			29	.01
F_2	90.33	436.60	23.13			238	-.02
Backcross 1	65.75	129.01	17.27			166	
Backcross 2	115.45	389.18	17.09			164	

Table 3. Continued.

Cross or Parental	Mean	Var.	C. V.	Hbs	Hns	n	d
Yaqui 50/Tordo				97.6	74.3		
F_1	86.41	18.25	4.94			29	-.24
F_2	91.15	586.96	26.58			278	-.12
Backcross 1	69.45	161.20	18.28			159	
Backcross 2	107.96	576.63	22.24			163	
Vicam 71/Sonora 64				79.8	79.2		
F_1	74.61	45.90	9.08			36	-.28
F_2	78.79	129.43	14.44			142	.40
Backcross 1	72.96	54.64	10.13			87	
Backcross 2	78.07	101.74	10.85			75	
Vicam 71/Yaqui 50				95.8	82.2		
F_1	105.20	24.29	4.68			34	.07
F_2	106.07	409.28	18.96			264	.09
Backcross 1	84.38	156.09	14.81			147	
Backcross 2	125.52	326.02	14.38			156	
Vicam 71/Olesen				82.7	74.5		
F_1	59.10	9.60	5.24			29	.07
F_2	57.53	58.09	13.25			129	-.07
Backcross 1	54.19	34.51	10.84			63	
Backcross 2	60.27	38.39	10.28			66	

Table 3. Continued.

Cross or Parental	Mean	Var.	C. V.	Hbs	Hns	n	d
Vicam 71/Tordo				93.2	88.2		
F_1	58.71	9.55	5.26			34	-.64
F_2	61.68	173.29	21.34			152	-.21
Backcross 1	58.35	72.53	14.60			82	
Backcross 2	64.60	121.12	17.04			83	
Tordo/Olesen				95.7	85.4		
F_1	51.89	5.24	4.41			36	.12
F_2	51.90	175.45	25.52			104	.13
Backcross 1	51.47	112.10	20.56			78	
Backcross 2	50.89	88.92	18.53			47	
Vicam 71	70.13	14.58	5.44			70	
Olesen	46.40	5.96	5.26			57	
Tordo	56.17	11.20	5.96			65	
Average				90.7	82.0		

positive. The degree of dominance varied and in the crosses Sonora 64/Tordo and Vicam 71/Tordo dominance was more towards the short parent than the midparent indicating that there were strong dominant effects for shortness of straw from this cultivar derived from Tom Thumb.

Only a slight degree of dominance for tallness was present in crosses involving Vicam 71 and Olesen dwarf. In these crosses additive gene action could not be ruled out as a major component of the genetic variability for plant height. Similar results were reported by Ficks and Qualset (1973) in a study using a Norin 10 derivative and Olesen. In crosses involving Tordo, however, non-additive gene action played a larger role because the degree of dominance for short straw was higher. Morris _et al._, (1972), reported similar results working with monosomics of Tom Thumb and two tall standard varieties.

As an ultimate goal the breeder of self-pollinated crops has to identify and select lines which possess superior agronomic characteristics. This is usually done after several generations of selfing. Success in selection will depend primarily on the type of gene action involved in the expression of the character(s) under consideration plus the amount of environmental influence. The breeder is mainly concerned with those effects which remain constant or can be fixed by means of selection. Heterosis, expressed as a percentage of the midparent or as a percentage of the high parent, is a means of detecting some of these gene effects by a simple comparison of means in the early generations. The superiority, or inferiority, of the F_1 hybrid may be due to intra-allelic interactions that are lost after inbreeding or to epistatic effects of an additive type that can be fixed by means of selection. When the F_2 generation is also evaluated for heterosis, then the amount of heterotic effects lossed after a generation of selfing, or the amount of inbreeding depression, may give some indications of the type of gene action involved in the expression of a particular trait.

Heterosis values in this study were high and positive for head grain weight and kernels per spikelet when the average values of the heterosis effects for all crosses were compared (Table 6). Head weight appeared to respond more to non-additive gene action as heterosis values were quite high in the F_1 (15.18 percent of $\overline{MP}$, 10.77 percent of $\overline{HP}$) and were greatly reduced in the F_2, (6.86 percent of $\overline{MP}$, 2.75 percent of $\overline{HP}$). The crosses having the highest heterosis values for head weight were Yaqui 50/Olesen and Vicam 71/Yaqui 50. The three parents involved in these crosses had the lowest head weight means. Therefore, high heterotic effects may very well indicate that the genes involved in these effects were different in each of the parental lines, and the possibility exists of finding recombinations which would have higher head weight than the parental

Table 4. Heterosis as percentage of the midparent (MP) and higher parent (HP) for **four characters** studied in the diallel cross of five spring wheats.

	PLANT HEIGHT				DAYS TO HEADING			
	F_1		F_2		F_1		F_2	
	MP	HP	MP	HP	MP	HP	MP	HP
Sonora 64/Yaqui 50	2.72	-17.40	.76	-18.99	1.94	-5.56	3.88	-3.76
Sonora 64/Olesen	4.06	-18.74	5.13	-17.90	8.13	5.03	4.29	1.30
Sonora 64/Tordo	-10.62	-24.91	3.81	-12.79	5.97	-1.04	3.43	-3.41
Yaqui 50/Olesen	.27	-32.73	-.83	-33.47	3.40	-1.52	3.06	-1.84
Yaqui 50/Tordo	-9.97	-36.36	-5.03	-32.87	2.02	1.14	1.72	1.01
Vicam 71/Sonora 64	-2.28	-9.64	3.20	-4.58	5.02	-1.49	2.21	-4.13
Vicam 71/Yaqui 50	2.18	-22.52	3.03	-21.88	1.00	- .38	1.14	- .20
Vicam 71/Olesen	1.43	-15.73	-1.26	-17.97	4.27	.59	5.37	1.65
Vicam 71/Tordo	-7.03	-16.28	-2.33	-12.05	1.51	1.03	1.23	.75
Tordo/Olesen	1.18	-7.62	1.20	-7.60	3.90	-.22	3.49	-.62
Average	-1.81	-20.19	.77	-18.01	3.72	-.24	2.98	-.92

	HARVEST INDEX				RACHIS INTERNODE			
Sonora 64/Yaqui 50	9.18	-9.20	4.01	-13.50	-.94	-6.37	-3.37	-8.67
Sonora 64/Olesen	2.52	.42	-2.09	-4.10	.11	-6.36	-.96	-7.36
Sonora 64/Tordo	1.64	1.09	.31	-.23	00	-3.17	-.19	-3.35
Yaqui 50/Olesen	15.13	-5.82	10.87	-9.31	-2.89	-13.81	-4.09	-14.87
Yaqui 50/Tordo	15.90	-4.03	2.54	-15.09	13.26	.53	6.08	-5.84
Vicam 71/Sonora 64	3.70	2.95	3.47	2.72	.97	-6.96	1.62	-6.36
Vicam 71/Yaqui 50	10.99	-8.23	6.91	-11.60	-.51	-12.92	-7.18	-18.76
Vicam 71/Olesen	1.16	-.20	-1.95	-3.26	-2.55	-4.11	-1.62	-3.20
Vicam 71/Tordo	-2.33	-2.52	-1.26	-1.45	-2.19	-12.48	-3.23	-13.41
Tordo/Olesen	.75	-.79	-3.06	-4.54	-.10	-9.31	-.92	-10.06
Average	5.86	-2.63	1.97	-6.04	.52	-7.50	-1.39	-9.19

Table 5. Heterosis as percentage of the midparent (MP) and higher parent (HP) for four characters studied in the diallel cross of five spring wheats.

	NUMBER OF SPIKELETS				DAYS TO MATURITY			
	F_1		F_2		F_1		F_2	
	MP	HP	MP	HP	MP	HP	MP	HP
Sonora 64/Yaqui 50	1.18	-6.24	.28	-7.08	-2.32	-5.28	-1.37	-4.37
Sonora 64/Olesen	2.97	-1.07	1.63	-2.36	1.16	-0.36	-0.23	-1.72
Sonora 64/Tordo	-3.37	-10.37	.88	-6.42	.28	-2.61	-1.46	-4.30
Yaqui 50/Olesen	.29	-3.42	1.36	-2.39	-1.80	-3.35	-0.58	-2.16
Yaqui 50/Tordo	1.47	1.35	.52	.40	-0.37	-0.53	-1.37	-1.53
Vicam 71/Sonora 64	.18	-4.98	1.59	-3.64	.18	-1.48	-0.33	-1.99
Vicam 71/Yaqui 50	3.12	.60	1.32	-1.15	-1.12	-2.52	-0.75	-2.16
Vicam 71/Olesen	.23	-1.09	1.16	-0.17	.64	.47	.47	.30
Vicam 71/Tordo	2.67	.28	.39	-1.95	-0.30	-1.55	-1.43	-2.68
Tordo/Olesen	.62	-2.99	-1.12	-4.66	-1.05	-2.46	-0.67	-2.08
Average	.94	-2.79	.80	-2.94	-0.47	-1.97	-0.77	-2.27

	HEAD LENGTH				GRAIN FILLING PERIOD			
Sonora 64/Yaqui 50	-0.48	-12.43	-3.99	-15.52	-8.19	-14.01	-11.27	-16.89
Sonora 64/Olesen	3.57	0.46	1.00	-2.03	-10.35	-11.20	-7.96	-8.84
Sonora 64/Tordo	-3.54	-13.00	0.00	-9.81	-9.70	-14.01	-10.42	-15.19
Yaqui 50/Olesen	-3.07	-16.92	-2.25	-16.22	-11.63	-16.48	-8.75	-13.75
Yaqui 50/Tordo	5.41	2.53	-2.60	-5.27	-5.17	-6.81	-8.99	-10.57
Vicam 71/Sonora 64	1.05	-1.94	3.14	.09	-8.89	-15.40	-5.33	-12.10
Vicam 71/Yaqui 50	2.21	-12.36	-6.39	-19.73	-5.22	-6.10	-6.54	-7.41
Vicam 71/Olesen	-2.60	-2.65	-1.42	-1.47	-6.63	-12.53	-9.54	-15.25
Vicam 71/Tordo	0.00	-12.18	-3.55	-15.30	-4.04	-6.56	-7.12	-9.56
Tordo/Olesen	.38	-11.88	-3.09	-14.93	-10.55	-14.03	-7.43	-11.03
Average	.29	-8.04	-1.91	-10.02	-8.04	-11.71	-8.33	-12.06

Table 6. Heterosis as percentage of the midparent (MP) and higher parent (HP) for five characters studied in the diallel cross of five spring wheats.

	KERNELS PER SPIKELET				YIELD PER PLANT			
	F_1		F_2		F_1		F_2	
	MP	HP	MP	HP	MP	HP	MP	HP
Sonora 64/Yaqui 50	5.76	-2.21	-2.58	-9.93	2.44	-2.71	-0.85	-5.84
Sonora 64/Olesen	7.84	3.68	3.63	-0.37	2.89	-7.15	-1.46	-11.07
Sonora 64/Tordo	7.75	-2.94	1.22	-8.82	-34.60	-35.17	-2.80	-3.65
Yaqui 50/Olesen	16.60	11.95	3.73	-0.40	9.54	-2.34	8.20	-3.55
Yaqui 50/Tordo	11.80	8.66	6.46	3.46	-11.30	-16.47	-17.00	-21.82
Vicam 71/Sonora 64	1.21	-7.72	.81	-8.09	-21.33	-27.23	-3.87	-11.09
Vicam 71/Yaqui 50	12.09	10.39	5.05	3.46	21.83	18.49	-12.34	-14.74
Vicam 71/Olesen	3.16	-2.39	1.47	-3.98	-16.63	-29.79	8.34	-8.77
Vicam 71/Tordo	9.50	8.03	5.43	4.02	-13.42	-20.56	-18.47	-25.19
Tordo/Olesen	.64	-5.98	6.18	-0.80	-6.12	-14.60	17.70	7.07
Average	7.63	2.15	3.14	-2.14	-6.67	-13.75	-2.25	-9.86

	KERNEL WEIGHT				TILLERS PER PLANT				HEAD WEIGHT			
Sonora 64/Yaqui 50	11.18	3.69	6.06	-1.09	-17.32	-27.50	-6.67	-18.17	19.02	10.83	3.80	-3.33
Sonora 64/Olesen	7.24	1.60	2.76	-2.64	-12.26	-17.13	-8.33	-13.42	19.82	13.33	7.93	2.08
Sonora 64/Tordo	4.85	1.95	4.10	1.21	-43.02	-43.27	-9.60	-9.99	10.23	10.00	7.31	7.08
Yaqui 50/Olesen	16.59	14.66	9.26	7.45	-18.39	-31.86	.06	-16.46	36.82	34.58	14.49	12.62
Yaqui 50/Tordo	7.49	-2.34	3.58	-5.89	-27.66	-36.81	-24.70	-34.22	21.52	13.39	9.86	2.51
Vicam 71/Sonora 64	4.97	3.27	2.38	.73	-27.69	-35.95	-8.70	-19.14	6.37	.83	4.61	-0.83
Vicam 71/Yaqui 50	9.83	4.01	3.84	-4.94	-4.19	-5.29	-18.64	-18.64	26.06	23.72	5.69	3.72
Vicam 71/Olesen	-2.15	-5.84	-6.00	-9.55	-16.61	-29.71	4.10	-12.26	1.63	1.39	-1.16	-1.39
Vicam 71/Tordo	1.59	-2.77	3.44	-1.01	-22.29	-31.43	-26.33	-35.00	11.89	6.28	8.81	3.35
Tordo/Olesen	-4.47	-11.87	-0.74	-8.43	-2.63	-7.66	4.92	-0.50	-1.54	-6.69	7.28	1.67
Average	5.71	.64	2.87	-1.76	-19.21	-26.66	-9.38	-17.78	15.18	10.77	6.86	2.75

cultivars, even if the main gene action was of the nonadditive type. The cross between Sonora 64 and Tordo, the two parents with the highest head grain weight means, showed some degree of heterosis which was not reduced in the F_2. Additive gene effects may be involved in the expression of this trait in this particular cross, and the possibility exist that genotypes may be selected with a higher head grain weight than both parents.

There was less heterosis for number of kernels per spikelet. In general, heterotic effects were significantly reduced in the F_2, indicating that non-additive gene action was important in the expression of this trait in the F_1. However, there were some crosses where reduction of heterosis in the F_2 was not as drastic, i.e. Yaqui 50/Olesen, Yaqui 50/Tordo, Vicam 71/Yaqui 50 and Vicam 71/Tordo. The small reduction in heterotic effects in the F_2, indicated that perhaps additive gene action played a bigger role in these crosses, and selection for higher number of kernels per spikelet is plausible.

Other traits showing significant heterosis, but of the negative type, were grain filling period (-8.04 percent of the $\overline{MP}$ and -11.71 percent of the $\overline{HP}$), number of tillers per plant (-19.21 percent of the $\overline{MP}$, -26.66 percent of the $\overline{HP}$), and grain yield per plant (-6.67 percent of the $\overline{MP}$, -13.75 percent of the $\overline{HP}$). Grain filling period did not show changes in heterotic effects from the F_1 to the F_2 (Table 5), hence additive gene effects may be important in the expression of this trait. None of the crosses had positive heterosis values. Because additive effects seemed important and significant differences were detected among the parental lines (Table 1), there is the possibility that transgressive segregation will occur. Therefore, families with a longer grain filling period could be selected. A long filling period may be a means of increasing seed set and kernel weight, two important components of yield.

A very large negative heterosis value for number of tillers per plant was observed in the F_1 but was reduced drastically in the F_2 generation (Table 6). This trait would be expected to respond to non-additive gene action and would be difficult to select for in early generations. Yield per plant followed a similar pattern as tillers per plant (Table 6). The negative heterotic value was not as large for grain yield as for tillers number, due perhaps to compensatory effects by the other yield components, except tiller number.

Kernel weight showed some heterosis in respect to the mid-parent when all crosses were averaged (Table 6). The cross between the two cultivars with the lowest kernel weight, i. e. Yaqui 50/Olesen, had the highest heterotic effects. Each parent may have contributed different genes that enhanced kernel weight in the F_1, and recombinations with higher kernel weight than both parents are possible provided it was not all due to non-additive gene action. The cross between the two cultivars with the highest kernel weight, Sonora 64/Tordo, showed very little heterosis. However, the heterosis values for this trait were positive with respect to both the midparent and high parent. Because these effects remained positive in the F_2, the genetic variance was probably additive and some lines with higher kernel weight than the parents could be selected from this cross. The amount of heterosis observed for the remaining traits was very small, and hence additive gene action was involved in the expression of these traits (Tables 4, 5, and 6). This was confirmed by the lack of a significant change in the heterotic values from the F_1 to the F_2 generations.

Crosses with the parental cultivar Tordo were the only ones in which negative heterosis values for plant height were observed, confirming that some non-additive gene action is involved in the expression of height in those crosses made with this cultivar. Non-additive gene action for reduced plant height could be very important in a hybrid wheat program because with heterosis for grain yield lodging becomes a big problem. Crosses between tall standard varieties and semidwarf wheats derived from Norin 10 usually have the greatest heterosis for grain yield. However, because tallness is usually dominant over shortness, the F_1 is tall and lodges very often (CIMMYT report, 1968). Tordo or Tom Thumb derivatives could be used as a means of producing short F_1 hybrids that do not lodge because of the dominance for short stature in the F_1 generation.

Days to heading showed almost no heterosis. In general, the F_1 crosses were a little bit earlier than the late parent and later than the midparent. Days to maturity followed the same trend as days to heading. Therefore, it seems possible to select for earliness, if desired, in early generations. Sonora 64 and Olesen would be the best parents for earliness.

Number of spikelets per spike showed no heterosis. The cross Yaqui 50/Tordo had the largest number of spikelets as well as the longest head size, a trait which also showed no heterosis. Vicam 71 and Olesen have very compact and small heads and when these cultivars are crossed to other parents the F_1 and F_2 generations showed negative heterosis values for head size and rachis internode length. This negative characteristic would have to be overcome when using Olesen and Vicam 71 as parents if an increase in head size is one of the objectives. From the analysis of heterosis, additive gene action was important in the genetic mechanism for earliness, plant height, rachis internode length, head length, and number of spikelets per spike. The possibility exists that selection could be practiced for these traits in early generations with good probabilities of success. Harvest index showed some positive heterosis values in relation to the midparent but none with respect to the high parent. Crosses between short and tall cultivars had the most heterosis with respect to the midparent and had the least heterosis with respect to the high parent.

For the wheats used in this study, a high harvest index was an indication of short plant height. Since effective selection for short strawed wheats is quite possible, the same would be true for high harvest index, a character that some investigators consider an indication of more efficient translocation of assimilates to the kernel (Syme, 1972). There were also indications, except with tiller number, that additive gene action was present in the expression of components of yield.

Heritability - The amount of variability observed for a trait in a population of plants may be due to: 1) differences in the genetic constitution of the individual plants, 2) differences in the environment to which each of the genotypes is being exposed, and 3) genotype-environment interactions. Therefore it is important to understand the relative role of heredity, the environment, and their interaction in the variability observed in the character(s) under study.

Broad sense heritability values estimate that proportion of the total variability which is due to genetic causes, without specifying as to the nature of gene action that is involved in the expression of the trait in question. Heritability in the broad sense is very useful when working with cross-pollinated or vegetatively propagated crops that can be used commercially as F_1 hybrids.

Narrow sense heritability is a more refined way of examining the relationship between environment and heredity. Narrow sense heritability estimates are computed on the basis of the additive genetic variance, and hence gives a better indication of the degree to which a progeny will resemble its parents in latter generation. Working with self-pollinated crops, it is the additive part of the genetic variance that is most important in terms of the effective progress that can be made through selection.

Broad sense heritability estimates in the present experiment varied from 14.5 percent for number of tillers per plant to 90.7 percent for plant height (Tables 3 and 10). More than one half of the phenotypic variability for the expression of plant height, days to heading, head length, days to maturity, number of kernels per spikelet, head grain weight, and grain filling period, was due to genetic reasons (Tables 3, 7, 8, 9, and 10). The environment accounted for more than one half of the total variability in number of tillers per plant, grain yield per plant, and harvest index (Tables 7 and 10). The range of variability for the heritability estimates was smaller for those traits that showed higher Hbs values while the opposite was true for those traits that had lower Hbs values. Plant breeders often encounter difficulty when trying to select in early generations for superior genotypes for traits such as tillering capacity or yield, because it is very difficult to separate the effects of the environment from those of heredity. Therefore, selection for these traits in relatively homozygous lines should be delayed to later generations, when

Table 7. Means, variances (Var.), coefficients of variation (C.V.), broad sense heritability (Hbs), narrow sense heritability (Hns), and number of observations (n) for Harvest Index, Days to Heading, Rachis Internode Length, in ten spring wheat crosses and their parents.

	HARVEST INDEX						DAYS TO HEADING						RACHIS INTERNODE LENGTH					
CROSS or PARENTAL	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	28.84	15.37	13.60			54	99.76	8.56	2.93			54	5.65	.126	6.29			54
Sonora 64	43.48	10.95	7.61			68	85.08	2.50	1.86			68	5.03	.294	10.78			68
Sonora 64/Yaqui 50				19.2	>100					71.4	64.5					42.9	41.2	
F1	39.48	7.17	6.78			33	94.21	20.11	4.76			33	5.29	.215	8.76			33
F2	37.61	13.81	9.88			53	96.01	36.39	6.28			100	5.16	.371	11.80			99
Backcross 1	41.50	13.66	8.91			30	95.76	33.62	6.05			54	5.16	.286	10.35			52
Backcross 2	34.91	54.64	21.17			7	100.47	15.68	3.94			68	5.32	.303	10.35			67
Sonora 64/Olesen				44.3	28.9					76.7	48.9					62.3	19.1	
F1	45.53	2.21	3.27			30	94.80	12.72	3.76			30	4.71	.083	6.14			30
F2	43.48	12.48	8.13			91	91.43	38.98	6.83			137	4.66	.441	14.25			137
Backcross 1	43.44	10.33	7.40			33	94.96	25.56	5.32			81	4.70	.405	13.54			81
Backcross 2	43.99	11.02	7.55			49	93.52	33.35	6.17			81	4.99	.393	12.57			81
Sonora 64/Tordo				49.2	41.3					78.7	67.9					57.2	56.4	
F1	44.43	7.28	6.07			31	97.03	14.76	3.96			31	5.20	.151	7.48			31
F2	43.85	16.92	9.38			74	94.71	37.59	6.47			138	5.19	.456	13.01			138
Backcross 1	46.76	15.45	8.41			19	98.94	20.75	4.60			84	5.29	.347	11.14			82
Backcross 2	43.99	11.40	7.68			62	93.11	28.91	5.77			88	5.05	.308	10.99			88
Yaqui 50/Olesen				46.1	32.8					74.3	42.2					69.2	19.1	
F1	42.70	2.37	3.61			29	98.24	4.26	2.10			29	4.87	.245	10.16			29
F2	41.12	15.72	9.64			77	97.92	32.22	5.80			213	4.81	.533	15.19			211
Backcross 1	43.54	15.26	8.97			57	98.20	27.72	5.36			162	4.56	.478	15.15			161
Backcross 2	36.78	11.02	9.03			53	101.23	23.13	4.75			153	5.11	.486	13.64			150
Yaqui 50/Tordo				59.7	36.4					63.2	32.4					63.6	26.2	
F1	42.18	3.05	4.14			29	100.30	12.67	3.53			29	5.68	.204	7.96			29
F2	37.32	21.48	12.42			63	100.61	25.35	5.00			235	5.32	.431	12.34			234
Backcross 1	41.07	16.93	10.02			21	100.52	19.28	4.37			159	5.62	.438	11.78			157
Backcross 2	36.01	18.21	11.85			37	102.50	23.22	4.70			148	5.51	.311	10.12			146
Vicam 71/Sonora 64				43.3	29.2					77.9	75.8					44.2	39.5	
F1	45.42	9.87	6.92			36	95.67	20.46	4.73			36	4.68	.147	8.20			36
F2	45.32	15.93	8.81			106	93.11	41.01	6.88			140	4.71	.319	11.99			140
Backcross 1	43.18	8.74	6.85			46	97.63	28.69	5.49			85	4.44	.238	10.99			84
Backcross 2	42.49	18.47	10.11			69	92.64	22.24	5.09			75	4.82	.274	10.86			75
Vicam 71/Yaqui 50				61.6	53.3					83.8	83.0					63.4	11.4	
F1	40.49	2.11	3.59			34	99.38	5.88	2.44			34	4.92	.145	7.75			34
F2	39.00	20.62	11.64			83	99.56	38.37	6.22			236	4.59	.332	12.55			236
Backcross 1	41.57	13.91	8.97			52	100.32	19.06	4.35			139	4.48	.309	12.41			137
Backcross 2	35.03	16.33	11.54			44	102.88	25.83	4.94			134	5.14	.317	10.95			134
Vicam 71/Olesen				61.1	34.6					62.3	47.0					58.6	50.4	
F1	45.25	5.48	5.17			29	97.69	11.94	3.54			29	4.20	.063	6.00			29
F2	43.86	16.64	9.30			26	98.72	24.86	5.05			101	4.24	.224	11.15			101
Backcross 1	43.05	14.48	8.84			25	97.63	25.36	5.16			51	4.41	.223	10.70			51
Backcross 2	43.63	13.35	8.37			7	99.67	12.68	3.57			45	4.34	.112	7.72			45
Vicam 71/Tordo				50.4	32.5					69.4	60.4					63.4	42.4	
F1	43.01	2.47	3.66			34	99.06	7.15	2.70			34	4.70	.082	6.09			34
F2	43.48	10.95	7.61			72	98.79	19.73	4.50			150	4.65	.288	11.55			150
Backcross 1	45.13	9.46	6.82			3	101.05	12.45	3.49			81	4.94	.227	9.64			81
Backcross 2	42.62	8.88	6.99			29	98.69	15.10	3.94			82	4.43	.227	10.77			81
Tordo/Olesen				61.5	34.0					63.3	58.3					69.1	60.7	
F1	44.98	3.61	4.22			36	97.83	9.91	3.22			36	4.87	.039	4.04			36
F2	43.28	16.35	9.34			14	97.44	26.04	5.24			79	4.83	.326	11.83			79
Backcross 1	45.07	12.14	7.73			17	96.09	18.05	4.42			65	4.58	.240	10.70			65
Backcross 2	40.73	15.00	9.51			3	101.46	18.84	4.28			35	4.86	.214	9.50			35
Vicam 71	44.12	6.26	5.67			69	97.12	4.22	2.12			69	4.24	.093	7.18			69
Olesen	45.34	7.70	6.12			57	90.26	11.98	3.83			57	4.38	.122	8.00			57
Tordo	43.95	7.57	6.26			63	98.05	6.76	2.65			65	5.37	.141	6.98			65
Average				49.6	35.9					72.1	58.0					59.4	36.6	

Table 8. Means, variances (Var.), coefficients of variation (C.V.), broad sense heritability (Hbs), narrow sense heritability (Hns), and number of observations (n) for Number of Spikelets per Spike, Head Length, Days to Maturity in ten spring wheat crosses and their parents.

	NUMBER OF SPIKELETS PER SPIKE						HEAD LENGTH						DAYS TO MATURITY					
CROSS or PARENTAL	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	25.14	2.13	5.80			55	14.24	1.50	8.60			55	145.85	6.35	1.73			55
Sonora 64	21.45	1.96	6.53			68	10.82	1.63	11.79			68	137.00	9.52	2.25			68
Sonora 64/Yaqui 50				72.0	44.0					49.3	45.2					47.2	45.4	
F1	23.57	1.75	5.61			33	12.47	1.51	9.87			33	138.15	6.01	1.77			33
F2	23.36	6.95	11.29			101	12.03	3.05	14.51			101	139.48	13.80	2.66			102
Backcross 1	22.49	4.24	9.16			54	11.59	3.29	15.65			53	140.51	10.72	2.33			55
Backcross 2	24.20	6.60	10.62			69	12.88	1.43	9.28			69	142.54	10.62	2.28			70
Sonora 64/Olesen				67.3	44.2					61.6	5.8					69.4	65.1	
F1	23.03	.72	3.69			30	10.87	.57	6.93			30	140.73	3.69	1.36			30
F2	22.73	4.55	9.38			137	10.60	2.43	14.71			137	138.80	17.66	3.03			137
Backcross 1	22.34	2.25	6.72			84	10.45	3.95	19.10			84	140.28	11.00	2.36			84
Backcross 2	21.60	4.84	10.19			81	10.75	2.18	13.74			81	139.89	12.82	2.56			81
Sonora 64/Tordo				65.4	54.5					45.9	45.3					38.8	36.8	
F1	22.48	2.32	6.78			31	11.71	1.55	10.60			31	141.58	9.45	2.17			31
F2	23.47	6.63	10.97			138	12.14	2.69	13.50			138	139.12	14.52	2.74			138
Backcross 1	24.33	6.19	10.23			85	12.73	2.14	11.49			86	142.89	11.19	2.34			85
Backcross 2	22.02	3.46	8.45			88	11.12	2.02	12.78			88	138.31	12.81	2.59			88
Yaqui 50/Olesen				69.3	31.0					75.1	65.3					74.2	52.8	
F1	24.28	1.21	4.52			29	11.83	1.63	10.79			29	140.96	2.96	1.22			29
F2	24.54	5.55	9.60			240	11.93	4.99	18.72			238	142.70	17.18	2.90			232
Backcross 1	23.99	5.55	9.82			166	10.82	3.14	16.38			166	141.78	9.96	2.23			167
Backcross 2	24.41	3.83	8.02			163	12.57	3.58	15.05			164	142.54	15.33	2.75			166
Yaqui 50/Tordo				67.1	36.7					63.1	16.6					61.4	53.5	
F1	25.48	2.67	6.41			29	14.60	1.51	8.41			29	145.07	9.56	2.13			29
F2	25.24	7.50	10.85			278	13.49	3.79	14.44			278	143.62	20.39	3.14			267
Backcross 1	24.90	7.94	11.32			159	13.83	4.03	14.52			159	143.47	13.48	2.56			160
Backcross 2	25.39	4.31	8.18			163	14.01	2.92	12.20			163	144.31	16.39	2.80			165
Vicam 71/Sonora 64				31.1	20.8					65.9	59.5					55.1	54.6	
F1	22.72	2.92	7.52			36	10.61	1.33	10.87			36	139.61	7.56	1.97			36
F2	23.04	3.56	8.19			142	10.83	3.43	17.10			142	138.89	16.87	2.95			142
Backcross 1	23.36	3.24	7.71			87	10.32	1.73	16.76			87	140.73	12.45	2.51			87
Backcross 2	21.45	3.14	8.26			75	10.34	3.09	17.00			75	137.15	12.07	2.53			75
Vicam 71/Yaqui 50				59.6	45.7					72.7	49.7					76.1	62.3	
F1	25.29	2.58	6.35			34	12.48	.93	7.73			34	142.17	4.21	1.44			34
F2	24.85	5.93	9.80			264	11.43	3.64	16.69			264	142.70	22.57	3.33			264
Backcross 1	24.67	5.59	9.58			147	10.95	2.22	13.59			147	142.17	12.57	2.49			145
Backcross 2	24.85	3.56	7.59			156	12.83	3.25	14.06			156	143.40	18.51	3.00			156
Vicam 71/Olesen				57.5	54.4					76.3	42.9					64.5	50.1	
F1	23.65	1.95	5.90			29	9.91	.41	6.47			29	142.38	5.38	1.63			29
F2	23.87	4.87	9.24			128	10.03	2.19	14.77			129	142.14	14.10	2.64			109
Backcross 1	23.25	3.54	8.09			63	10.25	1.58	12.27			63	140.71	10.21	2.04			58
Backcross 2	23.11	3.55	8.15			66	9.89	1.86	13.79			66	142.26	10.93	1.85			53
Vicam 71/Tordo				48.1	4.7					69.2	58.1					50.7	40.2	
F1	25.15	1.95	5.55			34	11.82	.82	7.64			34	143.11	3.50	1.31			34
F2	24.59	4.52	8.65			152	11.40	2.77	14.60			152	141.48	11.40	2.39			151
Backcross 1	25.50	3.36	7.19			82	12.61	1.78	10.57			82	143.77	8.15	1.99			82
Backcross 2	24.27	5.47	9.64			83	10.77	2.15	13.62			83	141.70	10.07	2.24			84
Tordo/Olesen				64.6	23.0					70.2	58.3					46.9	24.8	
F1	24.33	1.14	4.39			36	11.86	.48	5.84			36	141.80	2.79	1.18			36
F2	23.91	5.21	9.54			104	11.45	2.54	13.91			104	142.34	9.09	2.12			89
Backcross 1	24.00	4.95	9.27			78	10.97	1.21	10.03			78	141.94	7.74	1.96			71
Backcross 2	23.40	4.27	8.83			47	11.44	2.39	13.51			47	143.03	8.19	2.00			37
Vicam 71	23.91	2.48	6.58			70	10.18	.55	7.29			70	141.71	5.65	1.68			70
Olesen	23.28	1.78	5.73			57	10.17	.60	7.63			57	141.23	4.00	1.42			57
Tordo	25.08	2.61	6.44			65	13.46	1.19	8.10			65	145.37	7.70	1.91			65
Average				60.2	35.9					64.9	44.7					58.4	48.6	

Table 9. Means, variances (Var.), coefficients of variation (C.V.), broad sense heritability (Hbs), narrow sense heritability (Hns), and number of observations (n) for Grain Filling Period, number of Kernels per Spikelet, Kernel Weight in ten spring wheat crosses and their parents.

GRAIN FILLING PERIOD

CROSS or PARENTAL	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	45.76	18.00	9.27			54
Sonora 64	52.40	8.54	5.58			68
Sonora 64/Yaqui 50				44.1	40.0	
F1	45.06	15.81	8.82			33
F2	43.55	25.24	11.54			100
Backcross 1	44.91	23.54	10.80			54
Backcross 2	42.00	16.84	9.77			68
Sonora 64/Olesen				68.6	42.1	
F1	46.53	6.46	5.46			30
F2	47.77	29.31	11.33			137
Backcross 1	45.22	20.82	10.09			81
Backcross 2	46.68	25.47	10.81			81
Sonora 64/Tordo				61.4	36.3	
F1	45.06	9.26	6.75			31
F2	44.44	25.01	11.25			138
Backcross 1	43.79	17.11	9.45			84
Backcross 2	45.64	23.84	10.70			88
Yaqui 50/Olesen				45.0	51.6	
F1	42.93	6.21	5.80			29
F2	44.33	22.32	10.66			213
Backcross 1	43.57	17.64	9.64			162
Backcross 2	40.99	15.48	9.60			153
Yaqui 50/Tordo				24.9	22.9	
F1	44.17	10.79	7.44			29
F2	42.39	17.74	9.93			235
Backcross 1	43.01	15.89	9.27			158
Backcross 2	41.29	15.53	9.54			148
Vicam 71/Sonora 64				66.8	62.5	
F1	44.33	14.06	8.46			36
F2	46.06	27.77	11.44			140
Backcross 1	43.33	17.51	9.66			85
Backcross 2	44.68	20.68	10.18			75
Vicam 71/Yaqui 50				44.8	37.0	
F1	42.97	10.03	7.37			34
F2	42.37	19.99	10.55			236
Backcross 1	41.70	11.59	8.16			139
Backcross 2	39.29	20.99	11.66			134
Vicam 71/Olesen				54.6	46.4	
F1	44.96	15.82	8.85			29
F2	43.56	24.59	11.38			101
Backcross 1	43.41	25.59	11.58			51
Backcross 2	42.91	12.18	8.13			45
Vicam 71/Tordo				56.4	58.3	
F1	44.29	10.88	7.45			34
F2	42.87	20.73	10.62			150
Backcross 1	42.55	15.05	9.12			81
Backcross 2	43.11	14.33	8.78			82
Tordo/Olesen				57.0	78.9	
F1	44.19	10.27	7.25			36
F2	45.73	26.45	11.25			79
Backcross 1	46.38	17.90	9.12			65
Backcross 2	41.74	14.14	9.01			35
Vicam 71	44.91	5.05	5.00			69
Olesen	51.40	12.64	6.92			57
Tordo	47.40	11.18	7.05			65
Average				52.3	47.6	

KERNELS PER SPIKELET

CROSS or PARENTAL	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	2.31	.128	15.46			54
Sonora 64	2.72	.076	10.13			68
Sonora 64/Yaqui 50				34.0	15.8	
F1	2.66	.097	11.68			33
F2	2.45	.152	15.91			99
Backcross 1	2.54	.127	14.03			53
Backcross 2	2.68	.153	14.60			67
Sonora 64/Olesen				56.3	19.6	
F1	2.82	.051	8.04			30
F2	2.71	.155	14.54			136
Backcross 1	2.69	.163	15.01			81
Backcross 2	2.75	.117	12.44			81
Sonora 64/Tordo				62.3	19.9	
F1	2.64	.070	10.02			31
F2	2.48	.176	16.88			138
Backcross 1	2.48	.138	14.96			83
Backcross 2	2.64	.179	16.03			88
Yaqui 50/Olesen				45.4	32.8	
F1	2.81	.081	10.09			29
F2	2.50	.174	16.67			213
Backcross 1	2.56	.176	16.39			161
Backcross 2	2.42	.115	14.04			150
Yaqui 50/Tordo				34.5	24.1	
F1	2.51	.088	11.85			29
F2	2.39	.137	15.51			234
Backcross 1	2.36	.139	15.80			156
Backcross 2	2.42	.102	13.20			146
Vicam 71/Sonora 64				57.1	35.2	
F1	2.51	.057	9.55			36
F2	2.50	.122	13.93			140
Backcross 1	2.31	.071	11.53			84
Backcross 2	2.59	.130	13.92			74
Vicam 71/Yaqui 50				61.7	49.7	
F1	2.55	.047	8.52			34
F2	2.39	.173	17.40			236
Backcross 1	2.40	.125	14.74			136
Backcross 2	2.31	.135	15.91			134
Vicam 71/Olesen				70.8	36.4	
F1	2.45	.061	10.00			29
F2	2.41	.184	17.80			101
Backcross 1	2.36	.190	18.47			51
Backcross 2	2.37	.111	14.05			45
Vicam 71/Tordo				76.2	80.1	
F1	2.42	.045	8.73			34
F2	2.33	.171	17.77			150
Backcross 1	2.29	.105	14.15			81
Backcross 2	2.20	.100	14.33			81
Tordo/Olesen				68.8	23.9	
F1	2.36	.036	7.98			36
F2	2.49	.176	16.87			79
Backcross 1	2.46	.137	15.01			65
Backcross 2	2.68	.173	15.52			34
Vicam 71	2.24	.024	6.89			69
Olesen	2.51	.076	10.98			57
Tordo	2.18	.053	10.57			63
Average				56.7	33.8	

KERNEL WEIGHT

CROSS or PARENTAL	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	35.67	12.83	10.04			54
Sonora 64	41.23	5.99	5.93			68
Sonora 64/Yaqui 50				55.9	19.0	
F1	42.75	8.15	6.68			33
F2	40.78	20.39	11.07			100
Backcross 1	39.75	18.17	10.72			54
Backcross 2	37.27	18.73	11.61			67
Sonora 64/Olesen				69.7	41.5	
F1	41.89	6.41	6.04			30
F2	40.14	17.56	10.45			136
Backcross 1	38.20	13.96	9.78			81
Backcross 2	40.09	13.87	9.28			81
Sonora 64/Tordo				71.5	48.3	
F1	44.50	11.12	7.49			31
F2	44.18	33.34	13.07			138
Backcross 1	42.53	30.14	12.91			84
Backcross 2	43.18	20.45	10.47			88
Yaqui 50/Olesen				72.1	22.8	
F1	42.30	6.63	6.09			29
F2	39.64	27.56	13.24			213
Backcross 1	37.27	24.19	13.20			162
Backcross 2	39.80	24.66	12.48			153
Yaqui 50/Tordo				66.5	57.4	
F1	42.63	15.61	9.27			29
F2	41.08	39.64	15.32			234
Backcross 1	41.36	25.32	12.17			158
Backcross 2	38.97	31.19	14.33			146
Vicam 71/Sonora 64				59.9	58.1	
F1	42.58	8.68	6.92			36
F2	41.53	21.65	11.20			140
Backcross 1	41.18	15.45	9.55			84
Backcross 2	42.76	15.28	9.14			74
Vicam 71/Yaqui 50				67.1	32.9	
F1	41.50	8.11	6.86			34
F2	37.93	26.45	13.56			236
Backcross 1	38.74	16.84	10.59			138
Backcross 2	39.02	27.36	13.41			134
Vicam 71/Olesen				76.8	43.9	
F1	37.57	4.37	5.56			29
F2	36.09	18.88	12.04			101
Backcross 1	37.48	13.87	9.94			51
Backcross 2	37.71	15.60	10.48			45
Vicam 71/Tordo				28.3	12.1	
F1	42.44	12.83	8.45			34
F2	43.21	13.69	8.56			150
Backcross 1	42.85	15.09	9.07			81
Backcross 2	41.87	10.63	7.79			82
Tordo/Olesen				63.3	20.6	
F1	38.47	11.66	8.87			36
F2	39.97	24.20	12.31			79
Backcross 1	37.49	21.27	12.30			65
Backcross 2	39.36	22.15	11.96			35
Vicam 71	39.90	5.19	5.71			69
Olesen	36.89	3.57	5.12			57
Tordo	43.65	11.41	7.74			63
Average				63.1	35.7	

Table 10. Means, variances (Var.), coefficients of variation (C.V.), broad sense heritability (Hbs), narrow sense heritability (Hns), and number of observations (n) for Number of Tillers per plant, Yield per plant, Head weight in ten spring wheat crosses and their parents.

CROSS or PARENTAL	NUMBER OF TILLERS						YIELD						HEAD WEIGHT					
	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n	MEAN	VAR.	C.V.	Hbs	Hns	n
Yaqui 50	32.14	143.90	37.32			55	64.87	500.13	34.47			54	2.07	.144	18.35			54
Sonora 64	24.22	93.79	39.98			68	58.34	545.09	40.02			68	2.40	.098	13.05			68
Sonora 64/Yaqui 50				30.4	>100					13.4	77.5					35.3	23.1	
F1	23.30	47.22	29.49			33	63.11	452.92	33.72			33	2.66	.144	14.27			33
F2	26.30	136.39	44.41			101	61.08	576.42	39.30			100	2.32	.199	19.23			99
Backcross 1	21.68	47.01	31.62			54	48.67	201.29	29.15			53	2.28	.184	18.81			53
Backcross 2	23.67	80.87	38.00			69	57.05	404.64	35.26			68	2.40	.168	17.04			67
Sonora 64/Olesen				8.2	36.6					18.3	47.5					64.0	16.7	
F1	20.07	37.86	30.66			30	54.17	247.96	29.07			30	2.72	.085	10.68			30
F2	20.97	69.92	39.87			137	51.88	482.79	42.35			137	2.45	.239	19.95			136
Backcross 1	17.48	42.25	37.17			84	41.45	316.75	42.93			81	2.31	.207	19.69			81
Backcross 2	21.13	71.99	40.14			81	49.97	419.36	40.98			81	2.37	.231	20.27			81
Sonora 64/Tordo				7.0	>100					4.5	61.8					48.9	13.6	
F1	13.74	23.60	35.35			31	37.82	310.97	46.62			31	2.64	.164	15.34			31
F2	21.80	68.40	37.94			138	56.21	429.01	36.85			138	2.57	.257	19.73			138
Backcross 1	18.05	31.43	31.07			86	46.17	276.60	36.02			84	2.54	.237	19.17			84
Backcross 2	16.86	34.55	34.86			88	42.97	316.48	41.40			88	2.49	.242	19.76			88
Yaqui 50/Olesen				26.1	74.3					11.1	27.9					63.4	15.8	
F1	21.90	54.95	33.85			29	63.35	519.38	35.97			29	2.88	.081	9.91			29
F2	26.85	117.24	40.33			240	62.57	518.70	36.40			213	2.41	.273	21.66			213
Backcross 1	20.86	70.12	40.14			166	46.80	434.42	44.53			162	2.29	.341	25.48			161
Backcross 2	20.98	77.27	41.90			164	50.48	458.41	42.41			153	2.33	.162	17.24			151
Yaqui 50/Tordo				5.0	68.9					8.8	61.0					53.7	53.4	
F1	20.31	56.36	36.96			29	54.19	498.69	41.21			29	2.71	.171	15.27			29
F2	21.14	95.97	46.34			278	50.71	501.42	44.16			235	2.45	.322	23.11			234
Backcross 1	19.71	53.41	37.08			159	46.96	341.32	39.34			159	2.43	.297	22.45			156
Backcross 2	21.26	72.40	40.03			163	50.75	355.61	37.16			146	2.37	.175	17.67			146
Vicam 71/Sonora 64				9.0	87.9					8.6	76.5					53.8	7.7	
F1	20.11	45.53	33.55			36	49.95	532.94	46.21			36	2.42	.096	12.81			36
F2	25.39	89.27	37.21			142	61.03	570.12	39.12			140	2.38	.169	17.27			140
Backcross 1	20.71	63.37	38.43			87	47.93	415.72	42.53			85	2.23	.139	16.72			84
Backcross 2	15.65	36.72	38.71			75	37.84	288.48	44.88			75	2.40	.186	17.97			74
Vicam 71/Yaqui 50				7.2	24.5					9.7	46.7					52.4	41.6	
F1	30.44	58.98	29.20			34	81.33	528.60	28.27			34	2.66	.080	10.62			34
F2	26.15	110.47	40.01			263	58.52	558.87	40.40			236	2.23	.185	19.30			236
Backcross 1	24.44	100.70	41.06			147	56.16	536.44	41.24			138	2.28	.141	16.50			136
Backcross 2	24.17	93.20	39.95			156	52.35	320.42	34.19			134	2.21	.152	17.64			134
Vicam 71/Olesen				16.5	3.5					16.3	46.8					62.8	13.2	
F1	22.07	86.21	42.07			29	48.19	529.28	47.74			29	2.18	.088	13.66			29
F2	27.55	100.50	36.38			128	62.62	548.90	37.42			101	2.12	.182	20.11			101
Backcross 1	22.59	113.41	47.15			63	48.68	504.80	46.15			51	2.07	.178	20.38			51
Backcross 2	23.17	84.11	39.59			66	57.38	336.05	31.95			45	2.13	.162	18.90			45
Vicam 71/Tordo				13.0	77.3					8.8	45.1					63.6	62.3	
F1	21.53	76.92	40.74			34	54.53	395.36	36.46			34	2.54	.117	13.49			34
F2	20.41	89.44	46.34			152	51.35	458.55	41.70			150	2.47	.265	20.82			150
Backcross 1	18.10	58.19	42.15			82	44.94	294.54	38.19			81	2.49	.181	17.09			81
Backcross 2	21.64	51.53	33.18			83	49.86	415.65	40.89			82	2.24	.184	19.14			81
Tordo/Olesen				22.7	69.4					51.1	79.7					67.5	31.4	
F1	22.17	51.17	32.27			36	48.95	232.94	31.18			36	2.23	.066	11.53			36
F2	23.89	79.98	37.43			104	61.37	660.78	41.89			79	2.43	.280	21.74			79
Backcross 1	24.49	63.47	32.54			78	55.51	347.57	33.58			65	2.25	.212	20.46			65
Backcross 2	13.87	40.94	46.12			47	36.62	447.10	57.74			34	2.17	.260	23.50			35
Vicam 71	31.40	104.53	32.56			70	68.64	486.05	32.12			69	2.15	.040	9.29			69
Olesen	21.53	61.00	36.28			57	46.96	363.77	40.62			57	2.14	.075	12.81			57
Tordo	24.01	73.36	35.66			65	57.32	373.32	33.70			63	2.39	.132	15.21			63
Average				14.5	64.2					15.1	57.1					56.5	27.9	

the role of environment can be better assessed through replications over locations and years.

Narrow sense heritability estimates were in general smaller than Hbs values. There were, however, two exceptions: number of tillers per plant and grain yield per plant. Narrow sense heritability estimates were very high for these traits and in two crosses Hns estimates for number of tillers per plant were over 100 percent. Broad sense heritability estimates for tiller number and yield, however, were slightly less than those reported previously for wheat (Johnson, et al., 1966). In general, Hns values for grain yield and to a lesser degree for number of tillers per plant in wheat have been reported by other workers to be low (Alcala, 1973; Anwar and Chowdhry, 1969; Singh and Anand, 1971b) and even negative heritability values in both narrow sense and broad sense have also been reported for these two traits (Johnson, et al., 1966; Daaloul, 1973).

The analysis of variance showed that differences among parental lines and between the different generations for plant grain yield and number of tillers per plant were not as great as they were for all the other traits, even though the means of the parental cultivars were widely separated (Table 10). The effects of the environment on the expression of tiller number and grain yield may have been so great as to inflate the error term, making differences more difficult to detect. The same reasons may account for the discrepancies observed between Hbs and Hns. Sometimes the variances for tiller number and grain yield per plant in the F_2 were smaller than the parental and F_1 variances with the backcrosses variances being the smallest (Table 10). When using Warner's formula for calculating Hns (1952), the F_2 variances were doubled while the summation of the BC variances was quite small. Methods available to estimate heritability are based on the assumption that interactions between additive and non-additive effects, non-additive gene action interactions, and genotype-environment interactions have a value of zero. As a result the additive and/or dominance components of variance may be inflated (Allard, 1960). Inflation of the additive gene effects for tiller number and plant grain yield could have occurred in this experiment and as a consequence very high Hns estimations were obtained.

Narrow sense heritability estimates for plant height were consistently high for all 10 crosses (Table 3). Values ranged from 74.3 to 88.2 percent. Therefore, plant height is considered a highly heritable trait that can be selected for in the F_2 and F_3 generations. Narrow sense heritability values for days to heading were also high, with the crosses Vicam 71/Yaqui 50, Vicam 71/Sonora 64, and Sonora 64/Tordo having the largest values. For days to maturity Hns ranged from 65.1 percent in the cross Sonora 64/Olesen to 24.8 percent in the cross Tordo/Olesen. Most of the crosses had heritability values for this character of 50 percent or more, so selection for early or late material could be made in early generations. Length of grain filling period was also a trait with high additive genetic effects. Crosses with the highest heritability values in the narrow sense were Tordo/Olesen (78.9 percent), Vicam 71/Sonora 64 (62.5 percent), and Vicam 71/Tordo (58.8 percent).

Rachis internode length and head length had similar Hns values; the crosses Yaqui 50/Olesen and Tordo/Olesen had the highest Hns values. Tordo was a good parent in terms of head size; additive gene action was significantly present in the expression of this trait in all the crosses made with this cultivar.

Narrow sense heritability estimates for head grain weight and harvest index were low when averaged for all the crosses. However, there were two crosses with high levels of additive gene action for these traits. Vicam 71/Tordo had a Hns value for head weight of 62.3 percent and the cross Vicam 71/Yaqui 50 had a harvest index Hns value of 53.3 percent indicating that additive gene action could be important in the expression of these traits in these two crosses. Heritability estimates for harvest index were consistently lower than those for plant height, hence selection for short strawed genotypes would probably be a more efficient way of improving grain to straw ratios.

When all the crosses were averaged Hns estimates for the other yield components besides number of tillers per plant were relatively low. However, there were some crosses that showed high Hns estimates for some of the yield components. Sonora 64/Tordo had a Hns estimate of 54.5 percent for number of spikelets per spike. Vicam 71/Sonora 64 (58.1 percent), Yaqui 50/Tordo (57.4 percent) and Sonora 64/Tordo (48.3 percent) were crosses where additive gene action was important in the expression of kernel weight. For kernels per spikelet Hns was particularly high in the cross Vicam 71/Tordo, indicating that it should be possible to select plants with a large number of kernels per spikelet with the high kernel weight of Tordo.

The characters studied can be ranked as follows according to the magnitude of additive gene action involved in their expression as estimated by Hns: plant height, number of tillers per plant, days to heading, plant grain yield, days to maturity, length of grain filling period, head length, rachis internode length, harvest index, number of spikelets per spike, kernel weight, number of kernels per spikelet and head weight. However, the estimates of Hns for plant yield and number of tillers per plant were particularly high and there is the possibility that they are overestimations of the amount of addive gene action involved in the expression of this traits.

Correlations among agronomic traits - The practice of selection for several traits at one time requires a knowledge of the interrelationships that exist among and between them. Phenotypic correlations, which are very often used to evaluate associations among traits, are sometimes influenced to a large extent by environmental effects. Therefore correlations at the genotypic level may give a better idea of the gene associations existing in a population.

Genotypic correlations may be computed from phenotypic and environmental correlations and either narrow or broad sense heritability estimates. In self-pollinated crops narrow sense heritabilities are more appropriate for calculating genetic correlations because genetic associations with additive gene action will probably remain the same after several generations of selfing. However, in the present experiment, Hns estimates for number of tillers per plant and plant grain yield appeared to be overestimations of the additive components of variance; therefore, broad sense heritabilities were judged to be more appropriate for calculating genetic correlations involving these two traits. For the remaining 11 characters the genetic correlations were the actual breeding values because Hns estimates were used for their computation. The phenotypic, environmental and genotypic correlations were calculated for all possible combinations of 13 characters in every cross (Tables 11 to 20). Because a large number of observations were used to compute the correlations and degrees of freedom were quite large, probability levels of significance were not assigned.

In general the magnitude of the phenotypic and environmental correlations was consistent, to some extent, for all crosses. There was, however, a lack of consistency for the genotypic correlations.

Table 11. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Sonora 64/Yaqui 50.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.8490	.1188	.3886	.0131	.3957	.3477	-.0904	-.1880	.2599	.4183	.3837	.2673
	rE	.8748	.4362	.3367	.1565	.5917	.4175	-.3430	-.1033	.6286	.3043	.2132	.2613
	rG(1)	.8415	-.7617	.6947	-.7394	.4954	.5872	.3394	-.4742	-.8346	.8479	.9855	.3038
Tillers	rPh		.1660	.1461	-.1931	.0557	.3578	-.0329	.2540	.2358	.4254	.4369	.1060
	rE		.4578	-.0740	.0054	.1708	.3609	-.2993	-.0789	.6604	.1785	.1625	.1857
	rG(1)		-.3276	.9251	-.8203	.2613	.4794	.2617	.8146	.5476	.8502	.9408	-.1377
Spikelet No.	rPh			.1841	-.1409	.3400	.6157	.2146	.1504	-.1501	.6076	.3174	-.2903
	rE			-.0069	.0503	.3247	.4547	.0577	.3768	.3751	.4906	-.0859	-.1564
	rG			.7162	-.6045	.3981	.7939	.3545	-.1297	-.8531	.7530	.8612	-.6368
Kernel/Spkt	rPh				.1702	.8510	.4175	-.0927	-.0530	.0929	.3755	.4983	.3972
	rE				.3592	.8356	.3907	-.0788	-.0875	.0796	.2390	.4774	.0342
	rG				-.7298	.9349	.7687	-.1554	.0236	.1445	.7976	.6365	.1620
Kernel wt.	rPh					.4503	.0114	-.4610	-.5919	.1047	-.3137	-.2071	.3574
	rE					.7016	.0556	-.4756	-.4812	.0843	-.0098	-.0304	.5919
	rG					-.4937	-.0181	-.5883	-.9257	.1666	-.0223	-.6652	-.6358
Head Wt.	rPh						.4779	-.1616	-.2073	.0498	.3359	.0498	.4061
	rE						.1863	-.2707	-.1690	.3096	.3058	.1451	.3212
	rG						.1564	-.0522	-.3020	-.5280	.4252	-.1548	.7261
Height	rPh							.1712	.0323	-.1831	.5808	.4856	-.5036
	rE							.2862	.4615	.1469	.4498	.2192	-.3734
	rG							.0857	-.1525	-.3848	.7317	.7101	-.9303
Days to Heading	rPh								.5720	-.7767	.2853	.1265	-.4031
	rE								.7675	-.6741	.3013	.3032	-.4588
	rG								.4326	-.9166	.2823	-.0233	-.6983
Days to Maturity	rPh									.0675	.3625	.2487	-.3304
	rE									.0311	.5092	.3450	-.5169
	rG									.1166	.6149	.1230	.0438
Grain Filling Period	rPh										-.0761	.0347	.2330
	rE										.3293	-.0021	.1093
	rG										-.6230	.0885	.5661
Head Length	rPh											.8793	.0858
	rE											.8249	-.1420
	rG											.9525	.6120
Rachis Internode	rPh												.2827
	rE												.0523
	rG												.8770

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits, narrow sense heritabilities were used.

Table 12. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Sonora 64/Olesen.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.9109	.3306	.3544	-.0181	.4048	.4437	-.2431	.3819	.5646	.4344	.2904	-.0814
	rE	.9396	.4160	.2337	-.1219	.2675	.1632	-.0934	.2309	.5686	.4554	.2756	.2134
	rG(1)	.7933	.1748	.8712	.2401	1.0532	.9819	.6109	.7492	.6252	.3386	.3548	-1.0612
Tillers	rPh		.2626	-.0436	-.2013	-.1290	.2623	-.2496	.4187	.6065	.4078	.2933	-.1641
	rE		.3555	-.1982	-.3657	-.2566	.0445	-.1311	.3910	.5760	.4817	.3360	-.0946
	rG(1)		.0429	.9992	.3615	.8151	.9366	-.7981	.8543	1.0041	.5821	.0299	-.5695
Spikelet Number	rPh			-.0772	-.1982	.2163	.0982	.1253	.2665	.0965	.3634	-.1210	-.2161
	rE			-.2341	.0114	.1164	.0247	-.0091	.2741	.4540	.4646	-.0208	.0618
	rG			.2704	-.4780	.5040	.1494	.2800	.1967	-.3745	.1659	-.3683	-.7135
Kernels/Spikelet	rPh				.0254	.7927	.3268	.0234	.1465	.0587	.0904	.1379	.1627
	rE				.1471	.7843	-.0288	-.2546	-.2527	-.0238	.0660	.2041	.0077
	rG				-.2647	.8338	.8343	.6027	.7849	.2609	.3091	-.1380	.6591
Kernel Weight	rPh					.4513	.4089	-.1785	-.4384	-.1417	-.1057	-.0057	.1512
	rE					.6325	.1126	-.7218	-.6077	.1209	-.3177	-.4104	.4672
	rG					.0371	.6354	.4798	-.3152	-.5073	.8388	.9826	-.4334
Head Weight	rPh						.5047	-.0115	.0068	.0103	.1642	.0698	.1325
	rE						.4372	-.4139	-.4771	.1796	.0868	-.1193	.1830
	rG						.9167	.9047	.8008	-.4316	.8871	.9392	-.0379
Height	rPh							-.0122	.0344	.0468	.2724	.2482	-.3537
	rE							-.0780	.0258	.2776	.3327	-.4104	-.0711
	rG							.0165	.0383	-.0663	.6403	.9987	-.6707
Days to Heading	rPh								.4202	-.6663	.1265	-.0117	-.2948
	rE								.7848	-.5567	.3875	.4331	-.2398
	rG								.1573	-.8011	-.8452	-.9495	-.3997
Days to Maturity	rPh									.3696	.3556	.2761	-.1671
	rE									.2541	.5089	.4231	-.1512
	rG									.4878	.4984	.1454	-.2116
Grain Filling Period	rPh										.2648	.2377	.1454
	rE										.2104	.1130	.0170
	rG										.7002	.5655	.3856
Head Length	rPh											.8210	-.0799
	rE											.8535	-.1409
	rG											.7213	.2735
Rachis Internode	rPh												.0114
	rE												.0981
	rG												-.2681

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits, narrow sense heritabilities were used.

Table 13. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Sonora 64/Tordo.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.8481	.2787	.4836	.1291	.5279	.3136	-.2604	.1091	.3946	.1487	.0931	-.0286
	rE	.8526	.6351	.5266	.3435	.6794	.5408	-.2878	-.0112	.5718	.4125	.1552	.1098
	rG(1)	.7946	-.8936	.2433	-.7615	-1.1407	.5760	-.5781	.9154	-.4020	-1.0467	.0442	-.8128
Tillers	rPh		.0664	.1532	.1846	.4219	.0132	-.1100	.2614	.3234	.1778	.0351	.0267
	rE		.3485	.2485	.4985	.5889	.5193	-.3942	.1876	.6070	.4148	.0962	.2282
	rG(1)		-.8207	-.5192	-.8759	-1.0587	-.7224	.4834	.7326	-.9021	-.6629	-.1316	-.8346
Spikelet No.	rPh			-.1956	-.2259	.0471	-.1248	.1776	.2623	-.0145	.1974	-.3553	-.0221
	rE			.3128	.0777	.4726	.5404	.2134	.3647	.2157	.7007	.0913	.4878
	rG			-.7054	-.5137	-.9154	-.3852	.1578	.1490	-.2936	-.3062	-.7142	-.5779
Kernel/Spikelet	rPh				-.0087	.7083	.3014	-.1352	.0888	.2383	.2355	.3160	.0288
	rE				-.0921	.7911	.2521	.2379	.1796	.0716	.5119	.3558	.2588
	rG				.1631	.3050	.5231	-.6960	-.1441	.6963	-.3442	.3156	-.5185
Kernel Wt.	rPh					.5383	.6083	-.4215	-.6848	-.0078	-.2620	-.0711	-.1727
	rE					.4358	-.0084	-.6339	-.5996	.2920	-.1051	-.2234	.3569
	rG					.9639	.9496	-.7851	-.8113	-.4188	-.4406	.0670	-.8269
Head Wt.	rPh						.5003	-.3069	-.2392	.1977	.1350	.0950	-.1418
	rE						.4464	-.0626	-.0376	.2591	.5417	.1593	.1079
	rG						1.0048	-.9014	-.9450	.0247	-.9564	-.0100	-.9225
Height	rPh							-.2036	-.4660	-.1011	.0520	.1187	-.5299
	rE							.1724	.4282	.3544	.7207	.5278	.2014
	rG							-.3157	-1.0600	-.3739	-.2413	-.0195	-.9896
Days to Heading	rPh								.5771	-.7519	.2526	.0867	-.2038
	rE								.6925	-.5873	.3229	.2572	-.3604
	rG								.5305	-.9796	.2115	-.0154	-.0894
Days to Maturity	rPh									.0573	.3921	.1725	-.0140
	rE									.1384	.5164	.3978	-.1156
	rG									-.0835	.2167	-.0797	.1447
Grain Filling Period	rPh										.0028	.0364	.2266
	rE										.2429	.1545	.4820
	rG										-.3467	-.0995	-.1760
Head Length	rPh											.8217	.0431
	rE											.7734	.2521
	rG											.8784	-.1583
Rachis Internode	rPh												.1242
	rE												-.0752
	rG												.3362

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits, narrow sense heritabilities were used.

Table 14. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Yaqui 50/Olesen.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.8058	.1813	.1604	.2401	.3502	.3788	-.1721	-.0210	.2061	.2922	.2539	-.0253
	rE	.9666	.4076	.0402	.2350	.3436	.5134	-.2920	.2651	.4443	.6689	.4511	.2218
	rG(1)	.1312	-.7436	.6778	.2855	.3996	.5641	.1719	-.7961	-.3566	-.2946	-.8836	-1.0310
Tillers	rPh		.2421	-.3060	-.1677	-.2318	.0811	-.0667	.2050	.2491	.3218	.2521	-.0170
	rE		.3676	-.1532	.1078	-.1113	.4935	-.2737	.3664	.4926	.6301	.5371	.2593
	rG(1)		-.0717	-.6768	-1.0212	-.7091	-.2222	.3380	-.0307	-.1240	.0066	-.7309	-.6826
Spikelet Number	rPh			-.3123	-.4177	-.0912	.0967	.2517	.4583	-.3108	.5699	.1310	-.1729
	rE			-.1423	-.2492	.2143	.4498	-.1249	-.0892	.0202	.2898	-.0931	.0606
	rG			-.6114	-.8870	-.9313	-.1292	.9140	1.0114	-.8063	.9515	.8242	-.6716
Kernels/Spikelet	rPh				-.2933	.8147	.3117	-.1707	-.3058	-.0299	-.1649	-.0258	.0193
	rE				-.3925	.7512	.0699	.0561	-.3015	-.1954	.2016	.2393	.1132
	rG				-.0387	1.0966	.5556	-.5528	-.3268	.1982	-.5667	-.8080	-.1731
Kernel Weight	rPh					.6628	.4125	-.4670	-.5742	.1318	-.2565	-.0659	.0170
	rE					.6499	-.0232	-.2873	-.3403	-.0011	-.0478	-.0842	.1057
	rG					.7314	.9786	-.8868	-1.0629	.3862	-.6006	.0031	-.2162
Head Weight	rPh						.5196	-.1980	-.3949	-.0578	-.0469	.0014	-.0523
	rE						.3463	-.0440	-.3837	-.2068	.2845	.1366	.2152
	rG						1.0663	-.6479	-.5297	.3270	-.6248	-.6409	-.9408
Height	rPh							.0261	-.3373	-.2785	.1922	.1800	-.5602
	rE							-.1153	-.2009	.0234	.3840	.3097	-.2441
	rG							.1093	-.4237	-.4408	.1295	.1511	-.9172
Days to Heading	rPh								.5929	-.7478	.3989	.1673	-.1379
	rE								.1733	-.7604	.1790	.2869	-.2395
	rG								1.0642	-.7406	.6072	-.1017	.0305
Days to Maturity	rPh									.0666	.4321	.2589	.0967
	rE									.4657	.3303	.4168	.2102
	rG									-.2988	.5082	.0042	-.0521
Grain Filling Period	rPh										-.1437	.0026	.1849
	rE										.1028	.0848	.3639
	rG										-.3201	-.1607	.0550
Head Length	rPh											.8044	-.1572
	rE											.8661	.0621
	rG											.9783	-.4045
Rachis Internode	rPh												-.0705
	rE												-.0722
	rG												-.0690

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits narrow sense heritabilities were used.

Table 19. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Vicam 71/Tordo.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.8767	.4148	.4008	-.0069	.1899	.3747	-.3746	-.0170	.3361	.4014	.1304	.3416
	rE	.9055	.3801	.2927	-.1231	-.0662	.5041	-.4575	.1439	.5613	.4381	.4175	.2104
	rG(1)	.6592	.9398	1.0399	1.0012	.9768	.7514	-.4323	-.6554	-.0399	.5775	.8915	.7190
Tillers	rPh		.3225	.0147	-.2068	.0434	.1063	-.4266	.0717	.4664	.2770	.0722	.2322
	rE		.2925	.0452	-.3191	-.2773	.5717	-.4330	.3155	.5423	.3773	.3831	.0971
	rG(1)		.7169	-.0126	.5691	.7045	-.2247	-.7392	-.6755	.5052	.1786	-.8398	.7622
Spikelet Number	rPh			-.0166	-.1200	.3249	.1353	.0313	-.1384	-.0563	.4831	-.2520	.1062
	rE			-.4536	-.0520	.1712	-.0529	.1925	-.1693	-.2993	.6100	-.1467	.1888
	rG			.9325	-.9601	1.2990	.7517	-.5161	-.0771	.7997	.5908	-1.0168	-.3659
Kernels/Spikelet	rPh				.0782	.8451	.5422	.0101	-.0974	-.1080	.3249	.3578	.2482
	rE				-.1237	.3929	-.0308	-.0559	.4514	.2739	-.0081	.3982	-.0682
	rG				.4174	1.0439	.6507	.0371	-.4461	-.2735	.4797	.3826	.5354
Kernel Weight	rPh					.4159	.2566	-.1388	-.4834	-.2102	-.1190	-.0335	-.0733
	rE					.5153	-.2598	.1192	-.3574	-.3140	-.3859	-.3281	.1214
	rG					.4134	1.0415	-.7736	-1.0169	-.0757	.4345	.8828	-.8412
Head Weight	rPh						.6103	-.0255	-.2155	-.1589	.3957	.1682	.2234
	rE						-.3109	.2040	-.0097	-.2689	.0906	-.0381	.2212
	rG						.9118	-.1701	-.4214	-.0867	.5979	.3618	.2485
Height	rPh							.0207	-.2237	-.1974	.3456	.2444	-.0649
	rE							-.4674	-.0148	.4666	.0622	.1205	-.0445
	rG							.1668	-.3691	-.4196	.4635	.3483	-.0978
Days to Heading	rPh								.4312	-.7269	.0325	.0000	-.1970
	rE								.1258	-.8233	.0170	-.1495	.3113
	rG								.7508	-.6612	.0432	.1411	-.8079
Days to Maturity	rPh									.2706	.1158	.0320	.0141
	rE									.4312	.3353	.5757	.0337
	rG									.1142	-.1077	-.7409	-.0202
Grain Filling Period	rPh										.0382	.0150	.2030
	rE										.1298	.4303	-.2544
	rG										-.0276	-.3940	.7764
Head Length	rPh											.6879	.0506
	rE											.6932	.1618
	rG											.6998	-.0816
Rachis Internode	rPh												-.0262
	rE												.0611
	rG												-.1732

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits, narrow sense heritabilities were used.

Table 20. Phenotypic (rPh), environmental (rE), and genotypic (rG) correlations between all pairs of the thirteen characters measured for the wheat cross Tordo/Olesen.

		Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	rPh	.8262	.3448	.3117	.2096	.3734	.3145	-.5494	.0707	.5480	.2736	.0816	-.0280
	rE	.9241	.4950	-.0263	.1661	-.0219	.5416	-.5590	-.1545	.4622	.5694	.2827	.0855
	rG(1)	.7577	.1198	.9378	.9650	.9738	.2570	-.5443	.4618	.6292	.0302	-.0760	-.1837
Tillers	rPh		.4552	-.1422	-.1823	-.0576	.0366	-.4238	.1330	.4417	.2392	-.0121	.0566
	rE		.4558	-.2757	-.5061	-.3930	.5383	-.5061	-.0402	.4994	.5639	.3145	.0560
	rG(1)		.4532	.2973	.9905	.8562	-.3276	-.3752	.6897	.5671	-.2225	-.4496	.0598
Spikelet Number	rPh			-.2232	-.4082	.0860	-.1838	-.0037	.3320	.1565	.2921	-.2437	-.0809
	rE			-.2231	-.2773	.0309	.3190	.0000	.1513	.0639	.7180	-.0507	-.0417
	rG			-.2236	-.8792	.2364	-.6560	-.0101	.9080	.3069	-.3134	-.5776	-.1829
Kernels/Spikelet	rPh				.2967	.8565	.3619	-.2210	-.0685	.2368	-.0862	.0367	-.0074
	rE				.1668	.7444	-.1210	.0870	.0980	-.0936	-.1680	.0006	-.1637
	rG				.7528	1.0089	.8903	-.7233	-.5859	.6317	.0226	.0955	.3810
Kernel Weight	rPh					.6579	.3044	-.3390	-.2678	.1699	.1642	.2760	-.0086
	rE					.7063	-.1924	-.0616	-.5325	-.2725	-.3088	-.1328	.2314
	rG					.5372	.8819	-.8759	.6356	.6981	.9865	.9903	-.6654
Head Weight	rPh						.4885	-.3589	-.1124	.3115	.1223	.1659	-.0437
	rE						-.0966	-.0044	-.3120	-.2319	-.0668	-.1219	.0506
	rG						1.0024	-.8333	.4002	.8031	.3693	.5250	-.2379
Height	rPh							-.3749	.4255	.1074	.0238	.1122	-.4910
	rE							-.0462	-.0506	.0614	.5211	.3980	.1663
	rG							-.5152	-.8881	.1177	-.1485	.0234	-1.0070
Days to Heading	rPh								.2777	-.8062	-.2025	-.1950	.0277
	rE								.3142	-.8374	-.1746	-.2559	.0314
	rG								.2676	-.8224	-.2224	-.1537	.0252
Days to Maturity	rPh									.2665	.1548	-.0187	-.2384
	rE									.2207	.0377	-.0682	-.4506
	rG									.4037	.3516	.0474	.2722
Grain Filling Period	rPh										.2250	.1358	.0583
	rE										.2183	.2426	-.2725
	rG										.2363	.0953	.3089
Head Length	rPh											.8542	.3876
	rE											.6557	.0565
	rG											.9897	.8040
Rachis Internode	rPh												.4170
	rE												.1345
	rG												.7671

(1) Computation of genetic correlations for yield and tillers were done using broad sense heritabilities. For all the other measured traits, narrow sense heritabilities were used.

Some genetic correlations for certain traits consistently had high correlation values but others did not when assessed for each individual cross. Number of tillers per plant was highly positively correlated with plant grain yield at the genotypic level in seven of the 10 crosses (Tables 11, 12, 13, 15, 17, 19, and 20), while phenotypic and environmental correlations of the same two traits were always highly positively correlated. Number of kernels per spikelet and grain yield were highly positively correlated at the genotypic level in eight of the 10 crosses (Tables 11, 12, 14, 15, 17, 18, 19, and 20) but they were not correlated at the phenotypical and environmental level. This lack of association maybe due to the low heritability of yield per plant and the masking of genetic effects by the environment. The other two components of yield were less consistent in their genetic association with plant yield. Number of spikelets per spike was positively correlated with yield only in the crosses Vicam 71/Tordo and Yaqui 50/Tordo (Tables 15 and 19) and negatively correlated in three crosses (Tables 11, 13, and 14). Kernel weight was highly correlated with yield in six of the 10 crosses; however, three of the associations were negative (Tables 11, 13, 17, 18, 19, and 20). The three crosses showing high positive genetic correlations between plant grain yield and kernel weight were all possible combinations among the three dwarf cultivars. Progress in increasing grain yield through selection for high kernel weight in these three crosses is a strong possibility.

In the cross Vicam 71/Tordo there were high positive genetic correlations between grain yield and the four yield components; hence it is very likely that plant grain yield increase could be obtained in this cross through selection for high expression of yield components (Table 19).

The trait head grain weight was the recipient of the average contributions of spikelet number, kernels per spikelet, and kernel weight to plant yield. In five out of the 10 crosses head weight was positively genetically correlated with grain yield and only in two crosses was there a negative association between these traits (Tables 12, 13, 15, 16, 18, 19, and 20). Selection for increased head weight, in most of the cases, could be a means of increasing grain yield because head weight may be considered as an intermediate step between grain yield and its late components; i.e., kernels per spikelet, spikelet number and kernel weight. Head grain weight is a trait that deserves special attention because it could be easily implemented into a breeding program. A random sample of a fixed number of heads could be taken from those lines that looked promising in the field; they could be treshed and weighed and with this information the final selection could be made.

Other genetic associations that were fairly consistent among the crosses were number of tillers per plant and days to maturity. These two traits were highly positively correlated in 60 percent of the crosses (Tables 11, 12, 13, 15, 16, and 20). Number of kernels per spikelet and head weight were highly positively associated in terms of the genotypic correlation in 90 percent of the crosses. This association was also high for both phenotypic and environmental correlations (Tables 11, 12, 14, 15, 16, 17, 18, 19, and 20). High environmental correlations between agronomic traits may cause a problem when selection is based on correlated characters; however, the non-genetic influence caused by environmental interactions in the association of kernels per spikelet and head weight in this experiment may be overcome because of the consistent positive genetic correlation between these traits.

Kernel weight and plant height were genetically correlated in 50 percent of the crosses (Tables 13, 14, 18, 19, and 20). However, in this particular case the term plant height could be misleading: Three of the crosses were combinations among the three dwarf cultivars, another one was the cross Sonora 64/Tordo and only one cross involved the standard height parent, i. e., Yaqui 50/Olesen. This may suggest that the kernel weight-plant height association held true when the variability for plant height was not very large. Therefore those plants which were "tall" and also had high kernel weight, with the exception of the cross Yaqui 50/Olesen, could practically be considered dwarf wheats.

High negative genetic correlations were found between kernel weight and days to maturity in seven of the 10 crosses (Tables 11, 13, 14, 15, 16, 17, and 19). The genotypes which were early tended to have a heavy kernel weight. The late maturing genotypes had a lower kernel weight which may have resulted from rising temperatures and moisture stress conditions during the late part of the growing season.

Genetic correlations between head grain weight and plant height were positive and high in 70 percent of the crosses (Tables 12, 13, 14, 16, 18, 19, and 20), but again this association was present in most cases in those crosses involving the semi-dwarf wheat Sonora 64 and the three dwarf cultivars. The persistence of this type of association may indicate that in a cross between a tall standard variety and a dwarf cultivar, selection should be made for intermediate types in plant height and in a cross involving two short wheats selection should be in favour of relatively tall plants.

There was a high negative genetic correlation between plant height and harvest index in eight of the 10 crosses (Tables 11, 12, 13, 14, 15, 16, 17, and 20). In crosses where the genetic correlation for these two traits was not as high, dwarf parents were involved. High grain to straw ratios could be the result of increased rates of photosynthates translocated to the ear of the wheat plant due to sink-source relationships (Wallace, 1972). Also a high harvest index may be due to a reduction of height. With reduced plant height less nutrients are utilized for vegetative growth, and a relatively larger amount of assimilates are distributed to the grain (Borojevic, 1971).

Phenotypic, genotypic, and environmental correlations between days to heading and grain filling period (GFP) were high and negative in all 10 crosses. Days to maturity was never directly correlated with GFP. If length of GFP needs to be extended, the best indirect way of achieving it would be through selection for fast spike emergence. Increasing the duration of GFP could be a means of increasing the expression of number of kernels per spikelet and kernel weight, the two last yield components to develop. However, the genetic correlation between GFP with number of kernels per spikelet and kernel weight was high and positive in only two crosses (Tables 15, 18, and 20). Perhaps a high positive correlation between GFP with number of kernels per spikelet and kernel weight may have been observed more often if measurements of GFP were based on time from anthesis to senescence.

A very consistent association at the phenotypic, environmental, and genotypic level was between head length and rachis internode length. The observed correlations between these two traits were high and positive in all 10 crosses. An increase in the length of the head more often resulted in a more lax head rather than a higher number of spikelets per spike.

Some of the genetic correlations that were not consistent over all the crosses are of prime importance. Number of tillers per plant was negatively correlated with the other components of yield as follows: two crosses with number of spikelets per spike (Tables 13 and 15); in one cross with number of kernels per spikelet (Table 16); and in five crosses with kernel weight (Tables 11, 13, 14, 15, and 17). Tiller number per plant was found to have a large positive genetic correlation with the other components of yield as follows: spikelet number in one cross (Table 19); four crosses with kernels per spikelet (Tables 11, 12, 15, and 19); and two crosses with kernel weight (Tables 19 and 20). Therefore the possibility exists of increasing grain yield in several of the crosses studied by a combined increase of the components of yield without compensatory effects among them. This seems possible because yield components were often not correlated and even in some cases positively correlated. However kernel weight had a high and negative genetic correlation with tiller number per plant, spikelet number per spike and plant grain yield in some crosses (Tables 11, 13, 14, 15, 17, 19, and 20). These negative associations may be attributed to stress conditions that existed when this yield component was being finalized in its development. Most of the crosses showing this type of associations with kernel weight involved Yaqui 50 and Vicam 71, the two parents which had the largest number of tillers per plant and were late maturing. In general, the genetic correlations observed were characteristic of each individual cross, with the exception of those trait associations already mentioned that showed some consistency in their value and sign for most or all crosses. Many interrelationships differed from one cross to another due to different gene associations in the parental lines and/or the differences in their mean values of the characters under study.

For example, when Sonora 64 was crossed with Yaqui 50, (Son/Y), plant grain yield was highly negatively correlated with grain filling period and the genetic correlation of yield with head length and rachis internode length was high and positive (Table 11). These latter two characteristics are associated with the parental cultivar Yaqui 50 and this association may indicate that yield in this particular cross was mainly being transmitted by the parental variety Yaqui 50. However, when Sonora 64 was crossed with Olesen, (Son/On), grain filling period was highly positively associated with grain yield and head length while rachis internode length correlations with yield were small (Table 12). These same two crosses can be compared for other genetic correlations. When the cross was Son/Y, a positive correlation between plant tiller number and rachis internode was observed; with Son/On, there was no genetic association between these two traits. With Son/Y, there was a positive genetic correlation between spikelet number per spike with head length and rachis internode and a negative correlation with grain filling period. In the cross Son/On, associations between the same traits were negligible. With Son/Y, kernels per spikelet were positively correlated with head length and in the cross Son/On there was no correlation between these same traits. A negative genetic correlation between rachis internode length and kernel weight occurred in the cross Son/Y, and in Son/On there was a positive correlation between the same two traits. Grain filling period and plant height were positively associated at the genotypic level in the cross Son/On and negatively genetically correlated in the cross Son/Y.

The differences in genetic associations between these two crosses as well as among the other eight crosses should serve as an indication to the breeder that when selection is performed in these populations he has to remember the main characteristics of each of the parents of every cross and associate them with the potential of the individual plants or families that he is going to select. This could be true for almost any hybridization. Very often one of the genotypes involved in a cross is the source of high yield and the other parent is a source of a particular characteristic(s) that has to be incorporated. During selection the plant breeder must remember all those genetic associations between different agronomic traits in the high yielding variety, because by this means the capacity of high yield production may be identified. Once these characteristics are fixed, the incorporation of the new ones should be attempted. Otherwise, the probability of recovering or improving the yield potential of the best parental line may be reduced. All of this emphasizes the need for the breeder to be knowledgable of the genetic potential of the material in the field, and be perfectly cognizant of what he wants from each particular hybridization.

Path analysis - The study of association between traits by means of correlation coefficients serves as a guideline for the selection of desirable plant types. However, when several factors are considered at one time the relationships between the variables becomes more complex and a different type of analysis is needed to understand direct and indirect effects of variables that influence a complex correlation. The path-coefficient analysis developed by Wright (1921, 1923) and discussed by Dewey and Lu (1959) partitions the correlation coefficient into the direct and indirect effects and permits a more critical examination of the relative importance of each of the characters within the system.

The direct and indirect effects of eight agronomic traits with plant grain yield at the phenotypic level were evaluated by path coefficient analysis for each of the 10 crosses (Tables 21 and 22). Plant height showed a significant positive correlation with plant grain yield in only two of the crosses: i.e. Sonora 64/Yaqui 50 and Sonora 64/Olesen ($p = 0.05$). In eight of the crosses there was no significant correlation between yield and height. Neither direct or indirect effects

Table 21. Path-coefficients analysis of grain yield per plant vs eight agronomic traits at the phenotypic level, using replication means of the F1, F2, BC1 and BC2 for each wheat cross.

CHARACTER	CROSS Son/Y[1]	CROSS Son/On[1]	CROSS Son/Tor[1]	CROSS Y/On[1]	CROSS Y/Tor[1]
PLANT GRAIN YIELD AND PLANT HEIGHT					
Direct effect	.0335	-.0418	.0320	-.0097	.1085
Indirect effect via Tillers per Plant	.3993	.4926	.3892	.0340	.2167
Indirect effect via Spikelet Number	.0716	.0048	-.0163	-.0203	-.0594
Indirect effect via Harvest Index	-.0224	.0019	-.0120	-.0753	-.0470
Indirect effect via Kernels per Spikelet	-.0089	-.0100	.0405	.0528	-.0634
Indirect effect via Kernel Weight	-.0259	-.0586	-.0107	.0018	.2483
Indirect effect via Grain Filling Period	-.0030	.0584	.0007	.1192	.0300
Indirect effect via Head Weight	.1393	.1226	.0091	.0594	-.2158
Correlation (r2,3)	.5836*	.5700*	.4324	.1619	.2179
PLANT GRAIN YIELD AND TILLERS PER PLANT					
Direct effect	1.0455	.8196	.8759	.9269	1.1686
Indirect effect via Plant Height	.0128	-.0251	.0142	-.0004	.0201
Indirect effect via Spikelet Number	.0193	-.0488	.0467	-.0174	-.0660
Indirect effect via Harvest Index	-.0133	.0056	-.0030	-.0015	-.0006
Indirect effect via Kernels per Spikelet	.0093	-.0150	.0112	.0705	.3731
Indirect effect via Kernel Weight	-.0590	.0169	-.0386	.0003	.2456
Indirect effect via Grain Filling Period	-.0016	.0914	.0003	-.0747	-.0194
Indirect effect via Head Weight	-.2217	.0836	.0257	-.0721	-.8353
Correlation (r3,4)	.7913**	.9282**	.9325**	.8316**	.8862**
PLANT GRAIN YIELD AND SPIKELET NUMBER					
Direct effect	.0834	-.1101	.0898	-.0478	-.1729
Indirect effect via Plant Height	.0288	.0018	-.0058	-.0041	.0373
Indirect effect via Tillers per Plant	.2421	.3636	.4557	.3382	.4460
Indirect effect via Harvest Index	-.0205	-.0015	.0053	-.0490	-.0124
Indirect effect via Kernels per Spikelet	-.0130	-.0299	-.0060	.0420	.1157
Indirect effect via Kernel Weight	-.0358	-.0257	-.0194	-.0007	.1337
Indirect effect via Grain Filling Period	-.0028	.0349	-.0004	.0426	.0063
Indirect effect via Head Weight	.2003	.3719	.0576	.0214	-.0709
Correlation (r3,5)	.4827	.6051*	.5770*	.3425	.4828
PLANT GRAIN YIELD AND HARVEST INDEX					
Direct effect	.0313	-.0308	.0287	.0954	.0715
Indirect effect via Plant Height	-.0240	.0026	-.0134	.0077	-.0714
Indirect effect via Tillers per Plant	-.4457	-.1502	-.0902	-.0144	-.0103
Indirect effect via Spikelet Number	-.0545	-.0052	.0167	.0246	.0300
Indirect effect via Kernels per Spikelet	.0001	-.0708	.0160	-.1199	-.1574
Indirect effect via Kernel Weight	.0687	-.0960	.0331	.0010	-.2661
Indirect effect via Grain Filling Period	.0039	-.0378	.0001	-.0998	-.0464
Indirect effect via Head Weight	.0919	.4255	.0486	.2247	.6184
Correlation (r3,10)	-.3283	.0371	.0397	.1191	.1682
PLANT GRAIN YIELD AND KERNELS PER SPIKELET					
Direct effect	-.0271	-.1219	.1718	-.2178	-.6028
Indirect effect via Plant Height	.0110	-.0034	.0075	.0024	.0114
Indirect effect via Tillers per Plant	-.3583	.1008	.0569	-.3002	-.7233
Indirect effect via Spikelet Number	.0399	-.0270	-.0031	.0092	.0332
Indirect effect via Harvest Index	-.0001	-.0179	.0027	.0525	.0187
Indirect effect via Kernel Weight	.0025	-.0741	-.0300	.0017	-.2645
Indirect effect via Grain Filling Period	.0004	-.0161	.0002	.0034	.0023
Indirect effect via Head Weight	.3925	.5469	.1055	.5390	1.2746
Correlation (r3,12)	.0607	.3873	.3115	.0902	-.2505
PLANT GRAIN YIELD AND KERNEL WEIGHT					
Direct effect	.1384	-.1612	.1185	.0070	-.4804
Indirect effect via Plant Height	-.0063	-.0152	-.0029	-.0024	-.0561
Indirect effect via Tillers per Plant	-.4456	-.0862	-.2850	.0425	-.5975
Indirect effect via Spikelet Number	-.0216	-.0175	-.0147	.0048	.0481
Indirect effect via Harvest Index	.0155	-.0182	.0080	.0136	.0396
Indirect effect via Kernels per Spikelet	-.0005	-.0560	-.0435	-.0530	-.3318
Indirect effect via Grain Filling Period	.0045	-.0221	.0007	-.0253	-.0257
Indirect effect via Head Weight	.3153	.5534	.0537	.4775	1.1832
Correlation (r3,13)	-.0001	.1768	-.1652	.4647	-.2206
PLANT GRAIN YIELD AND GRAIN FILLING PERIOD					
Direct effect	.0086	.1120	.0020	-.1817	-.0672
Indirect effect via Plant Height	-.0116	-.0218	.0113	.0064	-.0485
Indirect effect via Tillers per Plant	-.2019	.6689	.1175	.3811	.3380
Indirect effect via Spikelet Number	-.0270	-.0343	-.0161	.0112	.0161
Indirect effect via Harvest Index	.0142	.0104	.0021	.0524	.0494
Indirect effect via Kernels per Spikelet	-.0012	.0175	.0212	.0041	.0203
Indirect effect via Kernel Weight	.0723	.0318	.0393	.0010	-.1835
Indirect effect via Head Weight	.1651	-.0621	.0387	.0007	.2063
Correlation (r3,15)	.0184	.7223**	.2159	.2751	.3309
PLANT GRAIN YIELD AND HEAD WEIGHT					
Direct effect	.5184	.6879	.1562	.6667	1.4346
Indirect effect via Plant Height	.0090	-.0075	.0019	-.0009	-.0163
Indirect effect via Tillers per Plant	-.4475	.0996	.1441	-.1003	-.6804
Indirect effect via Spikelet Number	.0322	-.0595	.0331	-.0015	.0085
Indirect effect via Harvest Index	.0055	-.0191	.0089	.0321	.0308
Indirect effect via Kernels per Spikelet	-.0205	-.0969	.1160	-.1761	-.5356
Indirect effect via Kernel Weight	.0842	-.1297	.0408	.0050	-.3963
Indirect effect via Grain Filling Period	.0027	-.0101	.0005	-.0002	-.0097
Correlation (r3,16)	.1842	.4647	.5015*	.4250	-.1645

[1] Son = Sonora 64, Y = Yaqui 50, On = Olesen, Tor = Tordo, Vc = Vicam 71
* significant at the 5% probability level ** significant at the 1% probability level

Table 22. Path-coefficients analysis of grain yield per plant vs eight agronomic traits at the phenotypic level, using replication means of the F1, F2, BC1 and BC2 for each wheat cross.

	CROSS Vc/Son[1]	CROSS Vc/Y[1]	CROSS Vc/On[1]	CROSS Vc/Tor[1]	CROSS Tor/On[1]
PLANT GRAIN YIELD AND PLANT HEIGHT					
Direct effect	.0147	.0572	-.0626	.0440	-.1167
Indirect effect via Tillers per Plant	-.1202	.0201	.2699	.3829	-.0385
Indirect effect via Spikelet Number	-.0151	-.0307	-.1466	-.0624	.0073
Indirect effect via Harvest Index	-.0074	-.1147	.0162	.0030	-.0016
Indirect effect via Kernels per Spikelet	-.0007	.0492	.4854	-.1017	-.0044
Indirect effect via Kernel Weight	.0241	-.0029	-.0198	-.0206	-.0080
Indirect effect via Grain Filling Period	-.0171	.0215	.0077	-.0034	.0034
Indirect effect via Head Weight	-.0236	-.0665	-.3697	-.0807	.1820
Correlation (r2,3)	-.1454	-.0667	.1806	.1612	.0235
PLANT GRAIN YIELD AND TILLERS PER PLANT					
Direct effect	.9683	.8203	.8705	.9662	.9881
Indirect effect via Plant Height	-.0018	.0014	-.0194	.0174	.0045
Indirect effect via Spikelet Number	.0299	-.0165	-.4471	.0000	.1020
Indirect effect via Harvest Index	.0078	.0157	.0136	.0036	-.0541
Indirect effect via Kernels per Spikelet	.0002	-.0370	.3393	.0448	-.2151
Indirect effect via Kernel Weight	-.0462	.0070	.5541	-.0448	.0243
Indirect effect via Grain Filling Period	-.0243	-.0301	.0156	-.0242	.0225
Indirect effect via Head Weight	.0291	.1355	-.4903	-.0271	.0392
Correlation (r3,4)	.9630**	.8962**	.8364**	.9358**	.9114**
PLANT GRAIN YIELD AND SPIKELET NUMBER					
Direct effect	.0427	-.1051	-.7034	.1471	.1250
Indirect effect via Plant Height	-.0052	.0167	-.0130	-.0187	-.0063
Indirect effect via Tillers per Plant	.6793	.1288	.5533	-.0002	.8062
Indirect effect via Harvest Index	.0041	-.0152	.0024	-.0003	-.0692
Indirect effect via Kernels per Spikelet	.0102	-.0379	.1297	.0407	-.2468
Indirect effect via Kernel Weight	-.0535	-.0350	.6868	.0016	.0150
Indirect effect via Grain Filling Period	.0027	-.0146	.0151	-.0093	.0153
Indirect effect via Head Weight	-.0546	.3550	-.2664	.0623	.0116
Correlation (r3,5)	.6258**	.2926	.4044	.2232	.6502**
PLANT GRAIN YIELD AND HARVEST INDEX					
Direct effect	.0176	.1273	.0711	-.0068	-.0895
Indirect effect via Plant Height	-.0062	-.0516	-.0142	-.0194	-.0022
Indirect effect via Tillers per Plant	.4292	.1012	.1668	-.5142	.5976
Indirect effect via Spikelet Number	.0100	.0126	-.0233	.0070	.0967
Indirect effect via Kernels per Spikelet	-.0113	-.1039	-.4862	.0386	-.2039
Indirect effect via Kernel Weight	-.0180	-.0254	-.3123	.0208	.0027
Indirect effect via Grain Filling Period	-.0187	-.0286	.0070	.0045	.0221
Indirect effect via Head Weignt	.1267	.2999	.8909	.0383	.1281
Correlation (r3,10)	.5294*	.3316	.2997	-.4313	.5517*
PLANT GRAIN YIELD AND KERNELS PER SPIKELET					
Direct effect	-.0260	-.1714	-1.4108	.1843	.2766
Indirect effect via Plant Height	.0004	-.0164	.0215	-.0243	.0018
Indirect effect via Tillers per Plant	-.0091	.1772	-.2094	.2346	-.7684
Indirect effect via Spikelet Number	-.0167	-.0232	.0647	.0325	-.1116
Indirect effect via Harvest Index	.0076	.0772	.0245	-.0014	.0660
Indirect effect via Kernel Weight	.0123	-.0441	-.0295	-.0015	-.0117
Indirect effect via Grain Filling Period	-.0280	-.0228	-.0093	-.0110	-.0227
Indirect effect via Head Weight	.2468	.5435	1.7095	.0792	-.1028
Correlation (3,13)	.1873	.5199*	.1612	.4923	-.6727**
PLANT GRAIN YIELD AND KERNEL WEIGHT					
Direct effect	.0784	-.1343	-.9665	.0575	-.0556
Indirect effect via Plant Height	.0045	.0012	-.0013	-.0158	-.0168
Indirect effect via Tillers per Plant	-.5712	-.0426	-.4991	-.7530	-.4313
Indirect effect via Spikelet Number	-.0291	-.0274	.4999	.0041	-.0338
Indirect effect via Harvest Index	-.0040	.0240	.0230	-.0025	.0043
Indirect effect via Kernels per Spikelet	-.0041	-.0563	-.0430	-.0049	.0583
Indirect effect via Grain Filling Period	.0009	-.0107	-.0070	.0242	-.0070
Indirect effect via Head Weight	.0681	.5487	.6090	.0586	.2478
Correlation (r3,13)	-.4565	.3027	-.3850	-.6318**	-.2341
PLANT GRAIN YIELD AND GRAIN FILLING PERIOD					
Direct effect	-.0487	-.0537	.0277	-.0403	.0359
Indirect effect via Plant Height	.0052	-.0229	-.0173	.0037	-.0111
Indirect effect via Tillers per Plant	.4837	.4605	.4885	.5814	.6180
Indirect effect via Spikelet Number	-.0024	-.0286	-.3820	.0341	.0532
Indirect effect via Harvest Index	.0068	.0677	.0180	.0007	-.0550
Indirect effect via Kernels per Spikelet	-.0149	-.0727	.4746	.0504	-.1743
Indirect effect via Kernel Weight	-.0015	-.0268	.2425	-.0345	.0108
Indirect effect via Head Weight	.1609	.3153	-.4717	-.0115	.2572
Correlation (r3,15)	.5890*	.6387**	.3802	.5841*	.7346**
PLANT GRAIN YIELD AND HEAD WEIGHT					
Direct effect	.2688	.6943	1.8771	.1108	.4838
Indirect effect via Plant Height	-.0013	-.0055	.0123	-.0320	-.0439
Indirect effect via Tillers per Plant	.1048	.1601	-.2274	-.2363	.0800
Indirect effect via Spikelet Number	-.0087	-.0537	.0998	.0827	.0030
Indirect effect via Harvest Index	.0083	.0550	.0338	-.0023	-.0237
Indirect effect via Kernels per Spikelet	-.0239	-.1342	-1.2848	.1318	-.0586
Indirect effect via Kernel Weight	.0198	-.1062	-.3135	.0304	-.0285
Indirect effect via Grain Filling Period	-.0291	-.0244	-.0070	.0042	.0191
Correlation (r3,16)	.3388	.5855*	.1903	.0892	.4310

[1] Son = Sonora 64, Y = Yaqui 50, On = Olesen, Tor = Tordo, Vc = Vicam 71
* significant at the 5% probability level ** significant at the 1% probability level

were important in the system. The exception to this may be the cross Sonora 64/Tordo where some indirect effects of plant height on grain yield via number of tillers per plant were observed. In the crosses Sonora 64/Yaqui 50 and Sonora 64/Olesen the direct effects of plant height on grain yield were negligible. However, positive indirect effects through tiller number and to a lesser extent the weight of grains per ear accounted for the overall significant positive correlation between yield and height in these crosses. In every case Sonora 64 was one of the parents and in all three crosses, including Sonora 64/Tordo, the tall parent had more tillering capacity. If selection is going to be applied to these three populations it is possible that the best lines could come from relatively taller plants than from the shorter ones.

The total correlation between the number of tillers per plant and grain yield per plant was high, positive and significant in all 10 crosses. The direct effects were always high and also positive and the indirect effects of tillers number via other traits were negligible except in the crosses Yaqui 50/Tordo and Vicam 71/Olesen. In these two crosses there were high negative indirect effects via head grain weight, indicating that any increase in the number of tillers per plant would lead to a decrease in weight of grain per ear and a reduction in yield. In the cross Vicam 71/Olesen there was also a positive indirect effect of number of tillers per plant via kernel weight but it was offset by a sizeable negative indirect effect through number of spikelets per spike. This is an example of one of the characteristics of Olesen dwarf, i. e. the head is so compact that an increase in kernel weight is the result of a decrease in the number of spikelets per spike. A positive and significant correlation between spikelets per spike and grain yield was observed in the crosses Sonora 64/Tordo ($p = 0.05$) Sonora 64/Olesen ($p = 0.05$), Vicam 71/Sonora 64 ($p = 0.01$) and Tordo/Olesen ($p = 0.01$). In three of the remaining crosses, i. e. Sonora 64/Yaqui 50, Yaqui 50/Tordo, and Vicam 71/Olesen, the total correlation was not statistically significant but it was high and had similar direct and indirect effects as those four previously mentioned. When the total correlation was partitioned into effects through other traits it was found that the direct effects of spikelet number on grain yield were negligible in all crosses except Vicam 71/Olesen. In this last cross there was a negative direct effect of spikelet number on grain yield; both of the parents of this cross had the smallest mean value for spikelet number, thus it is possible to assume that their yield capacity was associated with other yield components and not with number of spikelets per spike. In all seven crosses previously mentioned spikelet number had a positive indirect effect through tiller number per plant on grain yield. These associations accurately describe the parental cultivars, except for Vicam 71, in that tillering capacity was associated with longer heads and more spikelets per spike. In the cross Vicam 71/Olesen the positive indirect effects of spikelet number via kernel weight were more important than those via tillering and the two together may have offset the negative direct effects, resulting in a positive total correlation between spikelet number and grain yield.

There were only two crosses where a positive significant correlation was found between harvest index and grain yield, i.e. Vicam 71/Sonora 64 and Tordo/Olesen ($p = 0.05$). In both cases the direct effects were negligible and the significant correlation between these two traits was a result of positive indirect effects via number of spikes per plant. The cross Vicam 71/Tordo had a negative correlation between harvest index and yield per plant due to high indirect effects via number of tillers per plant. In other words, high grain to straw ratios were offsetting the tillering capacity of the plant and grain yields were reduced.

The phenotypic correlation between number of kernels per spikelet and plant grain yield was positive and significant in the cross Vicam 71/Yaqui 50 ($p = 0.05$) and negatively significant in Tordo/Olesen ($p = 0.01$). In both cases the direct effects were small and the significance of the total correlation was due to the indirect effects. In the cross Vicam 71/Yaqui 50 kernels per spikelet had a significant positive indirect effect on grain yield via its positive association with head grain weight. Similar indirect effects were observed in eight crosses out of the 10 but in most cases the total correlation was negligible due to negative indirect effects through number of tillers per plant. More kernels per spikelet were due to less number of tillers per plant. Because only negative indirect effects via tillering capacity were present in the cross Tordo/Olesen the total phenotypic correlation between kernels per spikelet and grain yield was negative. Number of kernels per spikelet may be a trait which is dependent for its full expression on its ability to compete for assimilates with earlier developed yield components as number of spikes per plant and spikelets per spike. This negative association, however, was offset in certain hybrid combinations as demonstrated with the crosses Vicam 71/Yaqui 50 and Vicam 71/Tordo. Both of these crosses showed positive indirect effects of kernels per spikelet via tiller number.

The cross Vicam 71/Tordo had a significant negative correlation between kernel weight and plant grain yield ($p = 0.01$). This negative correlation was the result of negative indirect effects via tillers per plant.

The cross Vicam 71/Olesen was an example of how complex the relationships among several traits can be. Positive indirect effects of kernel weight via head weight and spikelet number and strong negative direct effects plus negative indirect effects via number of tillers per plant resulted in a negative correlation between kernel weight and plant grain yield. In general, kernel weight had negligible direct effects on plant grain yield but had a large positive influence on yield via head weight and negative indirect effects through number of tillers per plant.

Grain filling period was significantly correlated with grain yield in 50 percent of the crosses. Direct effects of grain filling period were negligible in all crosses. The positive indirect effects via spikes per plant were high in almost all crosses and the positive indirect effects through head grain weight were not as high as those through tiller number but contributed in some instances to a significant total correlation. Head weight was significantly correlated with yield in only two crosses (p = 0.05). In the cross Sonora 64/Tordo the significant correlation was the result of the summation of positive indirect effects via yield components because direct effects were small. In the cross Vicam 71/Yaqui 50 the direct effects of head grain weight on plant grain yield were high and positive as it was for most of the other crosses. Usually these effects were offset by negative indirect effects via number of tillers per plant. Thus selection must be either for number of spikes per plant or head weight, because selection response to both of these traits seems unlikely to occur.

Number of spikes per plant was the only trait that showed consistent direct effects on plant grain yield. All the other direct and indirect effects as well as the total correlations displayed some degree of inconsistency from one cross to another. In general the other components of yield, i.e. number of spikelets per spike, number of kernels per spikelet, and kernel weight had no direct effect on grain yield but had positive indirect effects via head weight. Spikelet number was positively associated with number of tillers per plant, and kernels per spikelet and kernel weight were negatively associated with number of tillers per plant. However, there were several exceptions to these associations depending on the characteristics of the parental cultivars involved in each cross. Therefore each individual cross should be handled differently during selection.

Combining ability - Combining ability analysis has been used to estimate the relative magnitude of the gene action involved in the expression of a trait (Kronstad and Foote, 1964; Brown et al., 1966; Fonseca and Patterson, 1968). General combining ability effects (G.C.A.) and specific combining ability effects (S.C.A.) were computed for both the F_1 and F_2 generations (Table 23) for 10 agronomic traits: plant height, plant grain yield, number of tillers per plant, number of spikelets per spike, head length, days to maturity, kernels per spikelet, kernel weight, grain filling period, and head grain weight. There were significant differences ($p = 0.01$) in G.C.A. in both the F_1 and F_2 generations for the 10 agronomic traits measured with the exception of plant grain yield in the F_2 and head grain weight in the F_1 which were significantly different at the five percent

Table 23. Observed mean squares for general combining ability (G.C.A.) and specific combining ability (S.C.A.) for ten of the characters studied in the F_1 and F_2 generations.[1]

Source	D.F.	Plant Height		Plant Yield		Tillers Per Plant		Spikelet Number	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
G.C.A.	4	8708.57**	8642.43**	884.04**	210.22*	206.73**	141.04**	18.88**	15.76**
S.C.A.	10	49.65**	19.82*	271.80	141.35	74.47*	38.64	0.62	0.17
Error	42	4.99	9.13	174.48	78.11	45.79	20.95	0.38	0.27

Source	D.F.	Head Length		Maturity		Kernels Per Spikelet		Kernel Weight	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
G.C.A.	4	28.25**	23.07**	63.86**	70.80**	0.33**	0.30**	48.29**	72.62**
S.C.A.	10	0.50	0.31	7.77	2.70	0.10**	0.02	19.82**	7.38**
Error	42	0.26	0.23	4.66	2.28	0.02	0.02	2.89	2.34

Source	D.F.	Grain Filling Period		Head Weight	
		F_1	F_2	F_1	F_2
G.C.A.	4	47.34**	74.20**	0.14*	0.21**
S.C.A.	10	23.53**	21.22**	0.34**	0.06**
Error	42	5.38	3.88	0.05	0.02

[1] Using Griffing's model (1956)

* Significant at the 5% probability level

** Significant at the 1% probability level probability level. Testing of S.C.A. variance showed that there were highly significant differences (p = 0.01) for plant height in the F_1, kernels per spikelet in the F_1, and in both the F_1 and F_2 for kernel weight, grain filling period, and head weight. There were significant differences (p = 0.05) for S.C.A. for plant height in the F_2 and tillers per plant in the F_1. There were no statistical differences in S.C.A. in any of the two generations for plant yield, spikelet number, head length, and days to maturity. There were no S.C.A. differences for number of tillers per plant and number of kernels per spikelet in the F_2 generation. Additive genetic effects, which are estimated by G.C.A., were important in the expression of all traits studied. However, non-additive gene effects estimated by S.C.A. were also important in the expression of some traits. Therefore, measurement of the relative amount of each type of gene action involved in the expression of each trait in both generations would give a better indication of the potential of early generation selection (Table 24). High G.C.A./S.C.A. ratios indicate that the additive genetic variance is a sizeable proportion of the total genetic variance (Daaloul, 1973). Low ratios suggest that non-additive effects are proportionally important in the genetic expression of the trait and therefore selection may not be very effective. Large G.C.A./S.C.A. ratios revealed that a large part of the genetic variability associated with plant height, number of spikelets per spike, head length, days to maturity, and number of

Table 24. Components of variance for general combining ability (G. C. A.), specific combining ability (S. C. A.) and ratios of G. C. A. variances to S. C. A. variances for ten agronomic traits measured in F_1 and F_2 generations.[1]

Source	Plant Height		Plant Yield		Tillers Per Plant		Spikelet Number		Head Length	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
G. C. A.	1243.37	1233.33	101.37	18.87	22.99	17.16	2.64	2.21	4.00	3.26
S. C. A.	44.66	10.69	97.32	63.24	28.68	17.69	0.24	N. S.	0.24	N. S.
G. C. A. /S. C. A.	27.80	115.37	1.04	0.30	0.80	0.97	11.00	Large	16.67	Large
Error	4.99	9.13	174.48	78.11	45.79	20.95	0.38	0.27	0.26	0.23

Source	Maturity		Kernels Per Spikelet		Kernel Weight		Grain Filling Period		Head Weight	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
G. C. A.	8.46	9.80	0.044	0.040	6.49	10.04	5.99	10.05	0.013	0.027
S. C. A.	3.11	0.42	0.080	N. S.	16.96	5.04	18.15	17.34	0.290	0.040
G. C. A. /S. C. A.	2.72	23.33	0.550	Large	0.38	1.99	0.33	0.58	0.045	0.675
Error	4.66	2.28	0.020	0.020	2.89	2.34	5.38	3.88	0.050	0.020

[1] Following Griffing's procedures (1956)

kernels per spikelet was the result of additive gene action. With days to maturity and kernels per spikelet, the ratios were not very large in the F_1 but were greater in the F_2, indicating that non-additive gene action was present in the F_1 generation but was quickly lost after one generation of selfing. Therefore, it would be possible to effectively select for these traits as early as the F_2. The G.C.A./S.C.A. ratios for kernel weight and head weight were small in the F_1 but had the tendency to increase in the F_2. The possibility exists that genes which behave in a non-additive manner will not interfere with the additive gene effects after one or more generations of selfing. Grain filling period, number of tillers per plant, and plant grain yield, had low G.C.A./S.C.A. ratios for both the F_1 and F_2 generations, indicating a preponderance of non-additive (dominance and epistasis) gene action in their expression. The fact that the non-additive effects for these traits remained relatively important after one generation of selfing could mean that it may take several generations of selfing to have lower S.C.A. ratios. The combining ability analysis of variance did not detect plant yield and tiller number differences for S.C.A. whereas the G.C.A. effects were significantly different. The genetic differences observed for these two traits were probably due only to additive gene effects. However, after low G.C.A./S.C.A. ratios were calculated it is possible to assume that non-additive gene action was relatively more important than the analysis of variance showed.

Low G.C.A./S.C.A. ratios for these traits have also been reported by Daaloul (1973) and Paroda and Joshi (1970a). It is possible that in the present experiment genotype-environment interactions made the error term for tiller number and plant yield so large that no S.C.A. differences could be detected even if they existed. Daaloul (1973) reported a similar situation for tiller number in winter wheat. In the present experiment S.C.A. differences were difficult to detect for plant yield due possibly to a large dependency on plant tillering capacity. G.C.A./S.C.A. ratios increased from the F_1 to the F_2 for almost every trait, except number of tillers per plant and plant grain yield. Components of yield G.C.A./S.C.A. ratios were always higher in the F_2 than in the F_1, except tiller number, confirming that additive gene action is more preponderant in the expression of these traits than in grain yield per se. Hence selection for yield components may be a more efficient way of increasing total plant yield.

Identification of those parental cultivars that are "good combiners" or throw better progenies for a given trait is of paramount importance. Such knowledge provides information on which parental combinations have a better probability of producing better performing lines. For this purpose G.C.A. effects and S.C.A. effects were calculated (Tables 25 and 26).

Olesen and Tordo were the two cultivars that showed the best general combining ability for short straw. Estimates of S.C.A.

Table 25. Estimates of general combining ability effects for ten variables studied in the F_1 and F_2 generations.[1]

Parent	Height		Plant Yield		Tillers Per Plant		Spikelet Number		Head Length	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Vicam 71	-3.74	-3.84	4.55	3.13	2.51	1.79	0.16	0.13	-0.80	-0.81
Sonora 64	2.58	3.23	-2.87	-0.44	-2.17	-1.06	-1.28	-1.13	-0.50	-0.33
Yaqui 50	28.94	28.51	7.45	2.53	3.36	2.94	0.78	0.74	1.28	1.12
Tordo	-13.39	-12.06	-4.82	-2.54	-2.28	-2.31	0.59	0.56	0.87	0.81
Olesen	-14.39	-15.84	-4.30	-2.68	-1.42	-1.35	-0.26	-0.30	-0.86	-0.79
S. E. $(g_i - g_j)$#	1.19	1.61	7.06	4.72	3.62	2.45	0.33	0.28	0.27	0.26

Parent	Maturity		Kernels Per Spikelet		Kernel Weight		Grain Filling Period		Head Weight	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Vicam 71	0.09	0.00	-0.10	-0.07	-0.23	-0.24	-1.03	-1.23	-0.09	-0.06
Sonora 64	-2.37	-2.57	0.15	1.15	1.24	1.12	1.54	1.88	0.08	0.08
Yaqui 50	0.88	1.46	-0.01	-0.06	-0.72	-1.53	-1.39	-1.69	0.04	-0.08
Tordo	1.63	1.18	0.11	-0.08	1.39	2.12	-0.28	-0.51	0.03	0.10
Oleson	-0.23	-0.07	0.06	0.07	-1.68	-1.48	1.15	1.56	-0.06	-0.03
S. E. $(g_i - g_j)$#	1.15	0.81	0.08	0.08	0.91	0.82	1.24	1.05	0.12	0.08

#Standard error of the difference between two general combining ability effects where $i \neq j$.

[1] Using Griffings procedures (1956)

Table 26. Estimates of specific combining ability effects in the F_1 and F_2 generations for those traits that had specific combining ability differences in the analysis of variance.[1]

Cross or Self	Plant Height		Tillers Per Plant	Kernels Per Spikelet	Kernel Weight		Grain Filling Period		Head Weight	
	F_1	F_2	F_1	F_1	F_1	F_2	F_1	F_2	F_1	F_2
Vcm/Son	-1.37	0.63	-4.04	-0.07	0.65	0.62	-1.96	-0.25	-0.04	0.04
Vcm/Y	2.02	3.60	0.93	0.14	1.49	-0.62	-0.29	-0.18	0.26	0.04
Vcm/Tor'	-1.65	-1.33	-2.93	0.09	0.52	1.32	-0.39	-1.11	0.14	0.11
Vcm/On	0.10	-1.30	-1.04	-0.03	-1.55	-2.10	-0.07	-2.18	-0.13	-0.10
Son/Y	3.20	0.27	-1.64	0.02	1.44	0.33	-0.61	-2.04	0.11	-0.02
Son/Tor	-4.48	2.10	-5.25	0.10	0.80	0.45	-2.21	-2.46	0.09	0.07
Son/On	2.02	1.88	0.64	0.09	1.25	0.43	-2.14	-1.04	0.24	0.07
Y/Tor	-6.58	-3.94	-4.54	0.12	1.31	0.53	0.46	-0.89	0.22	0.10
Y/On	-0.33	-0.40	-3.89	0.26	3.66	2.58	-2.71	-1.46	0.45	0.21
Tor/On	2.24	0.92	2.50	-0.07	-2.05	-0.62	-2.07	-0.89	-0.18	0.04
S.E. $(S_{ij}-S_{ik})$#	2.92	3.96	8.86	0.18	2.23	2.00	3.04	2.58	0.29	0.18
S.E. $(S_{ij}-S_{kl})$##	2.67	3.61	8.09	0.17	2.03	1.83	2.77	2.35	0.27	0.17

Vicam 71 = Vcm
Sonora 64 = Son
Yaqui 50 = Y
Tordo = Tor
Olesen = On

[1]Using Griffing's model (1956)

Standard error of the difference between two specific combining ability effects where $i \neq j, k; j \neq k$

##Standard error of the difference between two specific combining ability effects where $i \neq j, k, l; j \neq k, l; k \neq l$

effects for plant height indicated that all crosses with the parental line Tordo, except Tordo/Olesen, showed very high negative S. C. A. effects, which means that Tordo is a good source for reducing plant height in the F_1 generation. Specific combining ability effects in the F_2 generation were similar for both Tordo and Olesen dwarf. Non additive effects might have been involved in the expression of height in the dwarf parent Tordo and were partially lost after one generation of selfing. The estimated S. C. A. effects in those crosses involving Vicam 71 and Olesen with Sonora 64 and Yaqui 50 were more consistent from one generation to another than those involving Tordo. This was especially true for the cultivar Olesen.

Yaqui 50 and Vicam 71 were the only parents showing positive G. C. A. effects for number of tillers per plant and grain yield in both generations. Tordo had the lowest G. C. A. effects for grain yield in the F_1 and Olesen the lowest in the F_2. There were only three crosses with positive S. C. A. effects for tiller number in the F_1 generation. These combinations were Vicam 71/Yaqui 50, a high x high general combiner, and Tordo/Olesen, a low x low general combiner. The former had two parents with the highest means for tiller number and because plant yield was so highly correlated with this yield component, grain yield per plant may be increased by selecting for tiller number. Yaqui 50, Tordo, and Vicam 71 were the best general combiners, in that order, for number of spikelets per spikes. Vicam

71 had an average number of spikelets per spike but high G.C.A. effects for this trait.

This could mean a possibility of improving yield in crosses with Vicam 71 by increasing the number of spikelets per spike. The crosses of Vicam 71 times Yaqui 50 and Tordo, which were two parental cultivars with high means and high general combining ability in both generations, may be a very good source of large number of spikelets per spike and high yield. Sonora 64 was the best source of earliness because it had the most negative values for G.C.A. effects for days to maturity. Tordo in the F_1 and Yaqui 50 in the F_2 had the highest G.C.A. effects for days to maturity, therefore they both can be considered as good sources for lateness.

Sonora 64 and Olesen were the best general combiners for number of kernels per spikelet. Tordo had high G.C.A. effects for kernels per spikelet in the F_1; however, F_2 G.C.A. effects revealed that some type of gene interactions were present in the expression of this trait in this cultivar and that these effects were lost after selfing. The best combination for kernels per spikelet in the terms of its S.C.A. effects in the F_1 was the cross Yaqui 50/Olesen.

Estimation of G.C.A. effects for kernel weight were high for Tordo and Sonora 64. Tordo showed very high G.C.A. effects in the F_2, almost twice as much as Sonora 64, while in the F_1 the difference was not as great between these two cultivars. Additive effects for kernel weight in crosses involving Tordo were significantly increased after selfing and the possibility of selecting for high kernel weight strains in crosses with this cultivar looks promising. The highest S.C.A. effects for kernel weight in the F_1 were observed in the cross Yaqui 50/Olesen which was a low x low general combiner combination. In addition both parental lines had the lowest mean values for this character. Therefore, it seems very unlikely that progress could be made through selection in this cross.

The cross Vicam 71/Tordo represents a combination of a very high general combiner for plant grain yield and tiller number with a very high general combiner for kernel weight. This cross also had the second highest S.C.A. effects for kernel weight. Theoretically the possibility exists of selecting genotypes with increased expression for the aforementioned yield components with a resultant increase in grain yield.

The cross Sonora 64/Tordo was a high x high general combiner combination for kernel weight which showed positive S.C.A. effects in both generations. The possibility exists for increasing kernel weight with this combination because these two cultivars had the highest mean value for kernel weight. Sonora 64 was the best general combiner for longer grain filling period and the only other cultivar that showed positive estimation of G.C.A. effects for this trait was Olesen. Only the cross Yaqui 50/Tordo, a low x low G.C.A.

combiner, showed positive S. C. A. effects for grain filling period. It would be very difficult to extend the length of grain filling period through non-additive effects because these effects influence the length of this agronomic trait to a large extent in a negative manner.

The best general combiners for head grain weight were Sonora 64 and Tordo. Their G. C. A. effects were not as consistent from the F_1 to the F_2 as with the other agronomic traits. The cross with the highest S. C. A. effects for head grain weight was Yaqui 50/Olesen. The crosses Sonora 64/Olesen and Yaqui 50/Tordo had high S. C. A. effects for head weight and both involved one parent with high head weight mean and high general combining ability. The F_2 generation may be used effectively for general combining ability studies. This seemed possible because the ranking of the parental cultivars for their G. C. A. effects was about the same from the F_1 and F_2 generations. This was true for most traits measured with the exception of head grain weight. Similar results have been reported by Paroda and Joshi (1970b). However, the reliance of the F_2 generation for estimating S. C. A. needs further testing because S. C. A. effects were not computed for several traits. In those traits where S. C. A. effects were calculated for both the F_1 and F_2 generations, the latter generation estimations of non-additive effects were similar to those observed in the F_1.

The parental lines used in this study differed in their general combining ability, which was related to the parental means for each of the traits studied. Usually high S. C. A. effects were associated with parents of low G. C. A. effects; however, there were exceptions for some traits. Combinations of high x high and high x low general combiners had high S. C. A. effects, indicating the possibility that some additive gene action may have been involved in the superior performance of these combinations.

SUMMARY AND CONCLUSIONS

Three genetically different dwarf cultivars of spring wheat were evaluated as potential sources of short stature to use in a wheat improvement program. The study involved a five parent diallel cross, space planted in a randomized block design with four replications. The five parents included a semidwarf, a standard height and three dwarf cultivars. The dwarf cultivars were: Vicam 71 a Norin 10 derivative, Tordo a Tom Thumb derivative, and Olesen dwarf. Sonora 64 was selected as the semidwarf and the standard height cultivar was Yaqui 50. The experimental population included the five parental lines, ten F_1 single crosses, ten F_2's from the single crosses, ten backcrosses to the short parent, and ten backcrosses to the tall parent. Information was recorded on individual plant basis for 13 agronomic traits which included: plant height, days to emergence, number of tillers, number of spikelets per spike, head length, days to maturity, grain yield, harvest index (grain to straw ratio), kernel weight, number of kernels per spikelet, rachis internode length, grain filling period (days from heading to maturity), and head grain weight.

All the characters studied were subjected to an analysis of variance to detect differences among the forty five entries in the experiment and between and within generations. To compare the reduction of plant height in the F_1 and F_2 generation by the different dwarf cultivars, degree of dominance was calculated for the ten hybrids. Information about the type of gene action for the agronomic characters studied was estimated by heterosis and heterobeltiosis values, broad and narrow sense heritability estimates, and combining ability analysis.

In addition, phenotypic, environmental, and genotypic correlations were used to estimate the degree of association between the agronomic traits studied for each of the 10 crosses. Path-coefficient analysis was used to provide a means of studying the indirect and direct effects of various agronomic traits in determining their final association with plant grain yield. The following conclusions were drawn.

1. There were genetic differences among the parental cultivars, their crosses, and generations for all the 13 agronomic traits studied.

2. Partial dominance for tallness was manifested for those crosses involving the cultivars Vicam 71 and Olesen dwarf. However, the degree of dominance was so small that some possibilities exist that the mode of gene action in the inheritance of plant height for these two dwarf sources is mainly of the additive type. This was especially true for Olesen dwarf.

3. The cultivar Tordo, when crossed to taller wheats, showed strong dominance effects towards short stature.

4. Strong heterosis for reduced plant height in crosses involving the cultivar Tordo were observed. This cultivar, or other Tom Thumb

derivatives, may be the best choice to produce short statured F_1 hybrids that do not lodge. Olesen dwarf crosses did not show dominance for short straw. However, this cultivar is very short and the F_1 values were always very close to the mid parent value for plant height. Olesen may also have some potential to be used as a source for short statured F_1 hybrids. The cross between Vicam 71, the Norin 10 derivative, and the standard height variety Yaqui 50 was significantly taller than the mid parent. Vicam 71 has limited possibilities to be successfully used as a parent for short statured single cross hybrids involving a tall standard cultivar.

5. All three sources of dwarfism and their resulting progenies displayed desirable agronomic characteristics. They have the genetic potential to be used as a source to produce superior dwarf and semi-dwarf wheats in a breeding program. Vicam 71 was a good parent in terms of grain yield and number of tillers per plant. Tordo was the best source for increasing the number of spikelets per spike, kernel weight and head grain weight. Olesen was a good progenitor for increasing number of kernels per spikelet. If these cultivars were to be ranked in terms of superior offspring for desirable agronomic traits, Vicam 71 would be first, Tordo second and Olesen dwarf third. However, each of these parents had some advantage(s) over the other two and all could be successfully used in breeding short statured wheats.

6. Plant height did not appear to have any direct effect on plant grain yield in any of the 10 crosses.

7. Fifty percent or more of the phenotypic variability present for plant height, days to heading, head length, kernel weight, number of spikelets per spike, rachis internode length, days to maturity, number of kernels per spikelet, head grain weight, grain filling period, and harvest index, was due to genetic variation. The amount of variation present for number of tillers per plant and grain yield was significantly smaller than that accounted for by the environment in most of the crosses.

8. The amount of genetic variability associated with days to heading, days to maturity, plant height, rachis internode length, number of spikelets per spike, kernels per spikelet, kernel weight, and harvest index, was mainly the result of additive gene action. Therefore, effective selection for these traits could be initiated as early as the F_2 generation.

9. Non additive and additive gene action were equally important in the genetic expression of grain filling period and head grain weight and as a result selection should be delayed until the F_3 or later generations for these characters.

10. The non-additive portion of the total genetic variance associated with number of tillers and grain yield per plant was relatively important; hence, if selection for these traits is going to be effective,

it should be delayed until the F_4 or later generations where a large degree of homozygocity has been obtained.

11. Genetic correlations between some agronomic traits were consistently high in most of the crosses studied. High positive genetic correlations were found between plant grain yield vs number of tillers per plant and kernels per spikelet, number of tillers per plant vs days to maturity, kernels per spikelet vs head grain weight, plant height vs head grain weight, and head length vs rachis internode length. High negative genetic correlations were found between kernel weight vs days to maturity, plant height vs harvest index, and days to heading vs grain filling period.

12. Most correlations among agronomic traits were different from one cross to another due to different gene associations in the parental lines. The genetic correlations between yield components varied in value and sign for the different crosses. Therefore, grain yield could be increased by a combined increase of more than one yield component because tiller number, spikelet number, kernels per spikelet, and kernel weight were often not correlated between one another and some times were even positively correlated.

13. With the large amount of additive gene action present in the expression of plant height and the consistently high negative genetic correlation of this trait with harvest index, phenotypic selection for

restricted plant height would be useful in obtaining lines with high grain to straw ratios.

14. Number of tillers per plant had a high direct effect on grain yield in all crosses. With the exception of two crosses indirect effects of this trait were negligible. Yaqui 50/Tordo and Vicam 71/Olesen presented high negative indirect effects of tiller number on plant grain yield via head grain weight. Kernels per spikelet and kernel weight had no direct effects on grain yield but their indirect effects via head weight were significant.

15. The F_2 generation can be used effectively to estimate G.C.A. effects from a diallel cross.

16. In general, high S.C.A. effects were associated with parents of low S.C.A. and vice versa. However, there were exceptions for some traits and crosses. High x high and high x low general combiner combinations had high S.C.A. effects, indicating the possibility that some additive gene action is involved in the superior performance of these combinations.

17. A wheat breeder should be aware of those genetic associations between different agronomic traits that occur consistently among crosses. A correct utilization of genetic associations could lead to the development of superior wheat cultivars. However, the breeder should not attempt to select the same plant type from every cross if he hopes to make progress by using the genetic variability available

in the crop. The genetic correlations in this study suggested that each cross has a particular combination of genes depending upon the parents involved. Every cross is potentially a source of better lines if when selecting the breeder remembers the reason why the hybridization was performed. It is very important to know the contributions of each parent in a cross combination and the most important trait associations present in each parent. Through the proper management of segregating populations of individual crosses superior genotypes could be obtained.

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APPENDIX

PEDIGREE AND DESCRIPTION OF CULTIVARS

Olesen. (Pitic "sib/Mazoe, S948-A1). Olesen is a very short, soft red, spring wheat cultivar bred by Dr. Robert Olesen in Rhodesia. It has very thick and strong culms, is awned and white chaffed, has small and clavate heads and is an early maturing cultivar. No information is available about its disease resistance.

Sonora 64. (Yaktana 54/2/Norin 10/ Brevor/3/ 2*Yaqui 54, II-8429-2Y-6C-6Y-4C-2Y-1C). Sonora 64 is a hard red spring wheat cultivar that was released as a commercial variety in Mexico in 1964. It has a semidwarf growth habit, averaging 80 to 90 cm in height. It is awned, white chaffed and has oblong heads of regular size. It has high grain test weight and good yield potential and breadmaking characteristics. It is currently susceptible to some of the prevalent races of leaf and stripe rust in Mexico. It is a very early and widely adapted cultivar due to its insensitivity to day length.

Tordo. (Nainari 60/2/Tom Thumb/ Sonora 64/3/ Lerma Rojo 64/Sonora 64, H-244-67-1Y-6B). Tordo is a hard red spring wheat almost as short as Olesen dwarf. The original source of dwarfing is the cultivar Tom Thumb which was originally from Tibet. It is an awned cultivar with brown chaff when ripe, with a long fusiform head. It is used as breeding material in the Maize and Wheat Improvement Center in Mexico. Its resistance to diseases and breadmaking characteristics are not well known. It is medium late in maturity.

Vicam 71. (Lerma Rojo 64/ Sonora 64//Napo 63, II-22398-39M-1R-0Y-101M-0Y). Vicam 71 is a soft white spring cultivar which was released as a commercial variety in Mexico in 1971. It has short and stiff stems, averaging 65 to 75 cm (triple dwarf) in height, is awned and has brown chaff, small oblong heads, medium test weight and soft and extensible gluten. It is resistant to the prevalent races of stem rust in Mexico and moderately resistant to leaf rust. It is a cultivar with a high yield potential, is late maturing and tillers profusely.

Yaqui 50. (Newthatch/ Marroqui, 120-3c(9-11c)-24c). Yaqui 50 is a hard red spring, tall standard cultivar which was widely grown in Mexico. It has thick culms which give it fairly good straw strength, is awnless and white chaffed, has long-laxe oblong heads. It has low test weight, but has good milling and baking quality. It has adult plant resistance to all known races of stem rust with the exception of race 15B. It is susceptible to the prevalent races of leaf rust in Mexico. It is a late maturing cultivar with good yield potential that has been replaced by semidwarf varieties.

Appendix Table 1. Summary of weather information from November 1972 to April, 1973 at CIANO Experimental Station, Ciudad Obregon, Sonora, Mexico. Wheat Physiology Meteorological Station.

Month	Temperature °C				Rainfall		Evapor-ation**
	Mean max		Mean min		mm		mm
	72 -73	long* term	72 -73	long* term	72 -73	long* term	72 -73
November	26.8	28.9	10.5	11.8	1.4	6.2	4.95
December	24.7	24.1	9.4	8.8	27.3	20.1	3.38
January	21.8	23.4	5.9	6.8	15.7	15.1	2.65
February	24.1	24.8	8.9	6.9	38.4	6.8	3.10
March	24.8	27.4	7.3	8.3	7.7	2.4	5.21
April	29.4	31.4	8.0	10.8	15.1	0.4	7.47

*1960 to 1972 = 13 years

**USWB Class A pan

Appendix Table 2. Summary of the genotypic correlations between thirteen agronomic traits and ten wheat crosses.

	Tillers	Spikelet Number	Kernels per Spikelet	Kernel Weight	Head Weight	Height	Days to Heading	Days to Maturity	Grain Filling Period	Head Length	Rachis Internode	Harvest Index
Yield	* 1,2,3,5,7,9,X	-1,-3,-4,9	1,2,4,5,7,8,9,X	-1,-3,-7,8,9,X	2,-3,5,-6,8,9,X	2,6,7,9	5,-8	2,3,-4	-1,-5,-7	1,-3	1,-4,5,9	-2,-3,-4,-8,9
**	7	1,-3	8	3,-3	5,-2	4	1,-1	2,-1	-3	1,-1	3,-1	1,-4
Tillers		-3,-5,9	1,2,5,-6,9	-1,-3,-4,-5,-7,9,X	2,-3,-4,-6,9,X	2,-3,9	5,7	1,2,3,5,6,X	2,-3,-5,-7	1	1,-4,5,9	-3,-4,-5,9
**		1,-2	4,-1	2,-5	2,-4	2,-1	2	6	1,-3	1	3,-1	1,-3
Spikelet Number			1,-3,5,9	-4,-5,-9,-X	-3,-4,-6,9	1,9	4,5,6,7	4,5,7,X	-1,-4,-6,-7,9	1,4,7	1,-3,4,7,-9	-2,-6
**			3,-1	-4	1,-3	2	4	4	1,-4	3	3,-2	-2
Kernels/Spikelet				-1,X	1,2,4,5,6,7,8,9,X	1,2,X	-8,-X	2	5,8	1,-4,5		8
**				1,-1	9	3	-2	1	2	2,-1	0	1
Kernel Weight					3,4,6	3,4,8,9,X	-4,-5,-9,-X	-1,-3,-4,-5,-6,-7,-9	8,X	2,-5,-7,X	2,-7,9,X	-3,8,-9,-X
**					3	5	-4	-7	2	1,-3	3,-1	1,-3
Head Weight						2,3,4,6,8,9,X	2,-3,-8,-X	2,-3,-6	8,X	2,-3	2,6	1,-3,-4,5,-6,8
**						7	1,-3	1,-2	2	1,-1	2	3,-3
Height								-X		1	1,2,7	-1,-2,-3,-4,-5,-6,-7,-X
**							0	-1	0	1	3	-8
Days to Heading								4,5,7,8	-1,-2,-3,-4,-5,-6,-7,-8,-9,X	-2,7	-2	-1,-5,-9
**								4	-X	1,-1	-1	-3
Days to Maturity											-9	
**									0	0	-1	0
Grain Filling Period										-1,2		9
**										1,-1	0	1
Head Length											1,2,3,4,5,6,7,8,9,X	-8,X
**											X	1,-1
Rachis Internode												1,-5,6,7
**												3,-1

Cross Number	
1	= Son 64/Y 50
2	= Son 64/On
3	= Son 64/Tor
4	= Y 50/On
5	= Y 50/Tor
6	= Vc 71/Son 64
7	= Vc 71/Y 50
8	= Vc 71/On
9	= Vc 71/Tor
X	= Tor/On

* Indicates cross number which showed high genetic correlations between the corresponding traits. A negative sign signifies the correlation was negative.

** Refers to total number of crosses where either high positive or negative correlations were observed.