

AN ABSTRACT OF THE THESIS OF

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Title : INTERRELATION OF THE COMPONENTS OF GRAIN YIELD IN A CROSS
BETWEEN DWARF AND SEMIDWARF WHEAT (Triticum aestivum L.) CULTIVARS

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Parents and progeny populations from a cross of 'Stephens' x 'Tibet dwarf' were grown in a spaced-planted experiment to obtain information concerning the nature of inheritance and possible associations between grain yield and the components of yield. Agronomic traits measured on an individual plant basis were: heading date, days to maturity, grain filling period, plant height, biological yield, number of spikes per plant, total length of spikes, spikelets per spike, kernels per spikelet, total kernel number, grain yield, kernel weight, harvest index, and chaff percentage.

The nature of gene action was estimated for each trait by comparing broad and narrow sense heritability estimates. Possible associations among traits were determined by phenotypic and genotypic correlations as well as by path coefficient analysis. This latter analysis was based on the genotypic correlations of total grain yield with five other traits.

Narrow sense heritability estimates were high for kernel

weight, spikelets per spike, heading date, kernels per spikelet, chaff percentage, and total kernel number. Intermediate estimates were found for plant grain yield, spikes per plant, plant height, harvest index, days to maturity and total length of spikes. A low estimate was realized for biological yield.

Narrow sense heritability values were higher than broad sense heritability for spikelets per spike, kernel weight, chaff percentage and heading date. These inflated estimates are attributed to sampling errors and/or uneven environmental influence on the various generations.

Path coefficient analyses suggested that among the yield components, the number of kernels per spikelet was most closely associated with grain yield, followed by the number of spikelets per plant, the number of spikelets per spike and kernel weight. Low direct associations with grain yield were found for both harvest index and plant height. A moderately high association between harvest index and grain yield was the result of an indirect association via spikelets per spike.

As suggested by both narrow sense heritability estimates and path coefficient analysis, selection for number of kernels per spikelet among the F_2 populations of the cross of Stephens and Tibet dwarf would result in increased grain yield in succeeding generations.

Path coefficient analysis indicated that the direct relation between grain yield and plant height was low, suggesting that short, high yielding plants could be selected within segregating populations resulting from this cross.

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YIELD IN A CROSS BETWEEN DWARF AND SEMIDWARF
WHEAT (Triticum aestivum L.) CULTIVARS

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INTERRELATION OF THE COMPONENTS OF GRAIN YIELD IN A CROSS BETWEEN DWARF AND SEMIDWARF WHEAT (Triticum aestivum L.) CULTIVARS.

INTRODUCTION

Increases in world wheat production in the last three decades have been accomplished through improved agronomic practices and the development of new cultivars. Statistics accumulated over the past 20 years reflect that global wheat production has risen at an annual rate of 3.4% (Byerlee and Hesse, 1983).

In part, the higher yielding potential of new wheat cultivars has been achieved through the manipulation of genes that reduce plant height. Dwarfing genes, coupled with stiffer straw, constitute the essence of success of the so called semidwarf cultivars. These wheats by in part reducing lodging have allowed for greater use efficiency of both water and fertilizers.

Concerns regarding yield instability have surfaced suggesting that in developed and developing nations the release of semidwarf cultivars based on 'Norin 10' dwarfing sources, greater fluctuations in annual wheat production due to weather pattern have resulted (Gale and Youssefian, 1985). Thus, wheat breeders are continually seeking new sources of dwarfing genes which will provide a greater grain yield stability.

The identification and assessment of different dwarfing sources is essential in three ways: a) to support efforts aimed at increasing grain yield potential by modifying plant architecture, b) to avoid the risk of disease epidemics posed by today's genetically nearly uniform cultivars, and c) to clarify the relation between

some dwarfing genes and yield instability.

Due to low heritability and the large environmental influence, estimates associated with grain yield increasing productivity on a per hectare basis are becoming more difficult to obtain. To understand and improve this trait, one approach has been to consider yield as the product of its components. For example, grain yield per plant can be considered as the product of the two primary components number of kernels per plant and average weight per kernel.

Each yield component is not genetically or environmentally determined and modified in the same way. Thus, the contribution of each yield constituent to total yield is different. An understanding of genotypic and phenotypic associations involved in the expression of the different components associated with grain yield is critical if selection is to be effective.

Success in increasing yields depends on the breeder's ability to select desirable plants among segregating populations. This task is facilitated by a knowledge of both the relative significance of the different components determining yield, and of the proportion of the observed total variation which is due to genetic factors. Consequently, the use of components in parent selection and in early generation progeny evaluation may prove to be a more efficient method of achieving larger grain yields than breeding for increased grain yield per se.

The major objective of the present study was to evaluate the components of grain yield in a cross between a newly introduced dwarfing source and a high yielding cultivar now in commercial

production. Of specific interest were the relationships between kernel weight and kernel number on a per spike, per spikelet, and per plant basis. Also of interest were the associations between all grain yield components and both plant height and harvest index.

LITERATURE REVIEW

Importance of Dwarf or Semidwarf Cultivars

One of the most complete reviews on dwarfing genes in wheat (Triticum aestivum L.) has been published by Gale and Youseffian (1985). They noted that Japanese breeders in the 19th century were probably the first to consciously employ short statured genetic sources. Today most of the short cultivars have one or more of the genes from two Japanese genotypes. These are the cultivars 'Akakomugi' and 'Daruma'. The later dwarfing sources (Rht1, Rht2) are found in the more commonly known cultivar Norin 10.

The need for short strawed cultivars which do not lodge under increased nitrogen fertilization and high soil moisture was emphasized more than three decades ago (Vogel, et al., 1956; Borlaug, 1957).

Short-statured wheat cultivars, introduced into the United States from Japan and Korea in 1947, have been used extensively by United States wheat breeders. Highly productive semi-dwarf cultivars have been selected from crosses of these wheats with locally adapted cultivars (Johnson, et al., 1966b; Vogel, et al., 1963).

The continued success of semidwarf cultivars has encouraged breeders worldwide to evaluate and incorporate dwarfing genes into their breeding programs. Extensive numbers of short statured wheat cultivars have been released (Maya, 1975; Gale and Flintham, 1984; Gale, et al. 1982).

There are major gaps in our knowledge of ideal dwarfing genes

to provide lodging resistance and maximum yield. Gale and Youseffian (1985) pointed out that most dwarfing genes appear to have deleterious effects on yield, however the genes contributed by Daruma and Akakomugi are apparently exceptions but reasons for this are not clear.

Effect of Dwarfing Genes on Yield

There are several reports discussing the effect of dwarfism on grain yield and grain yield components in wheat. Fisher, et al., (1981) observed that semidwarf wheats have a higher yield capacity which they attributed to greater CO₂ leaf permeability.

McClung, et al., (1986) employing the gibberellic acid test, screened F₂ wheat plants from crosses of four sources of the Rht1 allele and one normal (rht1) height cultivar. The F₂ seedlings that did not elongate in the presence of gibberellic acid were classified as homozygous semidwarfs. Seedlings where extensive elongation occurred were classed as being homozygous tall. While those having an intermediate response were considered heterozygous and discarded. Seed was increased for the F₃ families of the two remaining height groups and checked for segregation. The F₄ progenies and the five parents were evaluated using a split-split plot arrangement. This procedure permitted the observation of the effect of semidwarfism (Rht1 allele) on grain yield and the components of grain yield. Results indicated that the greater productivity of the semidwarfs was the result of greater production of kernels per spike.

Using the same principle, Brandle and Knott (1986) evaluated 64 F₂-derived F₄ lines produced from a cross between a semidwarf wheat cultivar 'CSP-44' ('Condor' sib, Rth1) and the tall cultivar 'Glenea' (rth1). 32 homozygous tall and 32 homozygous short lines were tested under two environmental regimes. Results from this study indicated that in most instances the semidwarf lines had more spikes per meter of row, more kernels per spike, and lower kernel weight. The percent change in the number of kernels per spike for the semidwarfs varied more in different environments than the other two components when compared to the tall cultivars. As a result, the semidwarf lines outyielded the tall lines under high rainfall or irrigated conditions, but yielded less in dry conditions.

Four short statured winter wheat cultivars differing in plant height were compared by Johnson, et al., (1966b) in replicated nursery plots over a four year period. Their results suggested that the two shorter cultivars evaluated produced higher yields by having a greater number of kernels per spike.

Johnson, et al., (1966a) reported on the inheritance mechanisms of several plant and seed traits in progeny involving a cross of two morphologically different winter wheat cultivars. Short plant height was associated with lower kernel weight, shorter spike length, shorter time to maturity, lower number of spikes per plant, lower number of rachis internodes and lower grain yield.

As observed by Gale and Youssefian (1985), many investigations of the relative grain yield of tall and dwarf wheats have involved comparisons of more recently developed dwarf cultivars with older

tall cultivars. In such comparisons, differences between Rht (dwarfing) and rht alleles could be confounded by other differences in genetic backgrounds.

A more meaningful way to relate height and the components of grain yield is with isogenic lines. Research reported between 1973 and 1984 on the pleiotropic effects of dwarfing genes on height, grain yield, components of grain yield and grain protein, using such methods, was summarized by Gale and Youssefian (1985).

Allan (1986) made multiple comparisons for grain yield, plant height, test weight, kernel weight, and tiller number among five reduced height, near-isogenic lines of wheat and their recurrent parent 'Burt'. Information was gathered specifically about the effect of the height-reducing genes Rht1, Rht2 and Rht3 had on the components of grain yield when placed under a common genetic background. The allele Rht3 (contributed by the cultivar 'Tom Thumb') caused negative effects on grain yield, test weight, kernel weight and tiller number. A single dose of Rht1 or Rht2 caused neutral or positive effects on grain yield and tiller number when compared with the standard height lines.

Components of Yield and Selection

Yield of cereals was described by Grafius (1956, 1964) as a product of components. As a way to visualize the problem he represented this concept in a geometric form. In this model, total yield is a parallelepiped (shape similar to that of a cube) with

edges X (number of spikes per unit area), Y (the number of kernels per spike), and Z (the average kernel weight). Grain yield (W), the volume of this rectangular parallelepiped is the product of the three components (X, Y, Z).

The geometrical model of yield implies that an increase in the volume (selection for higher grain yield) is obtained by increases along any axis. The greatest change in volume (greatest improvement in grain yield) is achieved by changes in the shortest edge. This concept is important because according to this analogy, yield can be increased more efficiently with a slight change in one of the critical components. Garfius also estimated that there might be disparities in the difficulty to modify the different edges due to an inherent resistance to change the characteristics of each edge. Also, adjusting one edge can be counterbalanced in the plant by changes in another edge so that in the model the volume of the cube may not change ("homeostasis for yield" according to the same author).

Many researchers have studied the relations between total grain yield and grain yield components in wheat. A soft white wheat, 'Lemhi', and a hard red wheat, 'Tatcher', were crossed by McNeal (1960). The two parents differed in the number of kernels per spike, kernel weight, spikelets per spike, kernels per spikelets, and plant height, but not in spikes per plant. The F_2 generation was evaluated for the components of yield and to obtain the F_3 generation. Narrow sense heritability estimates for grain yield and the various grain yield components studied, as expressed by the regression of F_3 on

F_2 , were low. However these regression coefficients did not constitute accurate estimates of heritabilities because they could also reflect differences in environment as the F_2 and F_3 were planted in different years.

Johnson, et al., (1966a) studied the inheritance of grain yield and other agronomic traits in a cross between two winter wheat lines. Parental lines, 'Seu Seun 27' and 'BlueJacket' had contrasting characteristics including plant height, spike length, yield of grain, maturity, and seed weight. The two cultivars, F_1 , F_2 , and backcrosses were grown in a randomized complete block field experiment with six replications. Plots were planted in rows 30 centimeters apart with five centimeters between plants. Narrow sense heritability for plant height, spike length, maturity, and kernel weight were sufficiently high to indicate that selection in the F_2 for these traits could be effective. In contrast, estimates of narrow sense heritability regarding the number of spikes per plant and grain yield were low indicating that direct selection for these traits would be ineffective.

In a similar study Ketata, et al., (1976) investigated the inheritance of grain yield and seven other agronomic traits. This study involved the parental lines, F_1 , F_2 , F_3 and Backcrosses of a cross of two winter wheat cultivars: 'Centurk' and 'Bezostaia 1'. The experimental design was a randomized complete block with six replications. Plots were spaced-planted. The two parents had contrasting traits, particularly in terms of tiller number and kernel weight. Analysis of means and variances did not provide

information as to whether segregates combining the higher tiller number of Centurk and large kernels of Bezostaia 1 could be obtained. The study did show however, given the estimates of heritabilities and genetic advances, that selection among F_2 plants of this cross should be highly effective for kernel weight. Selection for high tiller number probably would not be as successful despite the high estimate for genetic advance.

Maya (1975) used a five parent diallel cross of spring wheat to evaluate three genetically different dwarf cultivars as potential source of short stature in wheat improvement. The experimental material consisted of parental lines, F_1 , F_2 , and both backcrosses. Plots were planted in rows thirty centimeters apart with thirty centimeters between plants. The genetic correlations for individual crosses indicated that only a few of the traits studied were associated, and that the degree of association depended on the specific cross. However consistent high positive genetic correlations were found between grain yield and tiller number, and also for grain yield and kernels per spikelet. With the same consistency, high negative genetic correlations were found between kernel weight with days to maturity, and between plant height with harvest index.

Interrelations between components of yield have also been studied in durum wheats. Lee and Kaltsikes (1972) used a diallel cross and regression analysis to study four correlated sequential grain yield components of six parental durum wheat cultivars and the F_2 generation. They indicated that the phenotypic expression for

spikes per plant and grains per spikelet were independent of other traits. Spikelets per spike and 100-kernel weight were influenced by traits developed previously along the developmental sequence.

Many of the studies involving associations between grain yield components have reported negative correlations among these components. This appears to be a wide spread phenomenon among the major crop plants. Adams (1967), noted that such negative correlations are particularly prevalent under various kinds of environmental stress, but are not very common in spaced plant nurseries and in other non-competitive or non-stress situations. Based on the assumption that a genotypic correlation maybe derived from genetic linkage, pleiotropy, or from developmentally induced relationships between components, Adams further suggested that components of yield are essentially genetically independent, meaning that genes specifically regulating the formation of one component do not regulate the formation of the other components. He inferred that the negative correlations among the components of grain yield are developmental rather than genetic in origin. He postulated that the constituents of yield are caused by genetically independent components, developing in a sequential pattern, and are free to vary in response to limited input of metabolites. The experimental results of McNeal, et al., (1978), working with wheat, were consistent with this view.

Heritability estimates of the components of grain yield are an indication of the response to change through selection. High narrow sense heritability estimates in the F_2 of a self pollinated crop

species indicates effective selection on an individual plant basis is possible. Several workers have used different techniques for estimating the degree of heritability. Warner (1952) reviewed the techniques used for estimating the degree of heritability in crop plants. He described some of the drawbacks of those methods and proposed an alternative method to determine heritability from the variances of the backcrosses and the F_2 .

Many researchers (Kronstad and Foote, 1964; Fonseca and Patterson, 1968), have found higher narrow sense heritability estimates for the components of yield than for grain yield per se in wheat.

In winter wheat crosses, a large range of narrow sense heritability estimates for grain yield has been reported. Low values (0.26) were reported by Kronstad and Foote (1964); both high and low values (0.16 0.19) were reported by Ketata, et al., (1976).

In a study that included a 10 parent diallel cross, Kronstad (1963) concluded that a large percentage of the total genetic variation associated with the components of grain yield, kernel weight, kernels per spikelet, spikelets per spike and spikes per plant was primarily the result of additive type gene action.

Path Coefficient Analysis

The knowledge of phenotypic and genotypic correlations that exist between traits in a segregating population of wheat is important if progress is to be made in selecting superior genotypes.

The study of association between traits using correlation coefficients helps as a guideline for selection of desirable plant types. As previously noted, some traits such as grain yield are complex in their inheritance and final expression is influenced by other factors. When several variables are contemplated at one time, the relationship becomes more intricate. Different kind of analyses are needed to understand direct and indirect effects of variables that influence such complex associations.

Path coefficient analysis was originally introduced by Wright (1921, 1923, 1934). It is primarily a method of dividing a complex trait into component elements and interpreting linear relationships among a set of variables. It permits a more critical examination of the relative importance of each of the traits within the system. The concept of path coefficients, its statistical basis and its application in genetics, was reviewed by Li (1956). A path coefficient is a standardized partial-regression coefficient, and as such, evaluates the direct influence of one variable upon another allowing the separation of the correlation coefficient into components of direct and indirect effects.

Path coefficient analysis has been used by many researchers examining grain yield in many crops including wheat. Dewey and Lu (1959), investigated the interrelations of the components of yield in wheatgrass seed production. They carried out this analysis at the phenotypic level to arrive at the conclusion that under their conditions fertility and plant size were the most important components of seed yield.

Using a diallel cross involving 10 parents, Kronstad (1963) studied combining ability and path coefficient analysis to review the association of yield components in wheat. The variables kernel weight, number of kernels per spikelet, number of spikelets per spike, number of spikes per plant and plant height, were evaluated in terms of their association with grain yield. Data obtained from the path coefficient analysis indicated that the direct influence of the number of kernels per spikelet had the greatest impact on grain yield, followed by the direct effects of kernel weight and number of spikelets per spike. Both the number of spikes per plant and plant height had small negative direct effects on grain yield.

Fonseca and Patterson (1968), examined grain yield component interrelationships and narrow sense heritability estimates in a seven parent diallel cross, measuring the number of spikes per plot, kernels per spike, kernel weight, earliness and plant height. Using path coefficient analysis they concluded that each of the yield components had large direct effects on grain yield. However, there were also important indirect effects resulting from negative correlations among yield components.

Das (1972), using six Indian wheat cultivars, utilized path coefficient analysis at both phenotypic and genotypic levels concluded that, under his experimental conditions, grain weight and number of spikes per plant were the two most important component traits of grain yield.

In summary, the importance of using certain dwarfing genes has resulted in higher, but not more stable grain yields. The exact

nature how such dwarfing sources influence grain yield, apart from greater lodging resistance, remains unclear. Today, breeders are continuing to select new sources of short stature. To better understand the importance of reduced height on grain yield several investigators have used the component approach to examine grain yield. Depending on both the genetic material used and on the environmental stresses involved, the potential of negative direct or indirect responses exists. These associations may influence progress in selecting potential parents or progenies in subsequent generations for increasing grain yield.

MATERIALS AND METHODS

Experimental Procedures

Two winter wheat cultivars were used as parental material for this study. 'Stephens', a high yielding cultivar was developed by Oregon State Wheat Breeding Program. It is a soft winter wheat with a high yield potential, and is commercially adapted to the growing conditions observed in the Pacific Northwest. This cultivar has a semi-dwarf growth type with relatively moderate tillering capacity with large kernels and fertile spikes. Stephens was the result of a cross between 'Nord Desprez' and 'Pullman Selection 101'. This cultivar contains the Rht1 dwarfing genes from Norin 10 and 'Brevor 14'. The second parent, 'Tibet dwarf', presents a contrasting plant type. It is characterized by having a high tillering capacity, extremely short stature and relatively small kernels. When grown under Oregon conditions the yield of Tibet dwarf is low. This cultivar was part of collections from the Peoples Republic of China introduced into the United States by the Oregon State Wheat Breeding Program in 1981.

Crosses between the two cultivars were made in 1984. F_1 seed were produced in the greenhouse by hand emasculation and pollination. Stephens was used as the female parent. The F_1 was backcrossed in 1984 to each parent to produce backcross generations $B1 = (P_1 \times F_1)$ and $B2 = (P_2 \times F_1)$. A portion of the F_1 seed was also sown, to provide the F_2 generation. Later, part of the F_2 was also planted to obtain the F_3 seed. The 10 F_3 families from individual F_2 plants

were selected to obtain a range of height that would include short, intermediate and tall plants. The 10 F₃ families selected came from plants ranging from 29 cm. to 91 cm. in height.

A field study was conducted during the 1985-1986 growing season at Hyslop Agronomy farm. This experimental site is located 11 km. northeast of Corvallis, Oregon. The soils type at this location is a fine, silty mixed mesic Aquultic Argixeroll.

In the fall, prior to planting, 40 kg./ha. of Nitrogen and six kg./ha. of sulfur were applied; additionally, 90 kg./ha. of Nitrogen were applied in the spring. The two parents, F₁, F₂, F₃ and two backcross were planted on November 20, 1985.

The experimental design was a randomized complete block with four replications. Plots consisted of single rows of 10 plants spaced 25 cm. apart between rows and 25 cm. within rows. For the non segregating generations (Tibet dwarf, Stephens and the F₁), one row per plot was used. Three rows for each Backcross and five rows for the F₂ and a total of 10 rows for the F₃ (10 families coming from individual F₂ plants) were employed for the segregating population.

Barley was planted around the replications to minimize possible border effects and was removed prior to harvest. The experiment was sprayed twice as a preventive measure against Septoria Leaf Blotch and other fungal diseases using dichlorophenyl triazole at a rate of 0.7 kilograms of active ingredient per hectare. Examination of individual plants did indicate that fungal and viral organisms were present. Those plants that showed severe disease symptoms were omitted from this study. Plants with less severe symptoms but

showing less than five grams of grain yield were also omitted and not included in this study.

To facilitate statistical analysis, the final number of plants for each generation was standardized at 36, 28, 32, 76, 268, 64 and 68 plants of Stephens, Tibet dwarf, F₁, F₂, F₃, BC₁, BC₂ respectively, using a random procedure.

All measurements were made on individual plant basis:

Heading Date: number of days from 1st of January to the date when more than half of the spikes had emerged from the flag leaf sheath.

Days to maturity: number of days from the first of January to the date when more than half of the spikes were mature. Maturity was determined based on the change in color of the peduncle.

Grain filling period: number of days between heading date and maturity.

Plant height: distance (cm.) between the base of the culm to the base of the spike of the tallest tiller.

Biological yield: dry weight (gm.) of the aerial portion of the plant.

Number of spikes per plant: number of spikes at harvest (fertile tillers).

Total length of spikes: the spikes were arranged according to their size and placed in one centimeter classes. The measurement was done from the base to the tip of the spike (awns excluded). Each spike was recorded and placed into the closest length class. The total length was computed as the summation of the products of the length of each class and the number of spikes per class.

Mean number of spikelets per spike: summation of the number of spikelets of one spike per each of the classes described above times the number of spikes per class, divided by the total number of spikes.

Kernels per spikelet: total number of kernels divided by the total number of spikelets.

Total kernel number: total number of kernels per plant .

Total grain yield per plant: weight (gm.) of all kernels per plant.

Kernel weight: total kernel weight (gm.) divided by the total kernel number.

Harvest index: grain yield divided by above ground biological yield times 100.

Chaff percentage: percentage weight of chaff with respect to the total weight of the heads, calculated as weight of heads minus weight of clean kernels divided by the weight of heads, all multiplied by 100.

Analytical Procedures

Analysis of Variance

An analysis of variance, including all generations means, was conducted for each trait to determine whether differences existed among generations. Mean values were analyzed using the Waller-Duncan Bayes K-ratio T test (WDLSD) to observe which generation were different. Separation of means using the WDLSD test requires the use of a 'k' ratio (or error weight ratio), comparable to a significance

level. A ratio of 100, equivalent to an alpha level of 0.05, was used in these analyses. Generation means and variances were used to calculate mid-parent deviations, heritability in the narrow sense (H_n), and expected genetic advance or gain from selection (G.S.) for each trait.

Estimation of Heritability

Generation variances for each of the traits were used to determine broad sense heritability (H_b) and a narrow sense heritability (H_n).

The formula used to estimate genetic variability in the broad sense (Allard, 1960) was:

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

Narrow sense heritabilities were estimated using the formula proposed by Warner in 1952:

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

where: VF_1 , VF_2 , refer to the variance of the first and second filial generations. VBC_1 and VBC_2 allude to the variances of the backcrosses to the tall and short parent. Finally, VP_1 and VP_2 refer to the variances of Stephens and Tibet dwarf respectively.

Variance and Significance of Heritability Estimates

A variance for H_n (square of the standard error), was computed

following Ketata, et al., (1976) using the formula:

$$V(Hn) = 2 \left(\frac{(VBC_1 + VBC_2)^2}{dfF_2} + \frac{VBC_1^2}{dfBC_1} + \frac{VBC_2^2}{dfBC_2} \right) / VF_2^2$$

in this formula dfF_2 , $dfBC_1$, and $dfBC_2$ refer to the degrees of freedom associated with VF_2 , VBC_1 and VBC_2 , respectively.

Levels of significance for Hn were also evaluated according to the formulas by Cochran (1951) and Ketata, et al., (1976). The ratio $2VF_2/(VBC_1 + VBC_2)$ approximately follows an F distribution with n_1 and n_2 degrees of freedom (Merrington and Thompson, 1943) where $n_1 = dfF_2$ and $n_2 = (VBC_1 + VBC_2)^2 / \left[\frac{VBC_1^2}{dfBC_1} + \frac{VBC_2^2}{dfBC_2} \right]$.

Expected Gain From Selection

Expected gain from selection, (G.S.) was calculated following Allard (1960) as $G.S. = k \times s_p \times Hn$, where k is the selection differential in standard units, s_p is the phenotypic standard deviation (estimated here as the square root of the variance for the F_2 population) and Hn is the narrow sense heritability. When the most desirable 5% of the F_2 plants are selected $k = 2.06$.

Phenotypic and Genetic Correlations

Phenotypic, environmental and genotypic correlations were used to estimate degree of association between the agronomic traits studied. Following Falconer (1960), the F_1 correlation was regarded as environmental correlation, the F_2 correlations were considered as phenotypic and genetic correlations and were calculated following

Johnson, et al., (1966a), using the formula:

$$r_{G_{xy}} = \frac{\text{CovarXY } F_2 - \text{CovarXY } F_1}{\sqrt{((\text{VarX } F_2 - \text{VarX } F_1)(\text{VarY } F_2 - \text{VarY } F_1))}}$$

where: 'r_{Gxy}' represents the genotypic correlation between x and y, 'CovarXY F₂' represents the phenotypic covariance of the F₂ generation. 'CovarXY F₁' represents the covariance of the F₁ generation. 'VarX F₂' stands for the variance of the trait X on the F₂ generation. Similarly, 'VarX F₁', 'VarY F₂' and 'VarY F₁' represent generation variances of the trait X or Y.

A way of interpreting a correlation coefficient (r) is to look at the square of its value. This figure is called the coefficient of determination (R²). It can be interpreted as the proportion of variance in one of the variables that can be explained by variation in the other variable. This study presents the degree of association between variables using coefficients of determination.

Path Coefficient Analysis

The path coefficient analysis was carried out at the genotypic level as described by Dewey and Lu (1959). The nature of the direct and indirect effects are represented diagrammatically (Fig. 1).

Two path coefficient analyses were performed. The first path analysis showed the direct and indirect effects of four grain yield components and plant height on total plant grain yield. The second analysis showed the effects of the same four grain yield components;

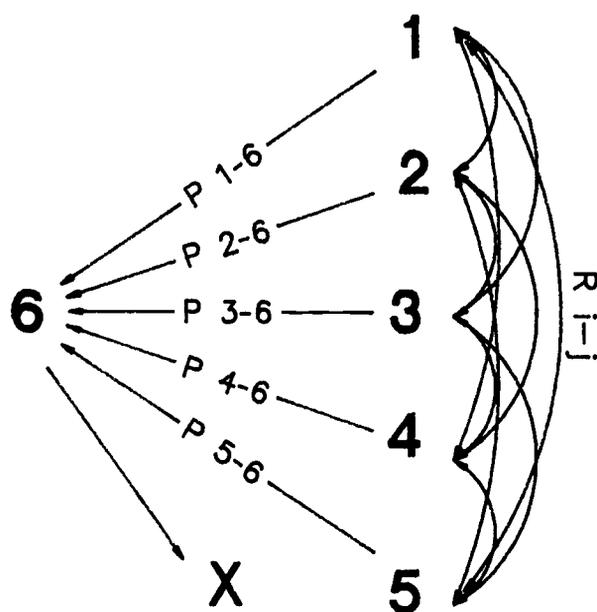


Fig. 1. A path diagram showing direct and indirect influences of different traits on grain yield of wheat.

In the path diagram the double-headed lines indicate mutual association as measured by correlation coefficients, r_{ij} , and the single arrowed lines represent direct influence as measured by path coefficients P_{ij} . the numbers represent the following traits: (1) Number of spikes per plant. (2) Spikelets per spike. (3) Kernels per spikelet. (4) Kernel weight. (5) Plant height or harvest index. (6) Grain yield per plant. (X) Residual factors.

additionally this time, height was replaced by harvest index as a factor determining grain yield. The path coefficients were obtained by solving the following simultaneous equations which express the basic relationships between correlation and path coefficients:

$$\begin{aligned}
 1) \quad r_{16} &= P_{16} + r_{12}P_{26} + r_{13}P_{36} + r_{14}P_{46} + r_{15}P_{56} \\
 2) \quad r_{26} &= r_{12}P_{16} + P_{26} + r_{23}P_{36} + r_{24}P_{46} + r_{25}P_{56} \\
 3) \quad r_{36} &= r_{13}P_{16} + r_{23}P_{26} + P_{36} + r_{34}P_{46} + r_{35}P_{56} \\
 4) \quad r_{46} &= r_{14}P_{16} + r_{24}P_{26} + r_{34}P_{36} + P_{46} + r_{45}P_{56} \\
 5) \quad r_{56} &= r_{15}P_{16} + r_{25}P_{26} + r_{35}P_{36} + r_{45}P_{46} + P_{56} \\
 6) \quad 1 &= P_{X6}^2 + P_{16}^2 + P_{26}^2 + P_{36}^2 + P_{46}^2 + P_{56}^2 + 2P_{16}r_{12}P_{26} \\
 &\quad + 2P_{16}r_{13}P_{36} + 2P_{16}r_{14}P_{46} + 2P_{16}r_{15}P_{56} \\
 &\quad + 2P_{26}r_{23}P_{36} + 2P_{26}r_{24}P_{46} \\
 &\quad + 2P_{26}r_{25}P_{56} + 2P_{36}r_{34}P_{46} \\
 &\quad + 2P_{36}r_{35}P_{56} + 2P_{46}r_{45}P_{56}
 \end{aligned}$$

The sub-indices in the previous equations indicate the following variables:

(1) number of spikes per plant, (2) mean number of spikelets per spike, (3) kernels per spikelet, (4) kernel weight, (5) height or harvest index (6) total grain yield per plant. The variable X consists of all residual factors that influenced grain yield. Direct effects (P) are symbolized by single side arrows. The correlations are indicated by the symbol (r) followed by the sub-indices of the respective traits. The 'R²' symbol appearing in both the path coefficient tables represents the summation of the products of the correlation coefficients (r) and the direct path coefficients (P).

RESULTS

Analysis of Variance

The results presented in this section were obtained by measuring 14 agronomic traits involving parents, F_1 and four segregating generations of a cross involving the cultivars, Tibet dwarf and Stephens.

Analyses of variance were conducted to test for differences between generations for each of the traits measured. Table 1 illustrates the results of these analyses. Differences were found among generations means for the following traits: yield per plant, spikelets per spike, kernels per spikelet, kernel weight, plant height, harvest index, grain filling period, chaff percentage, heading date, days to maturity, total kernel number, and biological yield.

Coefficients of variation (C.V.) were high for some traits, including total length of spikes (28.22%), total kernel number (37.47%) and biological yield (35.61%). The C.V. for total grain yield per plant was also high (42.43%), with the components of grain yield having lower coefficients of variation. Among the components of grain yield, the number of spikes per plant had the highest C.V. (23.27%), with other components of yield and traits measured, displaying coefficients of variation of less than 7%.

Total number of kernels per plant is an important constituent of yield. However, it is possible to further divide this variable into three components (spikes per plant, spikelets per spike, and

Table 1. Observed means squares from analysis of variance using a randomized block design for 14 characters involving parents, F1, F2, F3, BC1 and BC2 generations of a cross of two winter wheat cultivars grown at Hyslop Farm Research Station, 1986.

Source of variation	d.f.	Grain yld. per plant (g)	Spikes per plant	Spikelets per Spike	Kernels per Spikelet	Kernel Weight gx1000	Plant Height (cm)	Harvest Index (%)
Generations	6	759.5415	3.3050	2.1989	1.8608	92.5435	1198.0582	90.6423
Replications	3	81.6462	15.7962	1.9862	0.0237	1.7684	6.1040	4.3172
Error	18	160.9307	13.7209	0.1484	0.0162	2.7019	9.5397	4.1376
Total	27							
Significance level								
Generations		*	ns	**	**	**	**	**
Replications		ns	ns	**	ns	ns	ns	ns
C.V.		42.4298	23.2706	1.9763	6.7002	3.3104	6.8992	5.7393

* and ** indicate 5% and 1% significance levels, respectively.

Table 1. (Continued) Observed means squares from analysis of variance using a randomized block design for 14 characters involving parents, F1, F2, F3, BC1 and BC2 generations of a cross of two winter wheat cultivars grown at Hyslop Farm Research Station in 1986.

Source of variation	d.f.	Grain filling period (days)	Chaff (%)	Days to Heading	Days to Maturity	Total Length of Spikes (cm)	Total Kernel Number	Biol. Yield. (g)
Generations	6	126.9704	87.1004	264.5236	36.2169	779.016	185240.65	2759.390
Block	3	24.0091	3.6185	22.4197	0.7408	1500.125	25593.56	326.065
Error	18	7.2854	2.4838	7.4972	1.2097	2112.780	48583.37	841.844
Total	27							
Significance levels								
Generations		**	**	**	**	ns	*	*
Replications		*	ns	ns	ns	ns	ns	ns
C.V.		6.3542	6.8528	2.0610	0.6272	28.2252	37.4717	35.6124

* and ** indicate 5% and 1% significance levels, respectively.

kernels per spikelet) in the same way it is possible to divide grain yield into two components (total number of kernels per plant and weight per kernel). A path coefficient that includes all these causal relationships would be difficult to analyze and interpret. No similar studies have done so. Instead, many investigations have excluded the total number of kernels per plant, but included the rest of the yield components. This, and the relatively high coefficient of variation shown by the total number of kernels per plant, resulted in the total number of kernels per plant not to be considered as one of the components of grain yield but it was treated as a separate variable. Thus, for the remainder of this manuscript, reference to the components of grain yield will only include spikes per plant, spikelets per spike, kernels per spikelet, and kernel weight.

Separation of Means

Mean values were analyzed using the Waller-Duncan Bayes test (WDLSD) to determine which generation were different. This examination was not possible for two variables: total number of spikes per plant and total length of heads per plant as no differences for these traits were detected among generations.

Table 2 shows the grouping of ranked generation means following the WDLSD procedure. Generation means for each trait are displayed on each vertical column, with letters indicating differences within each column. In Appendix Table 1 generation means and

Table 2. Grouping of ranked generation means with Waller-Duncan Bayes Least Significant Difference procedure for 14 traits measured on individual plants from a cross between Stephens x Tibet dwarf.

Generation	Trait						
	Grain Yield (gm./pl.)	Spikes/Plant ¹	Spikelets per Spike	Kernels per Spikelet	Kernel Weight (gm.)	Plant Height (cm.)	Harvest Index (%)
Stephens	57.68 a	15.44	19.95 d	3.300 g	0.0567 l	74.31 p	44.35 v
Tibet dwarf	20.70 bc	17.36	18.09 e	1.546 h	0.0423 m	22.50 q	38.46 w
F ₁	24.54 bc	14.88	20.15 d	1.533 h	0.0531 n	40.63 r	32.49 xz
F ₂	26.66 bc	16.18	19.24 f	1.741 i	0.0485 o	41.99 r	33.72 z
F ₃	24.00 bc	14.97	19.96 d	1.731 i	0.0477 o	47.99 s	32.35 z
BC ₁	37.88 b	15.91	19.97 d	2.199 j	0.0527 n	56.88 t	36.32 w
BC ₂	17.85 c	16.96	19.07 f	1.246 k	0.0466 o	29.04 u	30.42 y

The generation means in each column displaying the same letter are not significantly different; (k = 100; alpha = 0.05).

(1) indicates that WDLSD examination was not conducted but all means are assumed to be statistically not different.

n: P₁ = 36, n: P₂ = 28, n: F₁ = 32, n: F₂ = 76, n: F₃ = 268, n: BC₁ = 64, n: BC₂ = 68.

Table 2. (Continuation) grouping of ranked generation means with Waller-Duncan Bayes Least Significant Difference procedure for 14 traits measured on individual plants from a cross between Stephens x Tibet dwarf.

Generation	Trait						
	Grain Fill. Period (days)	Chaff (%)	Heading Date	Days to Maturity	Length Sp. (cm.) ¹	Tot. No. Kernels	Biological Yield (gm.)
Stephens	37.25 cb	14.54 f	144.0 k	181.3 o	187.2	1016.1 w	129.81 w
Tibet dwarf	48.89 a	24.87 gh	123.0 l	171.9 p	147.4	489.1 v	53.93 x
F ₁	48.50 a	25.74 g	126.0 l	174.4 sr	158.9	461.1 v	74.84 yx
F ₂	33.72 cd	23.80 gh	132.8 n	174.9 s	161.8	549.0 v	75.95 yx
F ₃	32.35 de	23.36 h	137.4 m	175.2 st	149.7	503.3 v	73.42 yx
BC ₁	36.32 bc	19.67 i	140.7 km	176.6 t	174.6	719.3 wv	102.45 wy
BC ₂	30.40 e	29.01 j	126.2 l	173.2 rp	160.3	380.1 v	59.91 yx

The generation means in each column displaying the same letter are not significantly different; (k = 100; alpha = 0.05).

(1) indicates that WDLSD examination was not conducted but all means are assumed to be statistically not different.

n: P₁ = 36, n: P₂ = 28, n: F₁ = 32, n: F₂ = 76, n: F₃ = 268, n: BC₁ = 64, n: BC₂ = 68.

standard deviations for all 14 traits evaluated are presented.

Separation of the generation means of grain yield per plant, indicated that Stephens had the highest grain yield when compared to Tibet dwarf or to any of the resulting generations. Although the differences were not significant, all generations (excluding BC₂, backcross to Tibet dwarf) had a higher grain yield than Tibet dwarf. The grain yield of BC₁ (backcross to Stephens) was higher than the yield of BC₂.

Differences were found among generations when the trait spikelets per spike was considered. Tibet dwarf had the lowest number of spikelets per spike among all populations, followed by the backcross to Tibet dwarf (BC₂). It is interesting to note that with respect to spikelets per spike, the F₁ generation value was above that of either parent. There were differences between the means of the backcrosses. The backcross generations to Stephens (BC₁) was higher and different than the backcross to Tibet dwarf (BC₂).

Observation of the generation means for kernel weight showed that Stephens had heavier kernels than Tibet dwarf. The kernel weight of the progeny fell between the value of the parents. All progeny populations were different from either parent. The mean of the backcrosses deviated significantly from the mean of the F₁ and favored the mean of the recurrent parent. As occurred in traits like grain yield and spikelets per spike, there was a significant difference between the means of the two backcrosses for kernel weight.

Examination of plant height generation means reveals a large

difference in height between the two parents, with Stephens being the tallest. All progeny populations resulting from this cross had height values between the two parents. All generations (F_1 , F_2 , F_3 , BC_1 , BC_2) were different from their parents and in some cases were different from each other. For example, the mean plant height of the F_3 was different than the mean value of both the F_1 and the F_2 generations. The mean for plant height of the backcrosses were skewed towards the value of the recurrent parent.

Stephens had the highest harvest index among all populations (44.35%). Harvest index values of the progeny were situated below the values of the two parents. The highest value among the progeny was displayed by BC_1 . The lowest value was displayed by BC_2 .

Tibet dwarf and Stephens differed significantly in both heading date and days to maturity. The mean value for heading date of Tibet dwarf was 123 days. The heading date of Stephens was recorded 21 days later. The number of days to reach maturity was 181 for Stephens and 172 for Tibet dwarf. The difference between days to maturity and heading date constitutes the grain filling period. Tibet dwarf had a longer grain filling period (48.9 days) compared to Stephens (37.3 days).

It is important to note that the F_1 generation means for heading date, days to maturity, and grain filling period, were closer to the means of Tibet dwarf than to the values of Stephens. While there was no difference between heading date and grain filling period of F_1 and Tibet dwarf, there was a difference in days to maturity between the two traits. Stephens was different from the F_1

with respect to all three traits.

With reference to heading date, days to maturity and grain filling period, backcrosses and their corresponding recurrent parents were not different in most instances. There were however, differences between the backcrosses for all three traits.

There were differences in the chaff percentage of the parents. Stephens had the lowest chaff percentage among all populations (14.54%), with Tibet dwarf (24.87%) and BC₂ (29.01%) having the highest chaff percentage. There were no differences between the chaff percentage of F₁, F₂ or F₃ and Tibet dwarf. However, there were differences between the chaff percentage of these generations and Stephens.

Stephens had the highest total number of kernels per plant among all generations while BC₂ (backcross to Tibet dwarf) had the lowest. The high variability associated with this trait did not allow the observation of differences between generations other than the big difference between Stephens and the other populations. Thus, no differences between segregating generations were detected.

There was a large difference in biological yield between the two parents. Biological yield of Stephens was over twice that of Tibet dwarf. Biological yield of each backcross was similar to the biomass of the recurrent parent.

Heritability, Mid Parental Value and Genetic Advance

Estimates of broad and narrow sense heritabilities, variance,

mid parent deviation and expected genetic advance through selection are reported on Table 3. Broad sense estimates are particularly high for plant height (0.99), heading date (0.98), and grain filling period (0.95). The lowest values were found for chaff percentage (0.51), total length of spikes (0.62), and for the number of spikes per plant (0.63).

When narrow sense heritabilities estimates were examined, some confusing results emerged. Higher narrow sense than broad sense heritability estimates were obtained for spikes per spike, kernel weight, chaff percentage, and heading date. Spikes per spike and kernel weight had the highest variances for the narrow sense heritabilities (1.90 and 0.225 respectively). One narrow sense heritability estimate (kernel weight) was greater than 1.00. This estimate was also associated with relatively high variance, presumably due to sampling errors and/or uneven environmental influences on the various generations.

The highest narrow sense heritability estimates were obtained for spikelets per spike (0.95), kernel weight (1.2), grain filling period (0.91), and heading date (0.98). Biological yield displayed the lowest narrow sense heritability estimate (0.09).

In relation with grain yield or grain yield components, the parents showed performance clearly higher than that of the F_1 in the case of plant grain yield, spikes per plant and kernels per spikelet (see F_1 -MP values in Table 3). Other traits like plant height, harvest index, total kernel number total length of heads and biological yield also presented the same response.

Table 3. Estimates of broad sense heritability (Hbs), narrow sense heritability (Hns), narrow sense heritability variance (VHns), mid-parent deviation (F₁-MP), and expected genetic advance (G.S) for 14 characters in a winter wheat cross.

	Hbs	Hns	VHns	F ₁ -MP	G.S.**
1) Plant Grain Yield	0.74	0.35	0.106	-14.65	12.45
2) Spikes/ Plant	0.63	0.33*	0.098	-1.526	3.89
3) Spikelets/ Spike	0.80	0.95*	1.897	1.133	4.30
4) Kernels/ Spikelet	0.82	0.64*	0.067	-0.890	1.02
5) Kernel Weight	0.71	1.22*	0.225	0.0058	0.02
6) Plant Height	0.99	0.45	0.093	-7.778	15.33
8) Harvest Index	0.68	0.37	0.093	-8.917	8.61
7) Filling Period	0.95	0.91*	0.443	5.429	16.53
9) Chaff percentage	0.52	0.65*	0.065	6.033	7.86
10) Heading Date	0.98	0.98*	0.040	-7.545	19.52
11) Days to Maturity	0.74	0.32	0.101	-2.116	1.54
12) Total Length of Spikes	0.62	0.39	0.091	-8.352	77.98
13) Total Kernel No.	0.80	0.58*	0.078	-291.49	100.00
14) Biological Yield	0.70	0.09	0.140	-17.02	7.05

* Significantly different from zero at P= 10% level.

** Genetic advance (G.S.) represent the expected percent increase in the F₃ above the F₂ mean when the best 5% of the F₂ plants are selected.

Estimates of the expected gain from selection are also presented in Table 3. Genetic advance estimates (G.S.) varied from more than 100% in the case of total kernel number to 0.02% for kernel weight. It is important to note that G.S. is an estimate of the advance for each trait and not on grain yield per se. Genetic advance estimates presented in Table 3 are therefore not directly comparable between traits.

Association Among Traits

Phenotypic and genotypic correlation coefficients agreed very closely for most comparisons (Appendix Table 2 and 3). Coefficients of determination for phenotypic and genotypic associations are presented in Tables 4 and 5. Where negative correlation values were found the coefficients of determination are preceded by a negative sign in parenthesis.

Phenotypic coefficients of determination between grain yield and other variables included a wide range of values (Table 4). High values were found for grain yield and total kernel number (0.937), followed by the value for grain yield and biological yield (0.740). Intermediate values were expressed by the associations of grain yield with kernels per spikelet (0.545), with harvest index (0.447), and with total length of spikes (0.443). Low values (between 0.016 and 0.260) were recorded for the associations between grain yield and spikes per plant, spikelets per spike, kernel weight, plant height, filling period, chaff percentage, heading date, and days to

Table 4. Coefficients of determination of phenotypic associations from correlations between 14 traits measured in the F₂ generation of a cross of two winter wheat cultivars grown at Hyslop Farm Research Station, 1986.

Trait	2)	3)	4)	5)	6)	7)	8)
1) Plant Grain Yield	0.260	0.151	0.545	0.057	0.017	0.447	(-)0.016
2) Spikes/ Plant		(-)0.002	(-)0.002	0.002	(-)0.021	(-)0.003	(-)0.012
3) Spikelets/ Spike			0.123	(-)0.054	0.025	0.020	(-)0.161
4) Kernels/ Spikelet				0.002	0.074	0.662	(-)0.008
5) Kernel Weight					(-)0.000	0.100	0.130
6) Plant Height						(-)0.010	(-)0.002
7) Harvest Index							0.002

Trait	9)	10)	11)	12)	13)	14)
1) Plant Grain Yield	(-)0.223	0.022	0.021	0.443	0.937	0.740
2) Spikes/Plant	0.025	0.019	0.026	0.883	0.269	0.443
3) Spikelets/Spike	(-)0.051	0.169	0.038	0.015	0.206	0.164
4) Kernels/Spikelet	(-)0.500	0.007	0.000	0.012	0.565	0.232
5) Kernel Weight	(-)0.014	(-)0.127	(-)0.015	0.007	0.000	0.009
6) Plant Height	(-)0.091	0.002	0.001	(-)0.006	0.016	0.096
7) Harvest Index	(-)0.347	(-)0.004	(-)0.008	0.021	0.382	0.066
8) Filling Period	0.011	(-)0.948	(-)0.072	(-)0.009	(-)0.043	(-)0.048
9) Chaff percentage		(-)0.004	0.020	0.003	(-)0.207	(-)0.085
10) Heading Date			0.232	0.017	0.052	0.064
11) Days to Maturity				0.033	0.027	0.051
12) Total Head Length					0.439	0.613
13) Total Kernel No.						0.738
14) Biological Yield						

(-) indicates that the correlation that originated the adjacent coefficient of determination had a negative sign.

n: F₂ = 76

Table 5. Coefficients of determination of genotypic associations based of variances and covariances of the F₁ and F₂ generations of a cross of two winter wheat cultivars grown at Hyslop Farm Research Station, 1986.

Trait	2)	3)	4)	5)	6)	7)	8)
1) Plant Grain Yield	0.185	0.221	0.570	0.037	0.022	0.463	(-)0.015
2) Spikes/ Plant		(-)0.002	(-)0.009	0.015	(-)0.040	0.007	(-)0.009
3) Spikelets/ Spike			0.184	(-)0.119	0.031	0.040	(-)0.207
4) Kernels/ Spikelet				(-)0.000	0.093	0.662	(-)0.011
5) Kernel Weight					(-)0.000	0.043	0.203
6) Plant Height						(-)0.015	(-)0.002
7) Harvest Index							0.002

Trait	9)	10)	11)	12)	13)	14)
1) Plant Grain Yield	(-)0.257	0.029	0.083	0.398	0.947	0.743
2) Spikes/Plant	0.008	0.025	0.129	0.849	0.195	0.291
3) Spikelets/Spike	(-)0.112	0.206	0.048	0.018	0.294	0.230
4) Kernels/Spikelet	(-)0.564	0.010	0.001	0.009	0.585	0.277
5) Kernel Weight	0.037	(-)0.177	(-)0.007	0.022	(-)0.001	0.017
6) Plant Height	(-)0.178	0.002	0.002	(-)0.013	0.019	0.135
7) Harvest Index	(-)0.189	(-)0.003	(-)0.004	0.039	0.425	0.085
8) Filling Period	0.026	(-)0.964	(-)0.171	(-)0.005	(-)0.049	(-)0.054
9) Chaff percentage		(-)0.011	0.035	0.001	(-)0.315	(-)0.243
10) Heading Date			0.335	0.021	0.065	0.084
11) Days to Maturity				0.174	0.074	0.154
12) Total Length of Spikes					0.391	0.485
13) Total Kernel No.						0.728
14) Biological Yield						

(-) indicates that the correlation that originated the adjacent coefficient of coefficient determination had a negative sign.

n: F₁ = 32, n: F₂ = 76.

maturity.

Phenotypic coefficients of determination for the associations among grain yield components (spikes per plant, spikelets per spike, kernels per spikelet, and kernel weight) were low, ranging from 0.002 to 0.123. The highest value (0.123) described the degree of association between spikelets per spike and kernels per spike.

It is interesting to note that total kernel number and grain yield displayed one of the highest coefficients of determination in this study (phenotypic $R^2=0.937$). Total kernel number also displayed high phenotypic coefficients of determination with biological yield ($R^2=0.738$), somewhat intermediate values (from $R^2=0.206$ to $R^2=0.565$) with the components of grain yield excluding kernel weight. Total kernel number also had intermediate coefficients of determination with harvest index ($R^2=0.382$), chaff percentage ($R^2=0.207$), and with total length of spikes ($R^2=0.439$). A very low coefficient of determination was obtained between kernel weight and total kernel number ($R^2<0.00001$).

The association of biological yield with spikes per plant, spikelets per spike, kernels per spikelets presented intermediate values ($R^2=0.443$ to $R^2=0.164$), the highest being the association with the number of spikes per plant. The association between biological yield and kernel weight was low ($R^2=0.009$).

An interesting relationship was noted between grain filling period and both heading date and days to maturity. Phenotypic coefficients of determination only showed a high association of grain filling period with heading date ($R^2=0.948$) but not with days

to maturity ($R^2=0.072$).

The association of harvest index with other traits was notable, especially with those traits which reflected the ratio of grain to straw, like kernels per spikelet ($R^2=0.662$) and chaff percentage ($R^2=0.347$).

Most of the associations of both biological and grain yield with other traits showed the same sign and in most instances similar magnitudes. Only for two traits, harvest index and kernels per spikelet were the coefficients of determination with biological yield lower than for grain yield.

The coefficients of determination based on genetic correlations provided similar results to those observed with phenotypic correlations.

Genetic correlation coefficients among components of yield (six correlations between spikes per plant, spikelets per spike, kernels per spikelet, and kernel weight) indicated four small negative associations (Table 5, Appendix Table 3). These were found for both spikes per plant and kernel weight with spikelets per spike and kernels per spikelet.

Plant height and components of yield correlations showed that height had a small and negative association with the number of spikes per plant. The remainder yield components were positively associated with plant height. Coefficients of determination indicated that plant height accounted for less than 5% of the variability in the number of spikes per plant ($R^2=0.04$), and less than 10% of the variability of the other grain yield components

Path coefficient analyses were performed for a more complete analysis of the relation of grain yield with the components of yield, plant height, and harvest index.

Since genotypic and phenotypic correlations were similar, path coefficient analyses were calculated and analyzed based only on genotypic correlations. Two path coefficient analyses were performed. The first analysis showed the direct and indirect effects of four grain yield components and plant height on total plant grain yield. The second showed the same four grain yield components, excluded plant height, but included harvest index as factors determining grain yield.

Results of the first analysis are presented in Table 6. It can be observed that the association between spikes per plant and grain yield ($r=0.430$) is almost completely determined by the direct effect of spikes per plant, while only small (positive or negative) effects are exerted indirectly via the other components.

The association between spikelets per spike and grain yield ($r=0.470$) was primarily determined by the direct effect of the number of spikelets per spike ($P=0.279$) and by the indirect effect of the number of kernels per spikelet ($rxP=0.295$).

The third correlation, between kernels per spikelet and grain yield ($r=0.755$), was explained almost entirely by the direct effect of kernels per spikelet ($P=0.690$). Positive indirect effects were observed via spikelets per spike.

For kernel weight, path coefficient analysis showed a direct effect on grain yield (P) of 0.241. There was however, a notable

Table 6. Path coefficient analyses of direct and indirect effects of four grain yield components and plant height, on grain yield per plant. Computation based on genetic correlations.

Relationships of grain yield and:	association with yield (r)	Direct effect (P)	Indirect Effects Via:				
			Spikes per Plant	Spikelets per Spike	Kernels per Spikelet	Kernel Weight	Plant Height
Spikes per Plant	0.430	0.479	---	-0.014	-0.067	0.029	-0.003
Spikelets per Spike	0.470	0.279	-0.023	---	0.296	-0.083	0.002
Kernels per Spikelet	0.755	0.690	-0.047	0.119	---	-0.004	0.004
Kernel Weight	0.192	0.241	0.058	-0.096	-0.011	---	0.000
Plant Height	0.148	0.013	-0.095	0.049	0.210	-0.003	---

$R^2 = . (rxP) = 0.905$
 residual = 0.095
 n: $F_1 = 32$, n: $F_2 = 76$.

negative effect through the number of spikelets per spike. Thus, correlation between kernel weight and grain yield was 0.192.

The correlation value of $r=0.148$ between plant height and grain yield was primarily due to the positive indirect effect of kernels per spike ($r \times P=0.210$). The direct effect of plant height on grain yield was close to zero ($P=0.013$) suggesting that the association between height and grain yield was exaggerated because it included the indirect effects via kernels per spike.

Small residual effects indicated that the five traits included in the path coefficient analysis accounted for most of the total variation in grain yield, namely 90.5% ($R^2=0.905$).

As mentioned previously, a second path coefficient analysis was performed replacing plant height with harvest index as one of the factors affecting yield. Direct and indirect effects of four grain yield components and harvest index on total plant yield are presented in Table 7.

This second path coefficient analysis showed that the association between spikes per plant and grain yield ($r=0.430$), was almost completely determined by the direct effect of spike number on grain yield. Only small (positive or negative) effects were exerted indirectly through the other traits. Results from the first path coefficient analysis concerning the effect of the number of spikes per plant on grain yield were very similar.

The association between grain yield and the number of spikelets per spike ($r=0.470$) appeared to be mainly determined by the direct effect of spikelets per spike ($P=0.311$) and by the

Table 7. Path coefficient analyses of direct and indirect effects of four grain yield components and harvest index on grain yield. Computation based on genetic correlations.

Relationships of grain yield and:	association with grain yield (rg)	Direct effect (P)	Indirect Effects Via:				
			spikes per plant	spikelets per spike	kernels per spikelet	kernel weight	harvest index
Spikes per plant	0.430	0.447	---	-0.015	-0.046	0.023	0.020
Spikelets per spike	0.470	0.311	-0.022	---	0.204	-0.070	0.047
Kernels per Spikelet	0.755	0.476	-0.043	0.131	---	-0.003	0.192
Kernel weight	0.192	0.204	0.054	-0.107	0.007	---	0.049
Harvest index	0.680	0.236	0.037	0.062	0.387	0.042	---

$R^2 = . (rxP) = 0.897$
 residual = 0.103
 n: $F_1 = 32$, n: $F_2 = 76$.

indirect effect of the number of kernels per spikelet ($r_{xP}=0.204$). Other positive or negative indirect effects with the other traits were small in this second analysis.

The third association, kernels per spikelet and grain yield, ($r=0.755$) was determined largely by the direct effect ($P=0.476$). Harvest index had an indirect effect on this association ($r_{xP}=0.192$). In this second path coefficient analysis a relatively small indirect effect of spikelets per spike appeared to affect this correlation between kernels per spikelet and grain yield.

The second path coefficient analysis showed that kernel weight had a direct effect (P) on grain yield (0.204). The degree of association displayed by correlation coefficient was only $r=0.1922$. This means that other small and negative indirect effects accounted for the difference, reducing the apparent degree of association between kernel weight and grain yield shown by correlation. For the most part, a small negative indirect effect through the number of spikelets per spike further reduced this correlation.

Path coefficient evaluation indicated that the association between harvest index and grain yield was primarily due to the positive indirect effect of kernels per spike ($r_{xP}=0.387$). The direct effect of harvest index had a smaller contribution ($P=0.236$). This means that the correlation between harvest index and grain yield showed an exaggerated degree of the true association between the two variables.

The five traits in this second path coefficient analysis accounted for 89.7% of the total variation in grain yield, meaning

that the second analysis that included harvest index instead of height, also accounted for most of the variation in yield.

DISCUSSION

Analysis of Variance

To establish a frame of reference for this discussion, the parental cultivars and their progenies should neither be regarded as a sample portraying any larger winter wheat population nor as representing the same population grown under totally different environmental conditions.

Stephens displayed the highest values for most of the grain yield related traits. Tibet dwarf only showed a slightly higher, but non significant number of spikes per plant than Stephens. It is unknown, however, if this difference could be accentuated or minimized under different growing conditions such as low or high planting densities.

Although there were no differences among generations with respect to the number of spikes per plant, phenotypic correlations (correlation between traits from individual plants within the F_2 generation) indicated that there was a significant degree of association between the number of spikes per plant and individual plant grain yield (Appendix Table 2). Mean values were used in the analysis of variance of segregating populations, individual plant data was used for correlation.

The present study revealed that in eight out of the 14 traits measured, the F_1 had a lower value than the average of the two parents. In diallel crosses of 12 cultivars of hexaploid triticale, Carrillo, et al., (1983) found that in many cases the F_1 had lower

yields than the parental averages. This circumstance was explained by citing cytogenetic investigations of Merker (1973) which indicated that in some cases the F_1 had lower fertility than the parents due to the occurrence of greater number of meiotic disturbances in this generation. This could be also the case in the present study but there are no cytogenetic studies to validate this hypothesis.

Ketata, et al., (1976) studying a cross of winter wheat cultivars with contrasting plant types, reported the occurrence of the same phenomenon of negative F_1 -MP values in four of the eight agronomic traits measured. This included spikes per plant and kernels per spikelet but it was not the case for kernel weight, spikelets per spike or plant grain yield. The present study revealed the same events except in the case of plant grain yield where the F_1 was also inferior to the average of the parents.

Yield Components

As grain yields in wheat have been increased, higher levels of productivity have become increasingly more difficult to attain. Breeding for greater yield potential by selecting for grain yield per se may limit future progress given the complex nature of this trait. Attention to expression of individual components of grain yield may provide a better basis for selection of parents and in the evaluation of their progenies than selection for grain yield per se. Support for this line of thought includes strong evidence that the

grain yield components are less influenced by the environment than grain yield itself. As suggested by Falconer (1960), another reason to pay attention to individual components of yield and to their genetic relationships with grain yield is that changes brought about by selection might sometimes be achieved more rapidly for a related trait than for the desired trait itself.

Genetic Nature of the Traits

The F_1 generation had a greater number of spikelets per spike than the two parents. This could be interpreted as hybrid vigour indicating that the trait might be genetically influenced by non additive gene effects. However, the estimates of narrow and broad sense heritability (based not only on parents and F_1 but also on the segregating generations, including their means and variances) indicated that the total genetic variability was mostly due to additive gene action. Furthermore, the total genetic variability seemed to be smaller than the additive portion. Since broad sense estimates measure the total genetic variability, and narrow sense heritability is only the additive portion of this total, such results are contradictory. This inconsistency was explained by the high variance of the estimate of narrow sense heritability. This prevented reaching any conclusions about the nature of the gene action involved in the expression of this trait (number of spikelets per spike).

The F_1 generation showed a kernel weight value that was higher

than the mid-parental value. Broad and narrow sense heritability estimates which should help in the interpretation of these results presented the same inconsistencies as with number of spikelets per spike limiting again any conclusions.

Narrow and broad sense heritability estimates for the number of spikes per plant suggested that both additive and non additive gene action, in about the same proportion, determined genotypic variability of this trait.

In the case of kernels per spikelet, heritability estimates showed that additive gene action was responsible for about 75% of the total genetic variability.

Comparison of broad and narrow sense heritability estimates suggested that nearly 50% of the genetic variance of both harvest index and plant height was determined by genetic factors which were contributing to the additive genetic variability.

Comparison of narrow and broad sense heritabilities, suggested that almost all the genetic variability with respect to filling period was due to additive gene action. However, estimates of narrow sense heritability were highly variable indicating that this assertion was not well supported by the results in this study.

Narrow sense heritability estimates were high for heading date (0.978). In similar experiment, an using two winter wheat cultivars, Ketata, et al., (1976) also found very high estimates of narrow sense heritability for heading date (101%). Their calculation of gain from selection for this trait (G.S.) was 18.4% which is similar to the 19.5% observed in this study.

Correlations and Path Coefficient Analysis

Associations among the components of yield were relatively low as seen through the coefficients of determination. This agrees with the observations of Adams (1967). Working with beans he noted that in spaced plant nurseries and in other non competitive situations, correlations among the components of grain yield were generally low. It also agrees with the range of magnitude of correlation found by Carrillo, et al., (1983) for the components of yield. Using diallel crosses of a cereal such as triticale, the range of correlations for the yield components were much larger both in the studies of Fonseca, et al., (1968), (experiments with wheat planted on hill plots), and in the studies of Kronstad and Foote (1964) (spaced-planted wheat nurseries).

The correlation coefficient between spikes per plant and grain yield was almost equal to its direct effect as noted by the path coefficient analyses. Consequently, and assuming that the causal relationships expressed in the path coefficient analyses are correct, this correlation is the result of a true relationship and not the effect of spurious associations through indirect pathways via the other components. This factor, plus the relatively high magnitude of the association, indicates that direct selection for higher yield using this trait as selection criteria should be effective under the growing conditions employed in this study.

Path coefficient analysis estimated that in the relationship between spikelets per spike and grain yield that the direct effect

of the number of spikelets did not account for most of the correlation. In this instance both the direct effect of the number of spikelets and the indirect effect through the number of kernels per spikelet defined the association of spikelets per spike and grain yield. Although the magnitude of the direct effect of the number of spikelets on grain yield is not high, direct selection of higher number of spikelets per spike to achieve increased grain yield is possible but better results maybe achieved selecting instead for higher number of kernels per spikelet.

The direct effect of kernels per spikelet on grain yield accounts for most of the correlation between the number of kernels per spikelet and grain yield. Correlation values tended to overestimate the effect of kernels per spikelet on grain yield because it includes the positive indirect effect of the number of kernels per spikelet. However, direct selection for higher grain yield through this trait should be effective.

The direct path coefficient of kernel weight on grain yield accounts for most of the association between kernel weight and grain yield. However, it reveals that there is a slightly greater association between kernel weight and grain yield than what correlation value itself suggests. This is explained by a small but negative indirect effect through the number of spikelets per spike. This means that although selection of plants with heavier grains could be effective to increase grain yield there could be a compensation by a small reduction in the number of spikelets per spike.

The association between plant height and grain yield was low and non significant in this study. Even this low association between height and grain yield ($r=0.1295$) might be inflated because it also reflects the indirect positive effect of the number of kernels per spikelet on grain yield. Although this implies that height is not useful as selection criteria for obtaining higher yields, it also suggests that it might be possible to select short, high yielding plants within the segregating population of this cross.

Dwarfing genes of Tibet dwarf have not previously been evaluated by others with respect to their effect on grain yield. However, the results of this experiment agree with Kronstad (1963) who performed path coefficient analysis to observe direct and indirect effects of the components of grain yield including plant height on grain yield. The degree of association of plant height and grain yield, in absolute terms, was low with respect to the effect of other yield components. Only small indirect effects of height via kernel number were observed.

The results here are also similar to those of Maya (1975) regarding the small effect of plant height on grain yield. Using replication means of the F_1 , F_2 , BC_1 and BC_2 for each of the 10 crosses, he found that in eight crosses, there was no significant phenotypic correlation between grain yield and height. In general, path coefficient analysis showed that neither direct or indirect effects were important in the system. The exception to this was the observation of indirect effects of plant height on grain yield via tiller number in two crosses. This event was associated with the

tall parent having more tillering capacity. In the same study, in two crosses where the correlation of height and grain yield was significant, the direct effect of plant height on grain yield, as expressed by the path coefficient, was about 10 times less than the association reflected by correlation.

The path coefficient analysis used by Fonseca and Patterson (1968) indicated that the direct effect of height on grain yield was low ($P=0.023$), but higher than the association shown by the correlation coefficient ($r=0.295$). The direct effects (P) of the components of grain yield on grain yield were much higher in comparison; the direct effect of the number of spikes per plant was 0.976, the direct effect of kernels per spike was 0.718, and the direct effect of kernel weight was 0.317.

Examining the yield components, McNeal (1960) observed that plant height of the F_3 progeny from the cross of the two wheat cultivars, Lemhi and Tatcher, was significantly correlated with grain yield. However, the correlation value of 0.415 accounted for only 17.2% of the variation in yield.

The study of Gale and Flintham (1984) used a different methodology to evaluate a specific height reducing gene ($Rh3$) and grain yield. They evaluated the components of grain yield in near-isogenic tall and dwarf lines instead of using progenies from crosses between lines with differential plant height. The $Rh3$ dwarfing gene was associated with an increase in the number of kernels per spike, reduced the kernel size and the nitrogen content. The experimental method used permitted the observation that the

associated reduction in mean grain size was entirely attributable to inter-grain competition. The associated reduction in grain nitrogen content was only partially attributable to inter-grain competition. Similarly, in the present study, height had a small effect on grain yield via the number of kernels per spikelet as described by the first path coefficient analysis.

Results from the second path coefficient analysis, where harvest index replaced plant height as a variable, show similar direct and indirect effects of yield components on grain yield. The comparison of the two path coefficient analyses showed the following: (a) The correlation coefficient between spikes per plant and grain yield was almost equal to its direct effect. (b) For the association between spikelets per spike and grain yield, the direct effect of the number of spikelets did not account for the total correlation. In this instance both the direct effect of the number of spikelets and the indirect effect through the number of kernels per spikelet had an impact on the degree of association of spikelets per spike and grain yield. (c) The highest direct association was displayed by the direct effect of the number of kernels per spikelet on grain yield. Again, the correlation primarily originates in the direct effect of the number of kernels per spikelets and in the indirect effect via the number of spikelets per spike. In the second path coefficient analysis another indirect effect, this time via harvest index, was even more important than the indirect effect via spikelets per spike .

This suggests that direct selection through kernels per

spikelet should be effective, given the degree of direct association with grain yield, and considering that additive genetic effects accounted for a large portion of the total genetic variability.

The direct effect of kernel weight on grain yield accounted for most of the associations between these variables. This suggests that this correlation value alone represented the true relationship between the traits for this study. Direct selection through this trait should be effective in increasing grain yield as only a small negative indirect effect was observed through the number of spikelets per spike.

The net relationship of harvest index on grain yield, as discerned by path coefficient analysis, was lower than the degree of association between the same variables suggested by the correlation value. The indirect effect of harvest index on grain yield by means of the number of kernels per spikelet was high. Association of harvest index and grain yield then reflects the indirect effect of kernels per spike and not of harvest index per se on grain yield. This would agree with the reasoning that the number of kernels per spike is also a ratio of economic and biological yield. Based only on path coefficient analysis alone, selection for higher yields based on higher harvest index would be expected to be achieved indirectly through the increases in the number of kernels per spikelet.

SUMMARY AND CONCLUSIONS

Parental and progeny populations from a cross between Stephens and Tibet dwarf were grown in a space-planted experiment to obtain information concerning the nature of inheritance and the possible association between grain yield and the components of yield. Agronomic traits measured on an individual plant basis were: heading date, days to maturity, grain filling period, plant height, biological yield, number of spikes per plant, total length of spikes, spikelets per spike, kernels per spikelet, total kernel number, grain yield, kernel weight, harvest index, and chaff percentage.

Analyses of variance of generation means were conducted for all traits. To determine the nature of gene action for the selected traits broad and narrow sense heritability were estimated. Associations among traits were determined by phenotypic and genotypic correlations as well as by two path coefficient analyses.

From data resulting from this experiment the following conclusions were made:

1. The parents differed widely for 12 of the 14 traits measured. The two exceptions were the total number of spikes and the total length of heads.

2. A large part of the total genetic variation associated with the grain yield components was the result of additive gene action as indicated by high narrow sense heritability estimates for kernel weight, spikelets per spike, kernels per spikelet, and total kernel

number.

3. Selection for number of kernels per spikelet within the F_2 population of the cross of Stephens and Tibet dwarf would result in increased grain yield in succeeding generations as suggested by both narrow sense heritability estimates and the lack of any direct, or any sizable indirect, negative associations with grain yield and the other components of yield.

4. Narrow sense heritability values were higher than broad sense heritability for spikelets per spike, kernel weight, chaff percentage and heading date. These inflated estimates are attributed to sampling errors and/or uneven environmental influence on the various generations.

5. Correlation coefficients can be somewhat deceptive unless path coefficient analysis is employed to discern possible direct and indirect effects. This was specially true for the case of the association between grain yield and harvest index where correlation value was high but only a small direct effect was shown by path coefficient analysis. A considerable portion of the association between harvest index and grain yield was the result of indirect effects via spikelets per spike.

6. Although no difference in the number of spikes per plant was found between the parents, both correlation and path coefficient analysis indicated that it could be an important factor to be considered when selecting for high grain yield among the F_2 population.

7. When the association of plant height and grain yield is

considered both the correlation value and the direct effect obtained from the path coefficient analysis were low. This suggests that short but high yielding plants could be selected within segregating populations.

8. Gain from selection estimate obtained for total grain yield suggests that direct selection for this trait could be effective.

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APPENDIX

Appendix Table 1. Mean and standard deviation values for 14 traits from non-segregating populations when grown at Hyslop Farm Research Station, 1986.

Variable	Stephens		Tibet dwarf		F1 generation	
	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Plant yield (gm./pl.)	57.676	30.134	20.696	7.9626	24.538	8.7567
Spikes/Plant	15.444	7.8793	17.357	4.7859	14.875	3.5172
Spikelets/Sp.	19.949	1.1260	18.088	1.4612	20.152	0.9866
Kernels/Spkt.	3.3003	0.2931	1.5457	0.3374	1.5328	0.3274
Kernel Wght. (gm.)	0.0567	0.0045	0.0423	0.0025	0.0531	0.0041
Height (cm.)	74.306	2.7131	22.500	2.5459	40.625	1.6801
Harvest Index (%)	44.353	2.4244	38.459	6.5486	32.489	6.4092
Fill. Period	37.25	5.739	48.89	2.250	48.50	2.000
Chaff (%)	14.54	2.333	24.87	6.650	25.74	4.062
Heading Date	144.0	5.986	123.0	1.915	125.9	1.458
Days Matur.	181.3	2.196	171.9	1.008	174.4	1.162
Length Sp. (cm.)	187.2	103.5	147.4	41.49	158.9	37.97
Tot. No. Krnls.	1016	516.2	489.1	189.4	461.1	156.3
Biol. Yield (gm.)	129.8	66.07	53.94	18.92	74.84	19.88

n: P1 = 36, n: P2 = 28, n: F1 = 32.

Appendix Table 1. (Continuation) Mean and standard deviation values for 14 traits from segregating populations when grown on the Hyslop Farm Research Station, 1986.

Variable	F2 generation		F3 generation		BC1		BC2	
	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
Plant yield (gm./pl.)	26.656	17.108	23.997	14.319	37.880	20.314	17.847	8.3239
Spikes/Plant	16.184	5.7497	14.966	4.7879	15.906	5.3946	16.691	5.1144
Spikelets/Sp.	19.244	2.2093	19.962	2.3331	19.968	1.7985	19.073	1.3828
Kernels/Spkt.	1.7410	0.7786	1.7314	0.7984	2.1990	0.7383	1.2466	0.5303
Kernel Wght. (gm.)	0.0485	0.0076	0.0477	0.0068	0.0527	0.0057	0.0466	0.0036
Height (cm.)	41.986	16.409	47.985	20.786	56.875	18.804	29.044	7.9296
Fill. Period	42.13	8.810	37.80	10.57	35.86	8.055	46.97	4.432
Harvest Index (%)	33.72	11.39	32.35	11.14	36.32	9.984	30.40	10.59
Chaff (%)	23.80	5.863	23.36	6.483	19.67	3.952	29.01	5.548
Heading Date	132.8	9.684	137.4	11.86	140.7	8.889	126.2	4.101
Days Matur.	174.9	2.301	175.2	2.840	176.6	2.436	173.2	1.716
Length Sp. (cm.)	161.8	61.35	149.7	49.96	174.6	58.44	160.3	51.58
No. Krnls.	549.0	351.7	503.3	293.4	719.3	381.4	380.1	173.1
Biol Yield. (gm.)	75.95	36.23	73.42	30.97	102.5	45.65	59.91	20.43

n: F2 = 76, n: F3 = 268, n: BC1 = 64, n: BC2 = 68.

Appendix Table 2. Matrix of phenotypic correlations among 14 traits measured on the progeny of a cross between two diverse wheat cultivars grown at Hyslop Farm Research Station, 1986.

Trait	2)	3)	4)	5)	6)	7)	8)
1) Plant Grain Yield	0.50991**	0.38884**	0.73816**	0.23878*	0.12946	0.66833**	-0.12480
2) Spikes/ Plant		-0.03902	-0.04795	0.04627	-0.14580	-0.05093	-0.10841
3) Spikelets/ Spike			0.35053**	-0.23228*	0.15670	0.14159	-0.40128**
4) Kernels/ Spikelet				0.03798	0.27118*	0.81387**	-0.08789
5) Kernel Weight					-0.01120	0.31605*	0.36005**
6) Plant Height						-0.09838	-0.03893
7) Harvest Index							0.04195

Trait	9)	10)	11)	12)	13)	14)
1) Plant Grain Yield	-0.47239**	0.14798	0.14495	0.66568**	0.96788**	0.86023**
2) Spikes/ Plant	0.15732	0.13705	0.16171	0.93951**	0.51895**	0.66533**
3) Spikelets/ Spike	-0.22493*	0.41108**	0.19374	0.12240	0.45366**	0.40485**
4) Kernels/ Spikelet	-0.70713**	0.08429	0.01827	0.11037	0.75166**	0.48127**
5) Kernel Weight	0.11738	-0.35679*	-0.12311	0.08505	0.00169	0.09502
6) Plant Height	-0.30182*	0.04114	0.02504	-0.07694	0.12523	0.31035*
7) Harvest Index	-0.58901**	-0.05943	-0.08951	0.14499	0.61824**	0.25659*
8) Filling Period	0.10290	-0.97345**	-0.26831*	-0.09540	-0.20767	-0.21867*
9) Chaff percentage		-0.06008	0.14110	0.05652	-0.45536**	-0.29144**
10) Heading Date			0.48170**	0.12964	0.22819*	0.25245*
11) Days to Maturity				0.18035	0.16529	0.22527*
12) Total Length Spikes					0.66240**	0.78283**
13) Total Kernel No.						0.85920**
14) Biological Yield						

* Significance at the 5% probability level
n: F₂ = 76

** Significance at the 1% probability level.

Appendix Table 3. Matrix of genetic correlations among 14 traits measured on the progeny of a cross between two diverse wheat cultivars grown at Hyslop Farm Research Station, 1986.

Trait	2)	3)	4)	5)	6)	7)	8)
1) Plant Grain Yield	0.429827	0.470258	0.754684	0.192182	0.147696	0.680133	-0.123810
2) Spikes/ Plant		-0.048540	-0.097190	0.121399	-0.199400	0.083026	-0.092770
3) Spikelets/ Spike			0.428493	-0.344880	0.176294	0.199308	-0.455150
4) Kernels/ Spikelet				-0.015480	0.304129	0.813496	-0.104630
5) Kernel Weight					-0.010240	0.206180	0.450651
6) Plant Height						-0.120240	-0.047200
7) Harvest Index							0.047532

Trait	9)	10)	11)	12)	13)	14)
1) Plant Grain Yield	-0.506610	0.170831	0.288579	0.630476	0.973227	0.861685
2) Spikes/ Plant	0.088301	0.157650	0.359150	0.921598	0.441132	0.539772
3) Spikelets/ Spike	-0.335140	0.453289	0.218852	0.132321	0.541894	0.479698
4) Kernels/ Spikelet	-0.750880	0.100815	0.033995	0.093075	0.764860	0.526270
5) Kernel Weight	0.191533	-0.420720	-0.081320	0.148805	-0.029390	0.129068
6) Plant Height	-0.421930	0.041576	0.047822	-0.115330	0.136834	0.366797
7) Harvest Index	-0.434220	-0.055070	-0.060150	0.198140	0.652141	0.291321
8) Filling Period	0.159911	-0.982000	-0.413860	-0.066890	-0.220720	-0.232770
9) Chaff percentage		-0.104790	0.185635	0.028430	-0.561230	-0.493300
10) Heading Date			0.578332	0.146400	0.254300	0.290035
11) Days to Maturity				0.416722	0.272377	0.392557
12) Total Head Length					0.625163	0.696503
13) Total Kernel No.						0.853045
14) Biological Yield						

n: F₁ = 32, n: F₂ = 76.

Appendix Table 4. Summary of meteorological data for Hyslop Farm Research Station, Corvallis Oregon, 1985-1986.

	Average temperature, °C			Radiation Langley	Evaporation mm.	Relative Humidity (%)
	Max.	Min.	Mean			
September	22.0	7.6	14.8	342	107.25	45.53
October	17.6	4.7	11.1	225	74.25	51.48
November	7.1	-0.2	3.4	111	-----	67.66
December	4.5	-3.6	0.4	117	-----	70.77
January	9.7	2.1	5.9	89	-----	77.00
February	10.0	3.0	6.5	133	-----	73.62
March	15.6	5.3	10.4	290	-----	58.12
April	15.1	4.1	9.6	381	73.50	51.53
May	18.7	6.9	12.8	496	94.00	52.58
June	25.2	10.6	17.9	578	155.50	49.13
July	24.6	10.0	17.3	547	166.00	48.87
August	30.6	11.3	20.9	516	203.20	41.72

Appendix Table 4. (Continued) Summary of meteorological data for
Hyslop Farm Research Station, Corvallis Oregon, 1985-1986.

	Average Precipitation		Number days with at least:		
	* Monthly (cm.) daily				
			0.25 cm.	1.25 cm.	2.50 cm.
September	1.98	12	3	0	
October	9.88	14	8	4	0
November	11.91	16	11	2	1
December	9.45	9	5	3	1
January	16.59	26	16	5	0
February	25.15	20	15	8	4
March	7.72	17	9	2	0
April	4.67	16	7	0	0
May	6.35	13	7	1	0
June	0.79	4	2	0	0
July	2.92	6	2	1	0
August	0.00	0	0	0	0

* = Number of days with measurable precipitation.