

AN ABSTRACT OF THE THESIS OF

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Title: Estimates of Genetic Variability Resulting From Single, Top, and Double
Cross Populations in Durum Wheat (*Triticum turgidum* L. var. *durum*.)

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The success of a plant breeding program depends upon the availability of useable genetic diversity. Such diversity may be enhanced depending on the type of hybridization strategy employed. Segregating progenies resulting from F₂ populations, a double cross, and a top cross were compared for the amount of useable genetic diversity associated with six traits in durum wheat. The parental lines were three winter selections, H7092-11, H7092-52, and WD5, and two spring cultivars, WPB 881 and Altar 84. Traits evaluated were (1) plant height, (2) days to maturity, (3) harvest index, (4) kernel weight, (5) grain yield, and (6) pigment content.

Analysis of the population mean values suggested the superiority of the F₁ top cross for plant height, kernel weight, and grain yield. The F₁ top cross progeny also had the highest genetic variability for grain yield. F₂ population of the cross Altar 84 / H7092-52 gave the highest mean values for days to maturity and harvest index, and showed the highest genetic diversity for traits other than grain yield. The only population showing detectable genetic variance for pigment content was the F₂ progeny of the single cross WPB 881 / H7092-11. When genetic diversity was

detected, the double cross was approximately intermediate between the two F₂ populations from which it was derived. Transgressive segregation was more frequent in the top cross population for grain yield, kernel weight, and plant height.

No associations between grain yield and the other traits were noted for the F₂ population of the single cross Altar 84 / H7092-52 and the top cross population. For the second F₂ population (WPB 881 / H7092-11) and the double cross population, grain yield was found to be associated with harvest index and plant height.

The only consistent relationship across all segregating generations was a negative correlation between plant height and harvest index.

Based on the genetic diversity and the transgressive segregation observed, top crossing appears to be the more promising in improving grain yield in the experimental material investigated. For specific traits other than grain yield, it would appear that single crosses would be a more productive approach, however progress would depend on the specific parental combination. The double cross was inferior to the other crossing strategies for the traits measured.

Estimates of Genetic Variability Resulting from Single,
Top, and Double Cross Populations in Durum Wheat
(*Triticum turgidum* L. var. *durum*)

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Typed by Mourad Abdennadher

DEDICATED TO:

my parents,

Mohsen and Bassima

my sister,

Narjes

my brother,

Nabil

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ESTIMATES OF GENETIC VARIABILITY RESULTING FROM SINGLE, TOP, AND DOUBLE CROSS POPULATIONS IN DURUM WHEAT

(*Triticum turgidum* L. var. *durum*.)

INTRODUCTION

Present efforts in wheat breeding have been oriented toward the development of high yielding cultivars adapted to the improved management practices. Thus, it is thought that new wheat cultivars are becoming increasingly more homogeneous genetically and accordingly, more vulnerable to new diseases and adverse climatic changes. However, different surveys have shown that elite germplasm has a wider genetic base and provides more useful diversity than is generally thought (Asins and Carbonell, 1989). This genetic diversity among potential parents is quoted to be an important factor for obtaining hybrid vigor and positive transgressive segregation (Ghaderi et al., 1984). Hence, estimating the magnitude of the genetic variability and determining its pattern of distribution are essential if genetic diversity is to be effectively utilized.

Plant breeding programs depend not only on the availability of diverse germplasm but also on the efficiency of combining the right parents in order to accomplish an optimal diversity in the off-springs. Thus, the choice of the parental lines to hybridize and the order in which they should be combined are two issues of equal importance that should be approached judiciously ahead of any crossing operation. The use of double and three-way crosses have been suggested as a means

of enhancing the useable genetic variability in subsequent segregating populations. However, the use of multiple crosses increases geometrically the number of possible cross combinations, and hence, adequate models need be developed to predict the most appropriate combinations from the performance of a set of parental lines (Petpisit, 1980). In wheat, genetic diversity has been enhanced in the 1960's through the systematic hybridization of spring and winter gene pools and subsequent top crossing to either winter or spring germplasm (Kronstad, 1986). These crosses incorporated additional sources of disease resistance, dwarfism, and agronomic attributes.

The purpose of this investigation was twofold. First, to evaluate the performance and the potential transgressive segregation of the first segregating generations following single, double, and top crosses. Secondly, to compare these three types of crosses in generating useable genetic variability for specific traits. A secondary objective was to determine possible relationships among the traits evaluated in the segregating populations.

LITERATURE REVIEW

I- Genetic Variability Resulting From Different Hybridization Strategies

Genetic variability can be assessed by statistical methods that test the goodness of fit of models. These models estimate different components of gene action using mean values and variances of different generations as measured in designed experiments. A common experimental approach in wheat, to determine the nature of gene action, is to use early filial generations derived by intercrossing and selfing the parents and their F1s. Jinks and Pooni (1976) suggested the use of F2 top-cross generation in addition to the original six generations (the two parental lines, F1, F2, and reciprocal back crosses) as a more complete experiment. Jinks and Pooni (1976) proposed the same model as an ideal method for interpreting the genetic control including predicting cross performance for specific traits.

Much of the theory and experimental documentation concerning the nature of genetic variability resulting from different sequences of parents in crosses has been developed in relation to cross pollinated crops, namely, maize (*Zea mays* L.). This has also been true in predicting hybrid performance of F1 populations. A literature review concerning the use of different crossing strategies in self pollinating species like wheat reflects a reluctance of breeders to use techniques other than single crosses. However in some cereal breeding programs different combinations of parental lines, employing double and top crosses, have lead to successful results.

When employing more than two parents in crosses, the breeder faces the problem of how many parents to use and in what sequence. The number of cross combinations available increases geometrically with the number of parents. Hayes *et al.* (1955) showed that if p is the number of parental lines $p(p-1)/2$ single crosses, $p(p-1)(p-2)/2$ three way crosses, and $p(p-1)(p-2)(p-3)/8$ double crosses are possible if reciprocal crosses are assumed to be equivalent. Hence, the breeder must find a means to predict which inbred line could be beneficial if included in a single, three-way, or double cross and which parent combinations and sequences are to be used in order to enhance the recovery of desirable transgressive segregant.

Genetic variability in single crosses

Since the earliest days in corn breeding, breeders have tried to determine which inbred lines to combine in order to obtain a high and positive genetic variability in subsequent progenies. The diallel analysis has been used since the earliest days of hybrid maize to test the response of any inbred to produce superior hybrids in combination with other inbred (Allard 1960). Rinkle and Hayes (1964) showed that corn inbred lines with the highest general combining ability are more likely to result in higher yielding single crosses. Using diallel crosses Kronstad and Foote (1964) working with soft white winter wheat, and Bitzer and Fu (1972) working with soft red winter wheat reported that the general combining ability is the principal component of genetic variability for yield and the components of yield.

A high potential of genetic diversity is always sought in the F1 generation.

Such diversity can be accomplished by hybridizing genetically diverse parents (Jensen, 1988). This is in agreement with findings of Escuro *et al.* (1963), working with oat they showed that single crosses generated from unrelated or genetically diverse parents gave greater genotypic variances and significant heterosis for different agronomic traits. In wheat several investigations noted high heterotic expression when the F1s come from genetically diverse parents (Walton, 1969; Grant and McKenzie, 1970). Winter X spring crosses in wheat have been fruitful in increasing the genetic diversity and the yield at the same time (McKenzie and Grant, 1974).

Bailey *et al.* (1980) working on hybrid wheat tried to compare different models to predict the performance of F1 hybrids. They found that the model that estimates the best genetic effects includes data from the parents, F2, and three-way crosses.

Genetic variability in double crosses

Double cross analysis has not attracted much attention from wheat breeders, although the details of the approach were available as early as in 1962 (Rawlings and Cockerham, 1962). Singh (1986) pointed out that double cross analysis has a two fold purposes: i) it provides information about the relative importance of various components and subcomponents of genetic variation, and ii) suggests the desired order of parents in a cross combination.

Singh and Chandhry (1977), and Singh (1986) working on grain yield in barley and harvest index in wheat, respectively, found that the order of parents in hybrid

production by double cross combinations played a major role in their hybrid performance. This is in agreement with the previous work on corn (Jenkins, 1934; Doxtor and Johnson, 1936; Anderson, 1938; and Robert and Bryan, 1940). Jensen (1988) referred to the single crosses used in a set of double crosses as pseudo-parents. He contended that when the single cross hybrids are used as parents they introduce additional genetic variability.

A disadvantage of the double cross is the lack of direction of the origin of diversity that the three way cross offers to the breeder. Three modifications were proposed by Jensen (1988) in order to harness the double crosses for the breeder's need: a) use three adapted lines and one exotic line, b) hybridize a backcross and a single cross, and c) if desirable genotypes are available, use their single crosses as parental lines. Eckhardt and Bryan (1940) pointed out that the best way of making double crosses is by bringing similar inbreds together in the initial single crosses.

Jenkins (1934) advanced four methods of estimating the yield of double crosses in corn: a) predicting the yield of the double cross on the basis of the average yield of the possible six crosses of the four inbred lines used in making the double cross, b) predicting the yield on the basis of the average yield of the four single crosses not used in making the double cross, c) prediction based on the average yield of the four inbred lines in all possible combinations with ten other inbred and these averages are averaged, and d) prediction based on the average yield of the four inbred lines in top crosses. Doxtator et al. (1936) and Anderson (1938), both working with maize, found a correlation between the average yield of the four non-

parental single crosses and the average yield of the double cross. Similarly, Punzalan and Lambeth (1970) showed the applicability of Jenkins method b for predicting double cross performance for fruit quality attributes in tomato.

Genetic variability in top crosses

Three-way top crosses have been used extensively for testing maize inbreds for their general combining ability (Jenkins and Brunson, 1932). The three-way top cross was first developed to test the general combining ability of maize inbreds. Jenkins and Brunson (1932) gave exhaustive data advocating the use of top-cross test in favor of the diallel test to identify the more promising inbred. When inbreds developed for hybrid production were crossed with a wide range of germplasm, those which ranked the highest in yield, on the average, produce the best hybrids. The correlation for the yield between the inbred lines selected on the basis of the top-cross test and average single cross production ranges from .53 to .90 (Jenkins and Brunson, 1932); thus, they concluded that it should be possible to eliminate 50% of the inbred lines based on the top-cross test without danger of losing any superior material. The remaining inbreds would be tested in single cross combination.

The efficiency of the top cross test over the diallel test results from the reduced number of crosses that one had to make (Allard, 1960). The top cross test allows for the identification of more promising inbred lines from a group of size "n" with only "n" crosses. While the diallel test needs $n(n-1)/2$ crosses. However, several plant breeders prefer to test for general combining ability using line *per se* evaluation,

and, thus, eliminating the genetic contribution of the tester (Lonnquist and Lindsey, 1964).

In the production of hybrids, three-way top crosses have taken on a more importance role. Hybrid wheat (*Triticum aestivum* L.*aestivum*) developed by three-way crosses were found to show less heterosis than single cross hybrids, however, three-way crosses introduced more variability to the resulting populations (Bailey et al., 1980 and Petpisit, 1980). The three-way hybrids offered the opportunity for segregation and recombination in contrast to single crosses. Thus, they result in a genetically more heterogenous population. Allard and Bradhaw (1964) suggested that this heterogeneity offers a populational buffering, and accordingly provides for more adaptation. Working with sorghum [*Sorghum bicolor* (L.) Moench], Stephens and Lahr (1959) found that three-way hybrids are not necessarily more variable than single-crosses for traits such as date of bloom and plant height. Walsh and Atkins (1973), working with the same crop, reported that the mean performances of single and three-way crosses were not significantly different for grain yield and other agronomic traits. They did report that the variability among plants for plant height and days to midbloom is significantly greater within three-way hybrids than within single crosses. In accord with Jowett (1972), they recommended the use of three-way crosses in favor of the single-cross hybrids because of their stability under different environmental conditions.

Maize investigators, namely, Wheatherspoon (1970) and Lynch et al (1973) noted the average yield superiority for single crosses over three-way crosses and for

three-way crosses over double crosses. This superiority is more pronounced when the best selected crosses are compared. They explained these results suggesting more complete utilization of both dominance and epistatic effects in single and three-way crosses than in double crosses. They also indicated that single crosses are more sensitive to environmental stresses than three-ways or double crosses.

Three-way crosses have been shown to be beneficial for the integration of new genes from exotic germplasm. Thorne and Fehr (1970), working on germplasm introduction for soybean improvement, found that populations resulting from three-way crosses were more fruitful sources than populations from two-way crosses for the selection of high yielding lines. Also they noted that the genetic variability was not reduced by crossing an adapted X exotic F1 population to a second adapted parent. Similarly, Khalaf *et al.* (1984), working on the relative potential of the three types of crosses as sources of variability for soybean improvement, showed that progenies from three parent crosses were more variable and had higher frequencies of agronomically superior lines than progenies from either two or four parent crosses.

Several studies advocate the use of the mean of the non-parental single crosses in predicting the performance of three-way top crosses (Skaracis and Smith, 1984; Patanothai and Atkins, 1974).

II- Components of Genetic Diversity

Cultivated durum wheat *Triticum turgidum* L. var. *durum* originated from *Triticum dicocoides* (Cantrell, 1987) which was mostly found in Palestine, Syria, and Lebanon. Later, the domesticated lines belonging to *Triticum turgidum* spread to all Europe, the Middle East, and North Africa. Many investigators have shown the close relationship between the wide geographical distribution of durum wheat and the phenotypic diversity (Porceddu 1976, Spagoletti Zeuli et al.1985). Genetic diversity is due to the action of additive and epistatic genes and different methods have been proposed to determine genetic differences among material on the basis of quantitative characters (Cervantes et al.1978).

The improvement of all agronomic, milling, and baking traits require genetic diversity. Plant height and lodging resistance, spike characters, kernel weight, maturity, and grain yield are the most important characters as far as agronomic traits are concerned in durum wheat breeding. While, quantity and quality of the proteins, yield of semolina, and semolina color are the most important end products used traits.

Plant height

The average height of the durum wheat lines sown under the North Dakota conditions is 150 cm (Joppa and Williams, 1988). However, since the use of the cultivar Heiti in 1940 a considerable decrease of the height was obtained and

concomitantly a higher resistance to lodging. Semidwarf gene Rht1 was transferred on chromosome 4A to durum wheat from a hexaploid wheat containing the Norin-10 genes (Lebsock, 1967). Other semidwarf phenotypes were observed by Mekni (1971), however he could not identify neither the causal genes nor their chromosomal location. The International Maize and Wheat Development Center (CIMMYT) durums containing Heiti genes and one or more semidwarf genes average about 65 to 75 cm in height.

The effect of the semidwarf genes on yield is conflicting. Several studies investigating bread and durum wheat showed the positive effect of the semidwarf genes on yield and yield components (Kulshrestha and Jain.,1978, O'Brien and Pugsley., 1981, and Fischer *et al.*1981). While, Joppa (1973) and Allan (1980) working with durum and common wheats, respectively, found a negative correlation between the semidwarf genes and test weight and 1000 kernel weight. Similarly, Deckard *et al.*(1977), in a study involving both durum and bread wheats, found that the semi dwarfism had no effect on grain yield. Reduced plant height is correlated with a lower protein content due to the dilution effect of the increased grain yield (Vogel *et al.*, 1956; Gale, 1979; Gale *et al.*, 1981). Conversely, other researchers did not find a significant correlation between the semi dwarfism and grain protein percent and yield (Busch *et al.*, 1981; Joppa and Walsh, 1974; Pepe and Heiner, 1975).

Wehrhahn and Tai (1988) studying the genetic architecture of homozygous inbred back cross lines of bread wheat found seven genes controlling plant height

variation. Five of these genes have pleiotropic effects on heading date. Widner (1968) working on durum wheat found that general combining ability was predominant in the expression of plant height. Amaya *et al.* (1972) estimating the genetic effects influencing plant height in durum wheat, noted that additive genetic effects predominated. Chapman and McNeal (1971) showed that epistasis was involved in the expression of plant height in a spring wheat cross.

Several investigations have reported different heritability estimates for plant height in wheat. Ketata *et al.* (1976) estimated the heritability for height in the narrow sense of 0.64 in a winter wheat cross. This moderately high heritability was also found by previous studies, namely, Reddi *et al.* (1969).

Heading date and grain filling period

The durum wheats grown in North America are spring types. Despite the positive association between late maturity and yield, early maturity can be a desirable attribute in avoiding some biotic and abiotic stresses. The vegetative period (days to anthesis) and the grain filling period (post-anthesis) determine the length of the vegetative and reproductive cycle. Lebsock *et al.* (1973) studied four durum wheat crosses and found that maturity depended on the sensitivity of the parental lines for day length. Moreover, they found that the insensitivity to day length is under the control of a single gene with incomplete dominance.

Lelley (1976) stated that the differences in earliness between cultivars or crossing derivatives are easily shown by the visual determination of heading time.

Hence, breeders have been looking for early flowering lines and for the type of gene action involved in the expression of earliness.

The association between the vegetative period and yield is controversial. Aksel and Johnson (1961) working with barley (*Hordeum vulgare* L.) and Bingham (1969) working with common wheat (*Triticum aestivum* L.) observed a positive correlation between the length of the vegetative period (planting -to-anthesis) and high grain yield. Whereas, Gbeyeou et al. (1982b) and Leihner and Ortiz (1978) working with durum wheat observed non significant and negative correlations, respectively, between the same traits. Bingham (1969) explained the beneficial effect of a longer vegetative period by the development of a better sink capacity. The contribution of pre-anthesis reserves to grain yield is 5 to 10% in wheat and 20% in barley (Evans and Wardlaw, 1976). Gebeyeou et al. (1982a) investigated sixteen durum wheat cultivars and found that the length of vegetative growth showed a positive correlation with kernel per spike, kernel weight, and grain yield, however, only the correlation with kernel weight was significant ($r = 0.42$).

Wehrhahn and Tai (1988) working with common wheat showed that five genes were responsible for over 95% of the genetic variation for heading date in two pure lines. In addition, they found that these genes have pleiotropic effects on plant height. Anwar and Chowdhry (1969) and Bhatt (1972) found the heading date in spring wheat to be controlled by dominance effects. Whereas, Walton (1971) and Edward et al. (1976) working with spring and winter bread wheat, respectively, found that the heading date was controlled by genes with both additive and dominance

effects, thus they concluded that selection for this trait should be delayed until later generations. Similarly, Amaya *et al.* (1972), working with durum wheat, showed that heading date was controlled by genes with additive and dominance effects, and found that additive genetic effects predominated in controlling the expression.

Grain yield is largely dependent on sink capacity which is determined by initiation of floral structures during the vegetative period and the photosynthetic capacity during the grain filling period (Bingham, 1969). Several investigators pointed out the positive association between grain yield, grain filling, and the length of the grain filling period (Daynard *et al.*, 1971 and 1976; Spiertz *et al.*, 1971). Gebeyehou *et al.* (1982a) observed in sixteen durum wheat cultivars positive correlations between the length of the filling period and kernels per spike, kernel weight, and grain yield.

The most recent spring wheats developed in Mexico have their yields coupled with a relatively short vegetative and grain filling periods (Lelley, 1976). The reduction of the grain filling period is brought about by a higher grain filling rate. Nass and Reiser (1975) found that a high grain filling rate and a shorter grain filling period could produce high grain yields in areas with short growing seasons.

The association between pre and post-anthesis periods is controversial; Knott and Gebeyehou (1982) and Rasmusson *et al.* (1979) working with durum wheat and barley, respectively, observed a negative association between these two periods. Whereas, Gebeyehou *et al.* (1982b) did not find a similar negative correlation in durum wheat.

Spikelet fertility and kernel weight

Spikelet fertility was proposed as one approach to improve grain yield of semidwarf durum wheat (Leihner and Ortiz, 1978). Ledent and Moss (1979) observed that spikelet fertility is the most closely related trait with grain yield/ culm in wheat.

One effort to increase the spikelet fertility in durum wheat has been the use of the four-rowed spike or tetrastichon character (Hangerud and Cantrell, 1984). Koric (1973) identified three genes affecting this character. Luedtke (1980) observed that the four rowed durum wheats had a significantly higher spike fertility but lower spike weight because of lower kernel weight. Haugerud and Cantrell (1984) did not find a significantly higher grain yield when they compared the four-rowed spike lines to the normal cultivars grown in North Dakota. They concluded that the complex interaction of yield components with the four-rowed spike genetic system make it difficult to use this trait in the improvement of yield *per se* in durum wheat. Hence, the investigation of the genetic variability of spikelet fertility is a better mean for grain yield improvement in durum wheat.

Narrow sense heritability estimates of spikelet fertility have been reported to be low. Lee and Kaltsikes (1972) found a heritability estimate of 0.46 for kernel number/spikelet in durum wheat. Haro (1983) using parent-offspring regression in durum wheat cross found a heritability value of 0.39 for the same trait. Heritability of spikelet fertility in hexaploid wheat were reported to be 0.28 by Ketata et al. (1976) and 0.34 by Sidwell et al. (1976).

Grain yield of wheat depends not only on the number of spikes per unit of area, but also on kernel number and kernels weight. Busch and Kofoed (1982) used recurrent selection to improve kernel weight in spring wheat lines. The advancing cycles of selection were significantly associated with decreasing days to heading, number of spikelets per spike, number of kernels per cm of spike, and number of spikelets per cm of spike. While, cycles of selection were effective in increasing kernel weight and percent grain protein. Conversely, plant height, grain yield, and test weight did not differ over cycles of selection. Many studies had shown the negative phenotypic correlation between kernel number and kernel weight in wheat (Osman et al., 1983; and Haugerud and Cantrell, 1984). Simmons et al. (1982) investigating the development of spring wheat kernels as affected by reduced kernel number per spike and defoliation concluded that the response depended on the genotype, kernel position in a spikelet, and possibly the environment. Sidwell et al. (1976) did not find a significant phenotypically nor genotypically correlations between kernel number and weight.

Thousand kernel weight in durum wheats varies from 20 to 60g (Joppa and Williams, 1988). This trait is highly heritable (Baker et al., 1968), however, its value as a selection criterion for yield is questionable (Gebre-Mariam et al., 1988). An average broad sense heritability of 0.72 was estimated for kernel weight in four durum wheat crosses (Lebsock and Amaya, 1969). Sidwell et al. (1976) reported broad and narrow sense heritabilities of 0.5 and 0.43, respectively, in a hard red winter wheat cross. A narrow sense heritability of 0.65 in winter wheat crosses was

reported by Ketata et al. (1976) for this trait. In the former study the authors found additive effects were the predominant factor contributing to the genetic control of kernel weight. In common wheat several investigations reported partial dominance for heavier kernels with additive gene action being the major in the control of kernel weight (Bhatt, 1972). Estimates of gene number controlling kernel weight in durum wheat vary from one to four or more (Joppa and Williams, 1988).

Harvest index

Donald (1962) defined the harvest index as the ratio of grain yield to total biomass yield. Thus, a high harvest index expresses a better conversion of biomass into grain.

Wallace et al. (1972) stated that harvest index depicts the ability of the genotype to differentially partition the photosynthetates, i.e. a high harvest index represents an increased physiological capacity of the crop to mobilize photosynthetate and translocate it to organs of economical value. Donald (1968) contended that increasing wheat grain yield could be brought about by either increasing biological yield with a sustained harvest index or by increasing the harvest index alone. The limit to which harvest index can be increased is considered to be around 60% (Austin et al., 1980).

Many investigators have shown the positive correlation between harvest index and grain yield with values ranging from 0.62 to 0.96 (Thorne et al., 1969; Syme, 1970; Singh and Stoskopf, 1971; Kulshrestha and Jain, 1982). Rosielle and Frey

(1975) reported a selection efficiency of 43% when selecting for grain yield through harvest index in oat (*Avena sativa* L.). Syme (1972) found a high correlation ($r = 0.85$) between harvest index measured on a single plant basis and mean grain yield. He could estimate 72% of the grain yield variability of 49 spring wheats grown in the field from their harvest index values obtained from single plants grown in the green house. Similarly, Fischer and Kertesz (1976) found that harvest index of spaced plants was better than grain yield of spaced plants for prediction of wheat grain yield in large plots. Nass (1980) found that harvest index was a valuable selection criterion for grain yield in two crosses of spring wheat. However, he found selection was more reliable at higher population densities than at lower densities. Allan (1983) stated that the use of harvest index as a selection criterion for grain yield was more feasible among taller than shorter genotypes. Also, he found the harvest index increased proportionally with the number of dwarfing genes in the genome. Sharma and Smith (1986) reported that harvest index was negatively correlated with plant height and days to heading, whereas correlation between harvest index and biomass was not significant.

Moderate to high broad sense heritability estimates have been reported for harvest index. Bhatt (1977) estimated the harvest index heritability from two crosses of common wheat. He found the estimates to vary from 0.70 to 0.88. Sharma and Smith (1986) reported the range from 0.44 to 0.60 in a study of the inheritance of harvest index in three diverse populations of winter wheat. Rosielle and Frey (1975) found heritability estimates of harvest index to vary from 0.35 to 0.66 in oat lines

derived from bulk population.

Grain yield

Genetic diversity is the most important prerequisite for long-term improvement of grain yield in durum wheat (Cantrell, 1987). Genetic variation has been proven to be greater among lines from different origins than among those more closely related. Therefore diversity based on morphological characters and origin may give a good indication for the choice of breeding material (Spagnoletti Zeuli et al. 1985).

Diallel analysis has been used in many studies to ascertain the genetic system controlling grain yield in durum wheat. This method has shown that both general and specific combining ability were important in the expression of grain yield, with general combining ability being predominant (Kaltsikes and Lee 1971; Quick 1973; DePace et al. 1985). Due to the bias brought by the interaction between general combining ability and the environment, caution must be exercised in extending the results of the diallel analysis to the type of genetic effects controlling yield (Cantrell, 1987).

The nature and predominance of genetic effects controlling grain yield variability is conflicting. Jackson et al. (1968) studied the genetic diversity and the nature of gene effects controlling grain yield in six durum wheat crosses. They noted an increased genetic variance in the population derived from highly diverse parents with additive genetic effects being the major source of genetic variation for grain

yield. Conversely, Amaya *et al.* (1972) found the dominance effects to be relatively more important than the additive effects in four crosses of durum wheat. Gill *et al.* (1983) found that both dominance and additive effects were responsible for the variability of grain yield in durum wheat with dominance effects being more important. They asserted that a maximum gain may be achieved by breeding strategies that exploit both additive and non-additive genetic variance.

Grain quality

Durum wheat has unique quality characters making it useful for production of pasta, couscous, and even bread in some area of the world. Of the major quality traits in durum wheat are grain protein content, and color and texture of pasta products (Sarraf *et al.*, 1989).

Grain protein content determines the yield of semolina. It is highly influenced by the environment (Joppa and Williams 1988) and is related to the kernel vitreousness (Menger, 1973; Joppa and Williams, 1988). The variability in grain protein percentage is related to the ability of the cultivars to translocate organic compounds from the leaves and stems into the kernel. A wide variation for protein content among Ethiopian durum wheats was reported by Negassa (1986). Avivi (1979) and Sarraf *et al.* (1984) reported high percentage of grain protein in wild tetraploid wheat collections.

Several studies indicated a moderate heritability estimates on protein content in durum wheat (Johnson *et al.*, 1973; Avivi *et al.*, 1983). Sarraf *et al.* (1989)

reported the predominance of additive genetic effects in the control of grain protein content in reciprocal crosses made between six durum wheat lines. They quoted a narrow heritability estimate of 78%. This value is beyond the range (42-72%) advanced by Johnson *et al.* (1973) and Halloran (1981) working with durum and hexaploid wheats, respectively.

Semolina color is determined by the level of xanthophyll pigments present in the endosperm of durum wheat (Laignelet *et al.* 1972). Consumers tend to be attracted by pasta products with an amber yellow color. Grignac (1970) found a variation for the grain pigment content in durum wheat. Sarrafi *et al.* (1989), in agreement with Johnston *et al.* (1983), found additive gene effects to be responsible for variation in semolina color. This trait was found to be highly heritable by many investigators (Braaten *et al.*, 1962; Johnson *et al.*, 1983). These reports were in concordance with those of Sarrafi *et al.* (1989) and Grignac (1970) who reported 42% and 59%, respectively. Joppa and Williams (1988) indicated that the major genes controlling semolina color might be on chromosome 2A and 2B.

MATERIALS AND METHODS

Five durum wheat cultivars were used to develop the set of experimental material. The parental lines included 1) Altar84, a semi-dwarf spring durum wheat cultivar developed at the International Maize and Wheat Improvement Center (CIMMYT) - Mexico, 2) WPB 881, a semi-dwarf spring durum developed by a private company in Montana, 3) H7092-11 and H7092-52, two mid-tall winter type introductions from Turkey, and 4) WD5, an experimental winter selection from Nebraska. A more complete description of the parental material is provided in Appendix Table 1.

Crosses were made at the Hyslop Crop Science Laboratory near Corvallis, Oregon. Two single crosses, a double and a top cross were generated from the five cultivars. The single crosses were made in 1988. The parental lines of the first single cross were Altar84 and H7092-52, while WPB 881 and H7092-11 constituted the parental lines of the second cross. The following crossing season a double cross was generated from these two single crosses, i.e. WPB 881/ H7092-11 // Altar84/ H7092-52, and the single cross H7092-52/ Altar 84 was top-crossed to the experimental selection from Nebraska, WD5. Also, the two single crosses were selfed to obtain the two F2 generations which were designed as SC1F2 (Altar84 / H7092-52) and SC2F2 (WPB 881 / H7092-11).

During the 1989-1990 growing season eight entries consisting of four parental lines of the two single crosses, two F2 populations from single crosses, one F1

population from the double cross, and one F1 population from three way cross were planted at East Farm Field Laboratory on October 25th, 1989. The East Farm Site is located 1.6 km east of Corvallis, Oregon. The soil type is a chehalis silt loam.

Fifty kilograms per hectare of nitrogen, 60 kg per hectare of phosphorus, and 36 kg per hectare of sulfur were applied prior to seeding. One application of the herbicide Finesse (Chlorosulfuron) at a rate of 18 grams per hectare was applied during December 1989, after tillering, to prevent weed competition. The fungicide Tilt was applied at a rate of 280 grams per hectare during April, just after flowering, to control leaf rust (*Puccinia recondita*). A summary of climatic data occurring during the experimental period is presented in Appendix Table 3.

A randomized complete block design with four replications was used to determine if differences in the extent and nature of the genetic variability existed among the three types of crosses, single, double, and top crosses. All populations were hand sown, with the parents, F1s double, and top crosses spaced in single row plots. The spacing was 30 cm between and within rows. The F2 populations were space planted in two row plots with the same spacing as the other entries. Population sizes consisted of 15 plants per entry for parents, double, and top crosses, and 30 plants per entry for the F2s. Barley was planted to reduce possible bias due to lack of competition where plants were missing and along the borders.

Observations were taken on single plant basis. The following traits were measured:

- Plant height: length (cm) from soil surface to tip of main spike, excluding awns.

- Plant maturity: number of days from heading until all chlorophyll had disappeared from the main culm spike.
- Harvest index: grain yield divided by biological yield.
- Kernel weight: 200 kernels were randomly selected and recorded in grams.
- Grain yield: total grain yield recorded in grams.
- Pigment content: expressed as the absorbance of three grams of flour at 440 nm (AACC Method 14-50 modified by CIMMYT).

The following analyses were performed:

- Analyses of variance were conducted to determine if there were significant differences between entries for plant height, days to maturity, harvest index, kernel weight, grain yield, and pigment content.
- The frequency of positive transgressive segregants recovered from each cross and for each measured trait. For each measured attribute, plants performing better than the best parent in the contemplated cross were defined as transgressive segregant.
- The phenotypic variances among F2, double cross, and top cross populations were estimated by pooling variances among plants within replications for each cross. Environmental variance was estimated by averaging the pooled variances from non segregating populations (parental lines). The genetic variance for each segregating generation was obtained by subtracting the environmental variance from the phenotypic variance.
- Correlations between the agronomic traits for the different cross populations were also obtained.

EXPERIMENTAL RESULTS

The results of this investigation are divided into four sections:

1) informations obtained from the analyses of variance including mean values, ranges, and standard deviations for the six traits under investigation, 2) estimates of the genetic variances from the different crosses and for each trait, 3) presence of transgressive segregation, and 4) relationships between the different agronomic traits in each type of cross.

Analysis of variance

The observed mean squares for the six traits measured revealed that the four parents differed in all traits except pigment content (Table 1). Coefficient of variation values were low except for pigment content (20.2) and grain yield (18.3). A multiple comparison of the mean values of the four parents is given in Table 2. H7092-52 was the tallest parent, while WPB 881 was the shortest. Altar84 and H7092-11 were similar in height. H7092-11 and H7092-52 were earlier and higher yielding than either WPB 881 or Altar 84. WPB 881 had the lowest harvest index, kernel weight and grain yield, but reflected the highest pigment content even though there were no differences at the 5 percent level of probability.

In Table 3 observed mean squares among the different generations and parental lines are provided. The generations included the two F2 populations, a

Table 1. Observed mean squares for plant height, days to maturity, harvest index, kernel weight, grain yield, and pigment content for the four parental lines grown on the East Farm Experimental Site in 1989-90.

Source	Mean Squares						
	D.F	Plant height (g)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
Replications	3	18.90	10.05	1.85 E-3	0.36	10.61	54.02
Genotypes	3	164.08**	195.70**	3.96 E-3**	2.01**	1.59	523.80**
Error	25	10.52	12.56	1.02 E-3	0.14	4.25	42.08
C.V		3.19	4.80	9.30	3.51	20.18	18.36

** Significant at one percent probability level.

Table 2. Comparison of the mean performance for plant height, days to maturity, harvest index, kernel weight, pigment content, and grain yield of the four parents grown on the East Farm Experimental Site in 1989-90.

Parents	Means					
	Plant height (g)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
WPB 881	71.87 ^{c*}	69.65 ^e	0.20 ^g	10.10 ^k	7.42 ^m	10.18 ^z
Altar 84	78.75 ^b	69.42 ^e	0.25 ^f	10.95 ^h	6.88 ^m	17.17 ^y
H7092-11	76.62 ^b	77.38 ^d	0.21 ^g	11.23 ^h	6.71 ^m	24.21 ^y
H7092-52	82.75 ^a	78.72 ^d	0.23 ^{fg}	11.03 ^h	6.35 ^m	28.62 ^x

* Means with the same letter are not significantly different based on least square difference (LSD) range test at five percent probability level.

double cross, and a top cross. Differences were noted for all traits except pigment content. Coefficient of variation values were again high for grain yield (22%) and pigment content (>21%), whereas all the remaining traits had relatively low coefficient of variations (<9%).

Orthogonal contrast for crosses

Mean squares from orthogonal contrasts between different combinations of the three types of crosses and for the different traits are displayed in Table 4. Differences between the F2 generations of the two single crosses were found for plant height, harvest index, and kernel weight. The contrast of the two multiple crosses, double and top crosses, gave significant differences for plant height and kernel weight only.

Generation performances

Table 5 illustrates the mean values, ranges, standard deviations, and coefficient of variations for the traits under investigation. The comparison are made among two F2 populations generated from the single crosses Altar84 / H7092-52 and WPB 881 / H7092-11 and designated hereon SC1F2 and SC2F2, respectively, the double and top cross populations.

Plant height was found to be different among the four segregating populations (Tables 3 and 4), and the maximum average plant height was noted for the top cross at 109.31 cm. The second tallest generation was SC1F2 with a mean height of

Table 3. Observed mean squares for plant height, days to maturity, harvest index, kernel weight, grain yield, and pigment content for the four parental lines and segregating populations grown on the East Farm Experimental Site in 1989-90.

Source	Mean Squares						
	D.F	Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
Replications	3	16.88	9.11	1.93 E-3	0.07	11.01	13.43
Generations	7	850.55**	85.35**	4.51 E-3 **	2.01**	1.60	637.24**
Error	57	9.81	10.01	8.96 E-6	0.16	4.20	81.61
C.V. (%)		3.75	4.27	9.78	3.57	21.68	22.20

** Significant at one percent probability level.

Table 4. Contrasts of means showing sum of squares for plant height, days to maturity, harvest index, kernel weight, pigment content, and grain yield from single, double, and top cross populations grown on the East Farm Experimental Site in 1989-90.

Contrasting crosses	Mean Squares					
	Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
SC1F2 vs SC2F2	180.10 ^{**}	6.87	7.28 E-3 ^{**}	1.00 [*]	1.47	206.43
DC vs TC	2106.00 ^{**}	0.66	6.12 E-6	1.94 ^{**}	4.12	128.30

^{**} Significant at one percent probability level.

^{*} Significant at five percent probability level.

SC1F2: Altar84 / H7092-52.

SC2F2: WPB 881 / H7092-11.

DC: Altar84 / H7092-52 // WPB 881 / H7092-11.

TC: Altar84 / H7092-52 // WD5.

86.50 cm. Average height in SC1F2 was higher than that observed in the double cross population (86.50 versus 83.63 cm), however, this difference was not significant. The shortest population was SC2F2 with a mean value for height of 81.13 cm. Phenotypic variation, noted from the ranges, was maximal in SC1F2. While phenotypic variation values of the three remaining populations, SC2F2, double cross, and top cross were not different. The variation around the mean in each population, noted from the standard variation values, increased for plant height from top cross to double cross to SC1F2 to SC2F2.

The orthogonal contrast analysis did not reveal any difference among the segregating populations for days to maturity (Table 4). This was confirmed by the multiple comparison of means for days to maturity (Table 5). On the average all segregating populations were earlier than the Turkish entries, H7092-11 and H7092-52, and later than the two other parental lines, Altar84 and WPB 881.

The highest phenotypic variability, noted from the ranges, for the trait days to maturity was found in SC1F2, range = 23 days, and was minimal in SC2F2, range = 16 days. The two composite crosses did not differ for this trait with the top cross showing slightly more variability than the double cross. The distribution around the mean for the trait days to maturity was the largest in the double cross population, Standard deviation = 0.78, and the smallest in SC1F2, standard deviation = 0.42. The top cross population and SC2F2 gave the same standard deviation values, standard deviation = 0.69.

Coefficient of variation values for days to maturity were relatively low in all

Table 5. Mean, range, and standard deviation for plant height, days to maturity, harvest index, kernel weight, pigment content, and grain yield in single, double and top cross populations grown on the East Farm Experimental Site in 1989-90.

		Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
Altar84 / H7092-52 SC1F2	Mean	86.50	74.17	0.26	11.44	6.68	29.16
	Range	55.00	23.00	0.42	5.67	6.08	86.33
	C.V.	12.35	8.73	13.76	4.66	21.57	21.32
	Std.dev.	0.87	0.42	6.07 E-3	0.12	0.52	2.16
WPB 881 / H7092-11 SC2F2	Mean	81.13	73.68	0.23	10.97	7.09	23.56
	Range	30.00	16.00	0.30	3.30	7.37	61.81
	C.V.	4.93	4.54	7.35	3.74	23.78	21.06
	Std.dev.	0.69	0.69	8.30 E-3	0.09	1.03	1.56

Table 5 (Continued)

		Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
Altar84 / H7092-52 // WD5	Mean	109.31	73.82	0.25	11.86	7.02	36.86
	Range	31.00	19.00	0.32	4.44	4.09	102.82
	C.V.	4.98	5.22	6.97	4.32	21.96	23.78
	Std.dev.	1.05	0.69	9.46 E-3	0.17	0.59	3.53
Altar84 / H7092-52 // WPB 881 / H7092-11	Mean	83.63	73.18	0.24	11.13	6.06	32.14
	Range	29.00	18.00	0.32	4.76	5.27	86.33
	C.V.	5.93	4.43	7.42	3.94	20.02	22.64
	Std.dev.	1.02	0.78	9.44 E-3	0.15	0.57	2.99

segregating populations, < 9%. The highest coefficient was noted in SC1F2, C.V. = 8.73 %, while the lowest coefficient was reported in SC2F2, C.V. = 4.54%.

Differences among segregating generations for harvest index were detectable only between SC1F2 and SC2F2 (Table 4). Multiple mean value analysis was concordant with the orthogonal contrasts analysis (Table 5), indeed, the only difference was noted between mean values of the SC1F2 and SC2F2, (0.26 versus 0.23). Top cross and double cross mean values were not different from neither SC1F2's nor SC2F2's values.

Phenotypic variability, observed from the ranges, was maximal for harvest index in SC1F1, range = 0.42, while SC2F2, top cross, and double cross populations gave similar variability for this trait. The highest standard deviation for harvest index was noted from the multiple cross populations, (9.4 E-3). The F2 progenies gave lower standard deviation values for harvest index, relative to top and double cross populations, with SC1F2 showing less variability around the mean value than SC2F2, (6.07 E-3 versus 8.30 E-3).

The coefficient of variation for harvest index was moderately high in SC1F2, C.V. = 13.76%, while in the remaining population it was relatively low, < 9%.

The top cross generation had the maximum average kernel weight, 11.86 g. SC1F2 and the double cross population were similar for this trait, while SC2F2 had the lowest average kernel weight, 10.97 g.

Even though SC1F2 and the double cross population had lower average kernel weight than the top cross population, their phenotypic variability values, noted from

the ranges, were higher, with SC1F2 being more variable than the double cross population, 5.67 versus 4.76 g. SC2F2 had the lowest variability for this trait, range = 3.30 g. The standard deviation values for kernel weight were the highest in the multiple cross populations, 0.17 and 0.15 in the double and top cross populations, respectively. The lowest standard deviation for this trait was noted from SC2F2, standard deviation = 0.09.

The coefficient of variation values for kernel weight decreased from SC1F2 to double cross to top cross to SC2F2. The coefficients were low in all populations.

Mean value grain yield was the highest in the top cross population, 36.86 g. The double cross population had the second highest mean for this trait, however was not different from F2 populations.

For grain yield the trend of variation of the phenotypic diversity from one population to the other was similar to that of the averages. Indeed, the top cross population had the highest phenotypic variability noted from the ranges, range = 102.82 g, the double cross population and SC1F2 showed similar phenotypic variability for this trait, while SC2F2 had the lowest phenotypic diversity. The distribution around the mean for grain yield was the most important in the top cross population, standard deviation = 3.53, and the smallest in SC2F2, standard deviation = 1.56. SC1F2 and the double cross population gave roughly similar standard deviation values, 2.16 and 2.99, respectively.

Coefficient of variation values decreased from top to double to single cross. In all these populations high coefficient of variation values were reported, >20%.

Average pigment content did not differ from one segregating population to the other, with the highest value being recorded in SC2F2, 7.09 ppm. Also, the highest phenotypic diversity for pigment content was noted in SC2F2. The lowest phenotypic variability for this trait was noted in the top cross population. SC1F2 was less variable than SC2F2 and more variable than the double cross. SC2F2 gave an exceptionally high standard deviation value for pigment content (1.03), whereas all the other populations showed approximately similar standard deviation values. Coefficient of variation values for pigment content were high in all populations, > 20%, and the highest value was obtained in SC2F2, while the lowest coefficient was recorded from the top cross population.

A comparison of the mean performance of the parental lines and the segregating generations for the six traits can be found in Table 6.

The top cross exceeded its parental lines, H7092-52 and Altar84, for the mean values for plant height, kernel weight, pigment content, and grain yield and was equal to the best parental line for harvest index. However its mean value for days to maturity was intermediate between the two parents' averages.

The double cross population performed better than the four parental lines for the mean plant height; also, it had an average grain yield higher but not significantly different than the better yielding parental line. The mean value of days to maturity was less than those of the Turkish introductions, H7092-52 and H7092-11, but higher than those of the two other parental lines, WPB 881 and Altar84, for the double cross. The mean values for harvest index noted from this population was higher than

Table 6. Comparison of the performance of four parental lines and segregating generations, grown on the East Farm Experimental Site in 1989-90, for plant height, days to maturity, harvest index, kernel weight, pigment content, and grain yield.

Crosses	Means					
	Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Pigment content (ppm)	Grain yield (g)
Altar84	78.75 ^{c*}	69.42 ^{ef}	0.25 ^g	10.95 ⁿ	6.88 ^p	17.17 ^y
WPB 881	71.87 ^d	69.65 ^{ef}	0.20 ^h	10.10 ⁿ	7.42 ^p	10.18 ^z
H7092-52	82.75 ^c	78.72 ^d	0.23 ^{gh}	11.03 ^{mn}	6.35 ^p	28.62 ^x
H7092-11	76.62 ^c	77.38 ^d	0.21 ^h	11.23 ^m	6.71 ^p	24.21 ^x
SC1F2	86.50 ^b	74.17 ^e	0.26 ^g	11.44 ^m	6.68 ^p	29.16 ^x
SC2F2	81.31 ^c	73.68 ^e	0.23 ^{gh}	10.97 ⁿ	7.09 ^p	23.56 ^{xy}
DC	83.63 ^b	73.18 ^e	0.24 ^g	11.13 ^{mn}	6.06 ^p	32.14 ^x
TC	109.31 ^a	73.82 ^e	0.25 ^g	11.86 ^k	7.02 ^p	36.86 ^w

* Means with the same letter are not significantly different based on least square difference (LSD) range test at five percent probability level.

SC1: Altar84 / H7092-52.

SC2: WPB 881 / H7092-11.

DC: Altar84 / H7092-52 // WPB 881 / H7092-11.

TC: Altar84 / H7092-52 // WD5.

those of the parental lines except Altar 84. Similarly, the mean kernel weight value in the double cross population exceeded those of all parents except H7092-11. The average pigment content noted in this population was less than the parental lines' mean values, although, it was not significantly different from any of these mean values.

SC1F2 exceeded its parental lines, H7092-52 and Altar84, for plant height and kernel weight. It had a higher mean value, but not different, than the best parent for harvest index and grain yield. Also, it was intermediate between the two parental lines for average days to maturity and pigment content, even though it was not statistically different from the best parent for the former trait.

SC2F2 was found intermediate between the two parental lines, WPB 881 and H7092-11, for all measured traits. In general it gave mean values intermediate between the two parental lines' averages.

Transgressive segregation from F2, double, and top cross populations

The magnitude of transgressive segregation obtained from each population for the different agronomic traits can be depicted from Graphs 1 to 5.

Transgressive segregant performing better than the best parental line were clearly distinguishable for plant height, mainly for the top cross population. The height classes noted from the top cross population were shifted towards the high values (Figure 1).

All segregating populations gave few transgressive segregant for days to

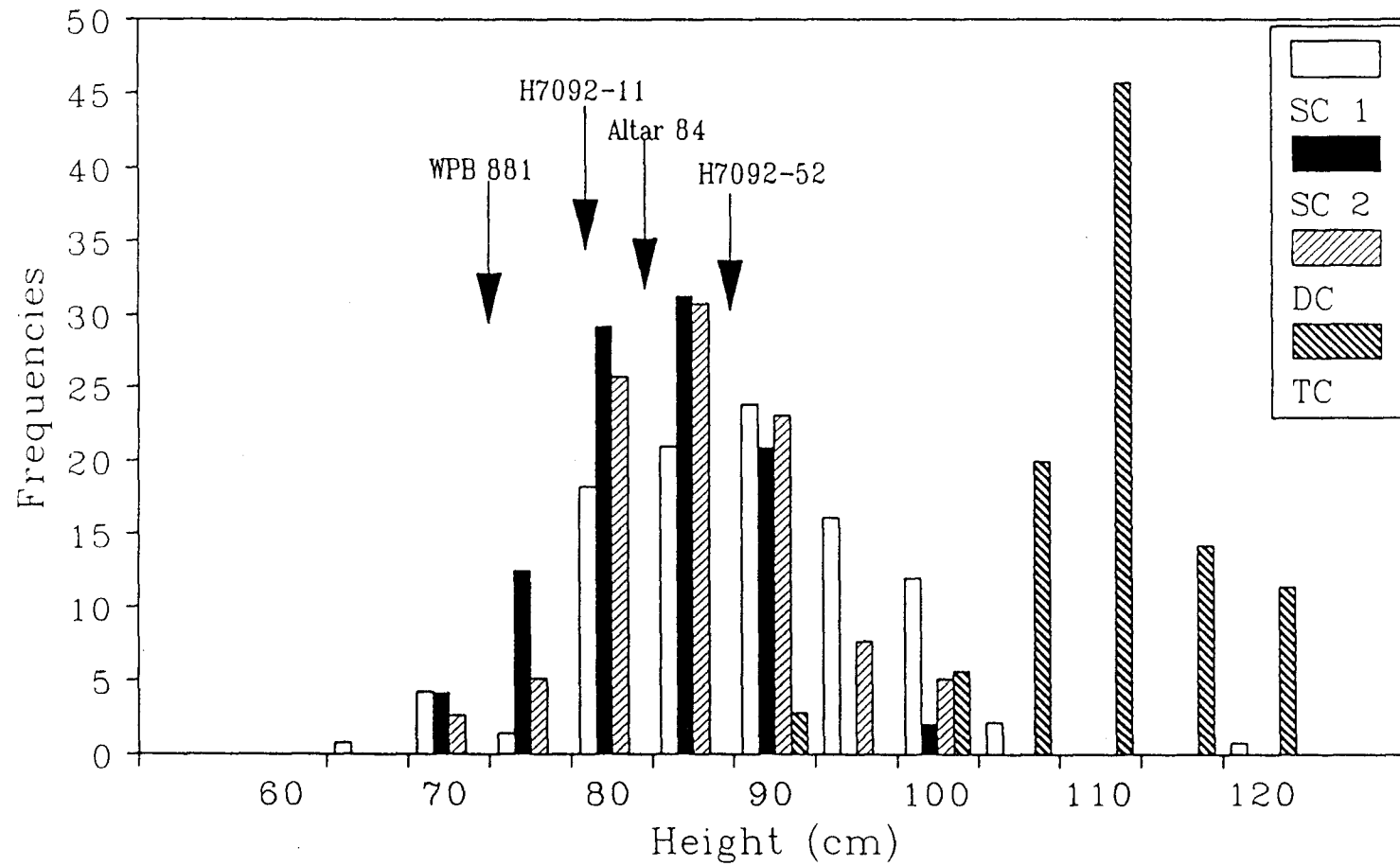


Fig 1. Frequency distribution of plant height in F2s, double, and top cross populations.

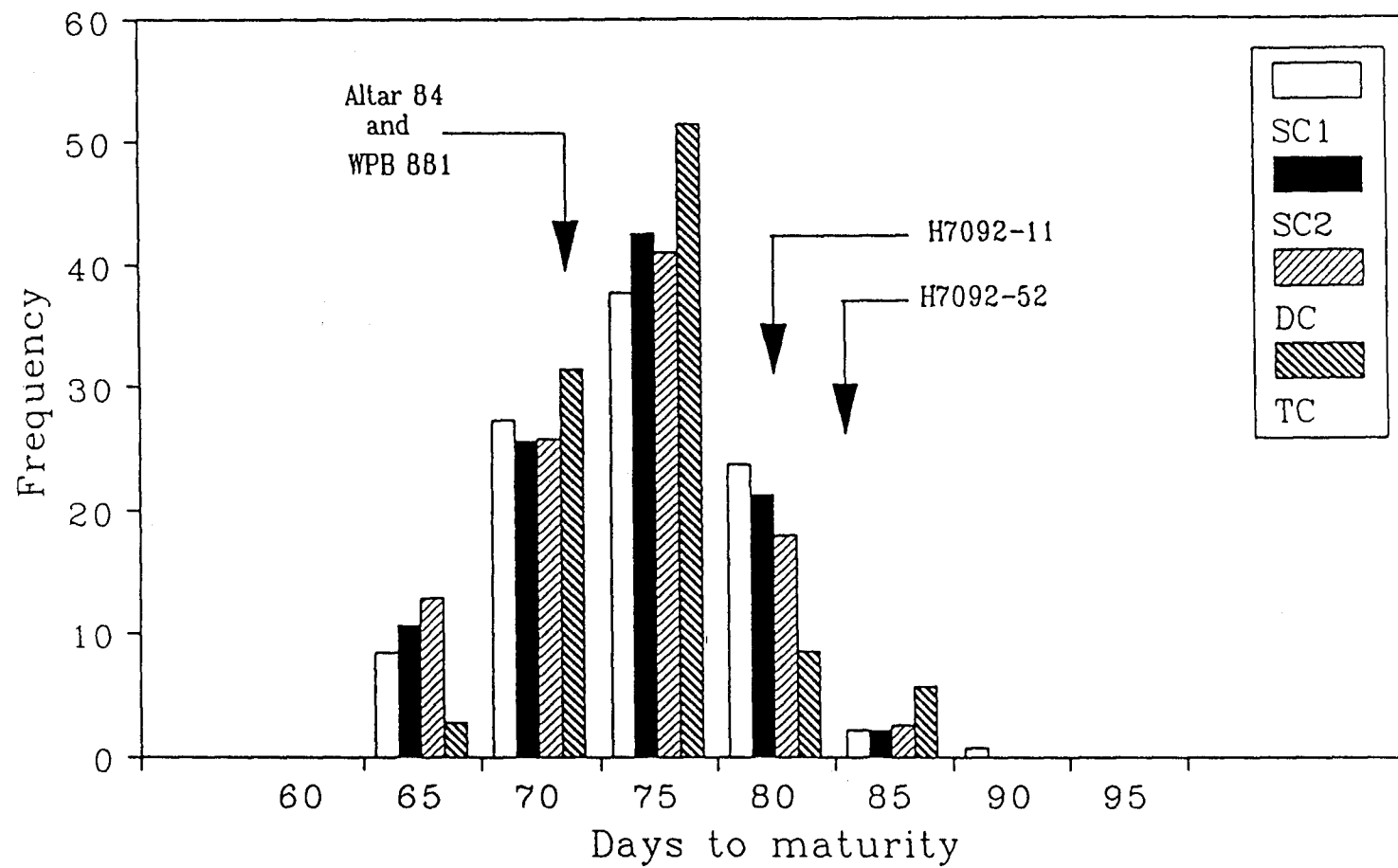


Fig 2. Frequency distribution of days to maturity in F2s, double, and top cross populations.

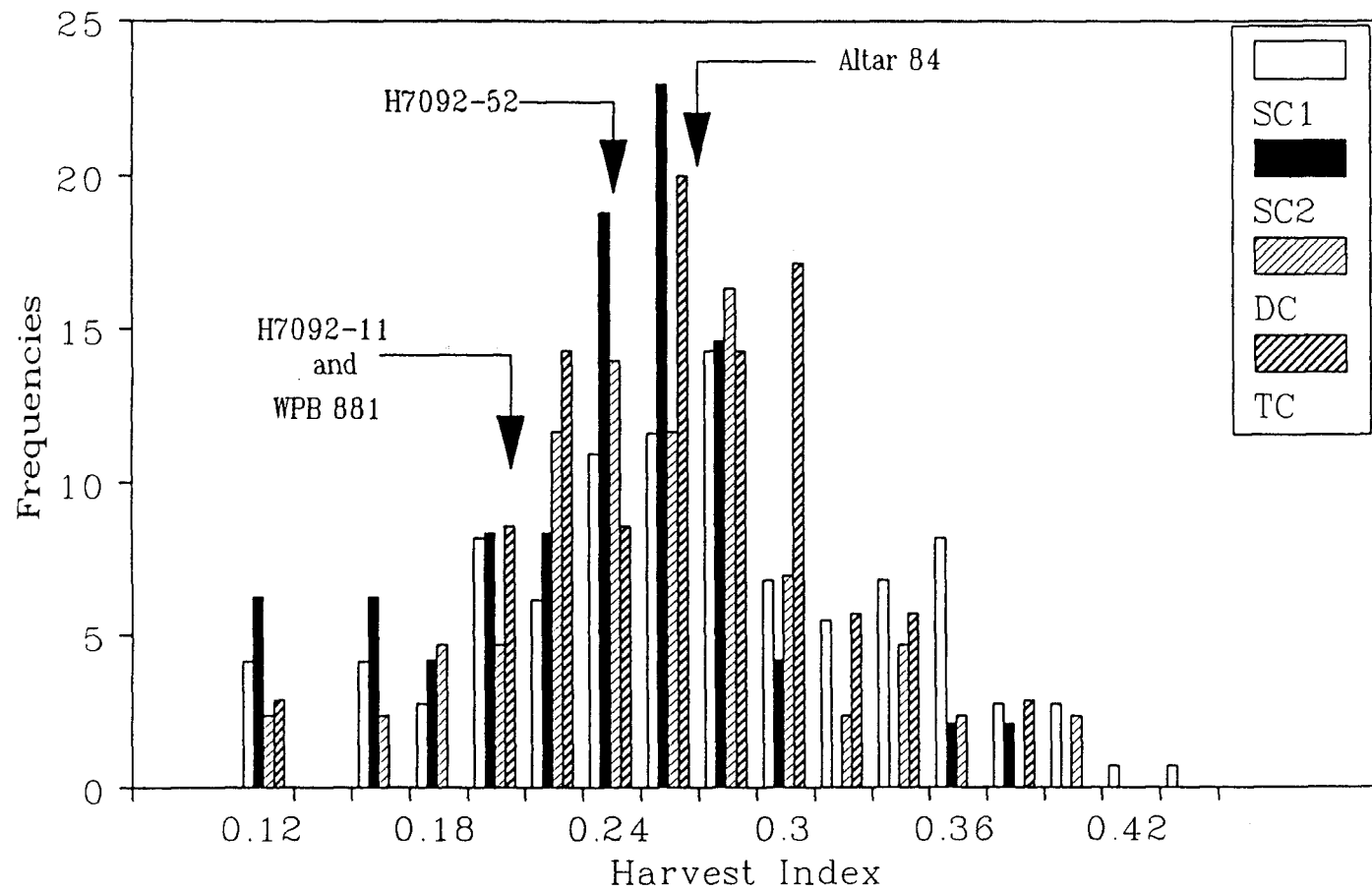


Fig 3. Frequency distribution of harvest index in F2s, double, and top cross populations.

maturity (Figure 2). For this trait, transgressive segregation was more apparent in SC2F2 than in SC1F2. This was expected as the parental lines of the first cross, WPB 881 and H7092-11, were characterized by lower days to maturity values than the parental lines of the second cross, Altar 84 and H7092-52. SC1F2 and the top cross population did not give rise to classes of days to maturity that surpassed drastically their common parental lines, Altar84 and H7092-52 (Figure 2).

Transgressive segregation for harvest index was more apparent in SC2F2 than in all other populations. This was expected as SC2F2 is generated from the two lowest performing parents for this trait. The highest classes of transgressive segregant for harvest index were obtained from SC1F2 (Figure 3). Top and double crosses did not differ for their ability to generate transgressive segregation.

Top cross population and SC1F2 gave the most conspicuous classes of transgressive segregation, and the highest classes for this trait were obtained from the top cross population (Figure 4). SC2F2 and the double cross population were similar in generating transgressive segregation for kernel weight. However, more classes in the low values of kernel weight were noted in the double cross population than in SC2F2 (Figure 4).

Distribution of the grain yield noted from the four populations were skewed towards values higher than those of the four parents (Figure 5). The most apparent of these classes were noted from the two multiple crosses. Among the four segregating populations, SC2F2 showed the lowest magnitude of transgressive segregation relative to grain yield.

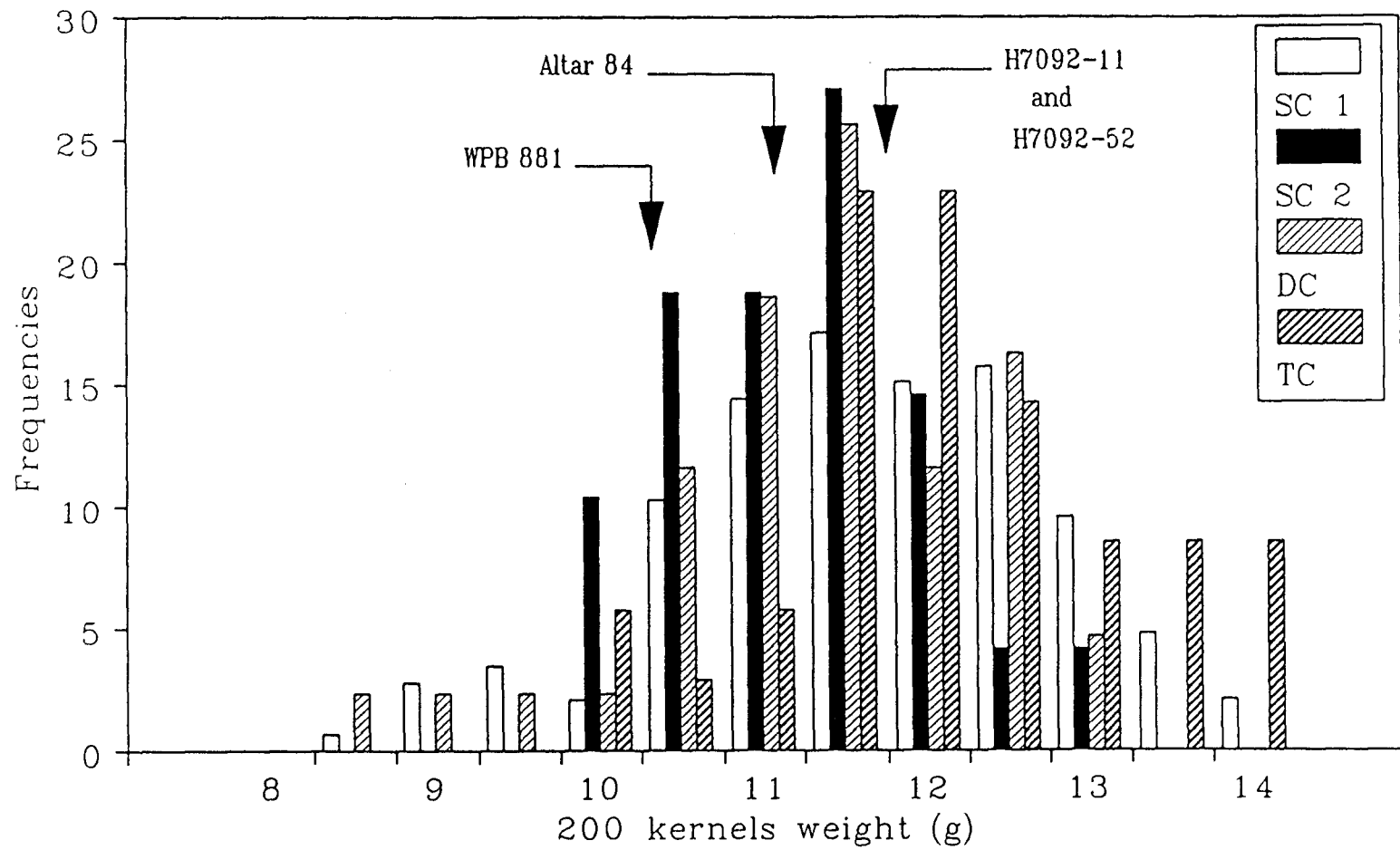


Fig 4. Frequency distribution of kernel weight in F2s, double, and top cross populations.

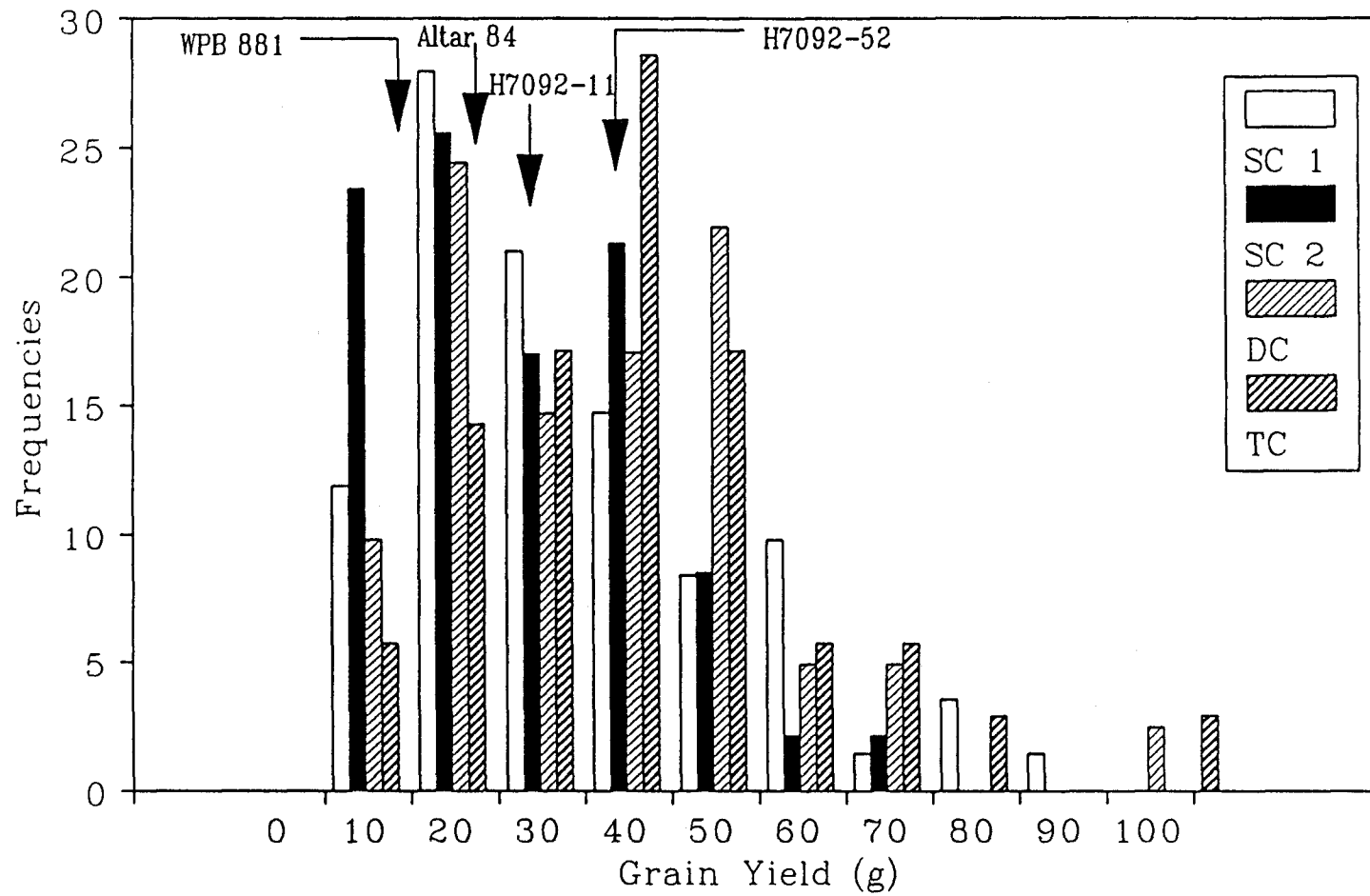


Fig 5. Frequency distribution of grain yield in F2s, double, and top cross populations.

Magnitude of genetic variances

Table 7 gives the genetic variances for the different cross combinations including the six traits. The SC1F2 (Altar84 / H7092-52) showed the greater variability when compared to SC2F2 (WPB 881 / H7092-11) for all traits except days to maturity and pigment content, where no detectable variability was observed in SC1F2. Genetic variability for pigment content was noted only from the single cross WPB 881 / H7092-11, however this cross had the lowest genetic variability for the other traits. The double cross (Altar84 / H7092-52 // WPB 881 / H7092-11) did not show detectable amounts of genetic variabilities for harvest index or pigment content. In general the genetic variability values noted for the double cross were lower relative to the variabilities observed from the SC1F2 (Altar84 / H7092-52). The double cross gave higher genetic variability than SC2F2 (WPB 881 / H7092-11) for days to maturity and kernel weight.

SC1F2 had the highest genetic variability for plant height, harvest index, and kernel weight. However, no detectable genetic variability was noted from this population. SC2F2 was the only population that gave detectable amount of genetic variability for pigment content. This population had the second highest genetic variability for plant height and harvest index, and the lowest value for kernel weight. Genetic variability noted from SC2F2 was lower than those of the top cross population and SC1F2, but higher than that of the double cross. The top cross population gave the lowest genetic variability values for plant height and days to maturity and like the double cross it did not show detectable genetic variability for neither harvest index nor

Table 7. Magnitude of genetic variances observed for plant height, days to maturity, harvest index, 200 kernels weight, grain yield and pigment content, generated from single, double, and top cross populations grown on the East Farm Experimental Site in 1989-90.

Crosses	Plant height (cm)	Days to maturity	Harvest index	Kernel weight (g)	Grain yield (g)	Pigment content (ppm)
Altar84/H7092-52 (SC1F2)	35.80	4.47	0.004	0.40	34.75	—
WPB 881/H7092-11 (SC2F2)	13.14	4.79	0.003	0.06	24.63	1.21
Altar84/H7092-52//WPB 881/H7092-11	12.00	6.41	— [*]	0.16	17.53	—
Altar84/H7092-52//WD5	9.73	1.10	—	0.16	56.80	—
Averages	17.67	4.19	0.002	0.20	29.04	0.31

* undetectable magnitude of genetic variability.

pigment content. Its genetic variability related to kernel weight was equal to the one observed from the double cross, while the highest genetic variability relative to grain yield was noted from this population.

The double cross population had the highest genetic variability for days to maturity, its genetic variability was higher than that of the top cross but lower than those of both F2 populations for plant height. It was intermediate between the two F2 progenies for genetic variability relative to kernel weight, and had the lowest genetic variability for grain yield.

Interrelationships among agronomic characters

The correlation coefficients between the different agronomic traits evaluated are noted in Table 8. The only consistent correlation across all populations was a negative association between plant height and harvest index.

Grain yield was not associated to any of the measured agronomic traits in SC1F2 and in addition to the association between plant height and harvest index kernel weight was positively correlated to plant height and harvest index. In SC2F2 grain yield was correlated to all traits and kernel weight was found to be positively associated with plant height. The top cross population showed the same correlations noted in SC1F2 except the association between kernel weight and plant height. The double cross population showed an association of the grain yield with plant height and harvest index; also, in addition to its negative association with plant height, harvest index was positively correlated with days to maturity.

Table 8. Correlation coefficients among plant height, days to maturity, harvest index, 200 kernels weight, and grain yield in two single crosses, a double cross, and a top cross grown on the East Farm Experimental Site in 1989-90.

		Plant height	Days to maturity	Harvest index	Kernel weight	Grain yield
Altar 84 / H7092-52 SC1F2	Plant height		0.046	-0.182*	0.300**	0.096
	Days to maturity			0.031	0.035	-0.086
	Harvest index				0.168*	-0.062
	Kernel weight					-0.092
	Grain yield					
WPB 881 / H7092-11 SC2F2	Plant height		-0.071	-0.173*	0.278**	0.336**
	Days to maturity			0.112	0.020	0.103*
	Harvest index				0.203	0.378**
	Kernel weight					-0.230**
	Grain yield					

Table 8 (continued)

		Plant height	Days to maturity	Harvest index	Kernel weight	Grain yield
Altar84 / H7092-52 // WPB 881 / H7092-11	Plant height		0.262	-0.360*	0.260	0.429**
	Days to maturity			0.388*	0.073	0.326
	Harvest index				0.273	0.490*
	Kernel weight					-0.220
	Grain yield					
Altar 84/H7092-52// WD5	Plant height		0.188	-0.403*	0.162	-0.015
	Days to maturity			0.285	-0.096	-0.043
	Harvest index				0.417*	0.194
	Kernel weight					-0.110
	Grain yield					

** , * Correlation coefficient significant at the 0.01 and 0.05 probability level, respectively.
Number of plants: N=70.

DISCUSSION

Increasing yield and other desired attributes in plant species can only be possible if there is available useable genetic diversity that allows for the manipulation and selection of the desired combinations of genes. Plant improvement program rely on information regarding the amount and nature of genetic variances, selection criteria, selection units, and selection methods (DePace et al., 1985). In self pollinated crops selection efficiency after crossing depends on the amount of additive genetic variance relative to the total phenotypic variance, the linkage relations of genes, and the shifts in gene frequency.

When the production of hybrids is sought, nearly homozygous inbred lines are used in different combinations in order to accomplish the maximum gain in grain yield. Thus, no genetic variability is sought in the F1 hybrids. However, in self pollinating plants, such as wheat, genetically homogeneous lines are usually used. In the past single crosses have often constituted the sole crossing approach in some breeding programs. However, to achieve more useable genetic variability different hybridization strategies are now being employed. Today, top and double crosses are more commonly encountered in the conventional breeding programs. Limited information is available regarding the beneficial use of these multiple crosses in contrast to single crosses in a wheat breeding program and the importance of what sequence the parental lines should be used.

Petpisit (1980) compared single, double, and top crosses for either hybrid

production or conventional breeding of common wheat. In the F1 generations he did not observe differences for mean grain yield between single and double crosses, whereas, F1s from three-way crosses yielded significantly less. No differences were detected among the three types of crosses for mean grain yield in the F2 generation. Other studies conducted in wheat showed that top crosses were advantageous over single crosses when the selection was oriented toward spike fertility and resistance to stem rust (*Puccinia graminis* f. sp. *tritici*) (Potocanac and Engelman, 1968).

In the present study the first segregating generation of three types of crosses: single, double, and a top cross, were compared for their mean performance, phenotypic variability as noted from the range and standard deviation values, and possible association between five agronomic traits. To evaluate the potential genetic variability resulting from different gene pools the parental lines selected were three winter selections, H7092-11, H7092-52, and WD5, and two spring cultivars, Altar84 and WPB 881. Among these parents WPB 881 performed poorly for all agronomic traits. This cultivar is known to have good milling quality attributes, which renders it interesting as a parent. The cultivar Altar84 excelled the Turkish introductions only in harvest index, however, the fall sowing date and the experimental sites selected reduced the potential yield of this spring type cultivar due to its limited winter hardiness. A spring planted yield trial also conducted at the Pendelton Site showed the superiority of Altar84 over three of the other parents for grain yield (appendix Table 2).

The F2 from SC1F2 (Altar 84 / H7092-52), showed a superiority over SC2F2

(WPB 881 / H7092-11) when comparisons are made of the mean values for plant height, harvest index, kernel weight, and grain yield.

Both the range and the standard deviation, used to compare the phenotypic variability noted from the two F₂ populations, suggested a higher phenotypic variability from SC1F₂ (Altar 84 / H7092-52) relative to SC2F₂ (WPB 881 / H7092-11). Similar results for plant height, kernel weight, grain yield, and pigment content were noted using the two measurements of variation. However, different results were obtained, using the two measurements, for days to maturity and harvest index. When phenotypic variability was contemplated using the range for days to maturity and harvest index, higher variabilities were noted in SC1F₂ (Altar 84 / H7092-52) relative to SC2F₂ (WPB 881 / H7092-11), while the contrary was suggested when using the standard deviation values. This inconsistency obtained for these traits emanate from the presence of extreme classes which bias the estimation of the variability. These extreme classes were the result of an apparent transgressive segregation in SC2F₂ (WPB 881 / H7092-11) and related specifically to the traits, days to maturity and harvest index. Transgressive segregation was found to be more conspicuous for days to maturity and harvest index in SC2F₂; whereas, more transgressive segregation was depicted in SC1F₂ than in SC2F₂ for plant height, kernel weight, and grain yield.

SC1F₂ (Altar 84 / H7092-52) exceeded SC2F₂ (WPB 881 / H7092-11) in genetic variability for plant height, kernel weight, and grain yield; while SC2F₂ resulted in more genetic variability for days to maturity and harvest index. SC2F₂ (WPB 881 / H7092-11) was the only population to generate detectable amount of

genetic variability for pigment content.

Overall superiority of F2 progeny of the single cross (Altar 84 / H7092-52) over the F2 progeny of the single cross (WPB 881 / H7092-11) is related to the superior performance of the two parental lines of the first cross over those of the second cross. The hybridization of the two genotypes representing the first cross resulted not only in higher mean value performance of its resulting F2 population, but also in more useable genetic variability. Several previous studies, with common and durum wheats have suggested the superiority of progenies resulting from the recombination and segregation of the genotypes of two high performing parental lines over those resulting from the hybridization of two low, or one low and one high parental lines (Bailey *et al.*, 1980; Bitzer *et al.*, 1982).

Use of multiple crosses, such as top and double crosses, to generate additional useable genetic variability was investigated in this study. Top cross progeny exceeded all segregating populations for mean values for plant height, kernel weight, and grain yield. Also, transgressive segregation was more apparent in this population for plant height, kernel weight, and grain yield. This superiority may be the result of either a better performance of the third parent, WD5, or extra epistatic interactions between the three genotypes involved in the cross.

Genetic variability of the top cross population was detected for all traits except harvest index and pigment content. Moreover, the top cross gave the highest genetic variability for grain yield. The top cross population also had the lowest values for genetic variability for the traits plant height and days to maturity.

Petpisit (1980) investigating the genetic variability for plant height and grain yield from F1 and F2 progenies resulting from single, double, and top crosses in common wheat, reported detectable variability only from the F1 progenies of the double crosses, and F2 populations of the three types of crosses.

According to the results of this study, the top cross appears to be the more appropriate in breeding for grain yield when using a cross between genetically distant parental lines, such as spring and winter types. For this purpose, using a third adapted cultivar similar in its genetic basis for desired quantitatively inherited traits as one of the parents of the single cross would help to create more useable genetic variability. In this investigation the hybridization of the cross Altar84 / H7092-52 to a third winter parent, WD5, helped enhance the useable genetic variability as evidenced by more desired transgressive segregation. Similar results were observed by Jensen (1988) in his cereal breeding program. He compared the use of different parental combinations when adapted and exotic entries were mated, and found that three way crosses were the most successful. He stated that "when adapted and exotic lines are mated a minimum requirement is that a third (adapted) parent is needed to channel the expressed variability into a high progeny potential range". Similar results were also obtained by soybean breeders when trying to improve yield by using exotic germplasm (Khalaf *et al.*, 1984). They found that a cross combination composed of 75% adapted and 25% exotic germplasm tended to generate greater genetic variability for grain yield than a cross between adapted and exotic germplasms. In common wheat, previous studies have shown the superiority of the

top cross over single cross in generating genetic variability for grain yield in the F₂ generations (Petpisit, 1980).

The mean values of the double cross population for the different traits did not surpass either of the top cross population nor the F₂ population from the first single cross (Altar84 / H7092-52). However, the double cross progeny did exceed the second F₂ population, generated from the single cross (WPB 881 / H7092-11), for plant height, kernel weight, and grain yield. When transgressive segregation was contemplated, the double cross excelled SC1F₂ (Altar 84 / H7092-52) for grain yield, and the SC2F₂ (WPB 881 / H7092-11) for all measured traits. The double cross also resulted in more apparent transgressive segregant than the top cross for days to maturity and harvest index.

The amount of genetic diversity associated with days to maturity was the highest in the segregating population from the double cross progeny. However, this population gave the lowest value for genetic diversity for grain yield. No genetic variation was detected in this population for harvest index and pigment content. In the present investigation the winter and spring parents represented two distant gene pools. When the F₁ progeny of a double cross is sought for the production of hybrids, the product of the four gene pools in the final single cross is advantageous over the hybridization of the two gene pools in the parental single crosses (Eckhardt and Bryan, 1940). Indeed, more variability would result from the former hybridization as more opportunities for new recombinations of the gene pools would be allowed by this procedure. Thus, a double cross obtained by first hybridizing the

two Turkish introductions (winter types) and Altar 84 with WPB 881 (spring types), is expected to result in less variability, in the F1 progeny, than the double cross combination used in the present study, where winter X spring F1 parents were employed.

In a previous study with common wheat Petpisit (1980) noted a decrease in the genetic variabilities for plant height in the F2 populations from double to single to top crosses. Similarly he reported the highest genetic variability for grain yield in F2 populations from the double crosses, followed by the top cross generations which exceeded the single crosses. In the F1 he noted detectable amount of genetic variability only from the F1 double cross progeny.

A negative relationship between plant height and harvest index was the only consistent association observed in all populations. Grain yield was not correlated to any of the other agronomic traits in SC1F2 nor in the top-cross population, while it was positively associated with plant height and harvest index in SC2F2 and double cross populations. Since the R' values of all the observed associations were small, they would not influence the direct or indirect selection for any of the traits measured in these populations.

In this study the F2 population generated from the single cross Altar84 / H7092-52 and the top cross gave higher potential segregates and more genotypic variability than either the single cross WPB 881 / H7092-1 or the double cross for grain yield. Thus, a conventional breeding program should rely equally on the single and top crosses based on the magnitude of genetic variability generated from for the

specific traits of interest. According to the results of this study and previous studies, the double cross might be suitable provided the right combination of the parental lines are used. The use of double cross combination appeared to be more appropriate, in this study, when improving traits such as earliness and kernel weight.

The results obtained point out the importance of the judiciously selection of the parental lines to combine in the different crosses in order to accomplish the maximum genetic diversity in the subsequent generations for the improvement of specific traits.

SUMMARY AND CONCLUSIONS

The objective of this study was to investigate the effectiveness of different crossing strategies to generate useable genetic variability. Three winter durum wheat selections: H7092-11, H7092-52, and WD5, and two spring durum type cultivars: Altar 84 and WPB 881, were used to generate two single crosses: Altar84 / H7092-52 and WPB 881 / H7092-11, a double cross: Altar84 / H7092-52 // WPB 881 / H7092-11, and a top cross: Altar84 / H7092-52 // WD5. F₂ populations were generated from the single crosses, while F₁s resulted from the double and top crosses. Segregating populations along with the parental lines, except WD5, were planted in randomized complete block design on the East Farm Crop Science Experimental Site. Plant height, days to maturity, harvest index, kernel weight, grain yield, and pigment content were recorded from individual plants from each population.

Analyses of variances were performed to determine possible differences among parents and segregating populations. Genetic variances including evidence of transgressive segregation were assessed for each population. Relationships between the different agronomic traits were also investigated.

The following conclusions were drawn:

1. Differences among parental lines and segregating populations were noted for mean values for plant height, harvest index, kernel weight, and grain yield. The one exception was for pigment content where no differences were detected.
2. Mean value performances for plant height, days to maturity, harvest index, kernel

weight, and grain yield of the F2 population generated from the single cross Altar84 / H7092-52 excelled those of the F2 population generated from the single cross WPB 881 / H7092-11.

3. Highest mean value for grain yield was obtained from the top cross F1 population followed by those of the double and single crosses, F1 and F2 respectively.
4. Mean value performances for the top cross population also exceeded the F2 progeny mean values of the parental single cross, for plant height, kernel weight, and grain yield.
5. Mean value performances of the double cross population did not excel either F2's mean values for any trait. In general, it was intermediate between the two F2 populations.
6. Transgressive segregation for grain yield was more apparent in the top cross progeny yield followed by the double cross population. The top cross also resulted in more transgressive segregant than double and single crosses for kernel weight; however, it had the lowest frequency for days to maturity and harvest index.
7. The two F2 populations were the most appropriate in generating transgressive segregant for days to maturity, harvest index, and pigment content. Also, the F2 population of the single cross Altar84 / H7092-52 excelled the top and double crosses in generating transgressive segregant for plant height.
8. When genetic variabilities from the different populations were contemplated, the top cross population gave the highest genetic diversity for grain yield followed by

the F2 generation of the single cross Altar84 / H7092-52. The lowest genetic variability for this trait was noted from the double cross.

9. The F2 progenies of the single cross Altar84 / H7092-52 showed the highest genetic variabilities for plant height and kernel weight. F2 population of the single cross WPB 881 / H7092-11 was the only population among all segregating generations to show detectable genetic diversity for pigment content.
10. The only consistent relationship between the different agronomic traits was a negative association between the plant height and harvest index across the different populations.

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APPENDICES

Appendix Table 1. Description of the parental lines used in the experiment conducted on the East Farm Experimental Site during 1989-90.

Cultivar	Origin	Type	Description
WPB 881	Montana U.S.A	Spring	White awned smidwarf cultivar with small spike size. Yielded less than 3 tons per hectare in the Pendelton area. High protein content and gluten strength.
Altar 84	Mexico (CIMMYT)	Spring	Black awned semidwarf cultivar with large spike. Yielded more than four tons per hectare in the Pendelton area. Moderately high protein content, and high gluten strength.
H7092-11	Turkey	Winter	Black awned tall introduction with small spike. Yielded more than 3.5 tons per hectare in the Pendelton area. Low protein content and gluten strength.
H7092-52	Turkey	Winter	Black awned tall introduction with large spike. Yielded more than 3.5 tons per hectare in the Pendelton area. Low protein content and gluten strength.

Appendix Table 2. Plant height and yield of the four parental lines grown in a yield trial at the Pendelton experimental site in 1989-90 growth season.

Cultivar	Height (cm)	Yield (g m ⁻²)
WPB 881	85.00	225.51
Altar 84	86.00	361.96
H7092-52	96.20	341.41
H7092-11	92.00	339.90

Appendix Table 3. Weather summary of the 1990 crop year in East Farm.

Month	Maximum temperature (°C)	Minimum Temperature (°C)	Monthly mean Temperature (°C)	Monthly precipitations (mm)
September	34	2	18	15
October	25	-5	11	66
November	18	-3	9	98
December	15	-2	6	77
January	16	3	6	237
February	18	-8	5	145
March	21	-2	9	55
April	26	0	12	56
May	29	0	12	36
June	35	7	16	38
July	37	7	20	11
August	38	6	20	43