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Title: INHERITANCE AND ASSOCIATION OF EARLINESS AND GRAIN YIELD IN FOUR WINTER X SPRING WHEAT CROSSES (TRITICUM AESTIVUM L. EM THELL.)

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Parental and segregating populations derived from four winter x spring wheat crosses were investigated to obtain information concerning the inheritance and association of earliness, grain yield and yield-related traits. Feasibility of selecting in early generations for these characteristics was also evaluated. Four winter wheat cultivars (Hyslop, Yamhill, Bezostaia 1, and Sprague) and one spring wheat cultivar (Inia 66) were chosen on the basis of their relative maturity and contrasting agronomic characteristics. Parents, F_1's, F_2's, and reciprocal backcrosses to both parents were planted in the fall in a space-planted randomized complete block design. The two environmentally diverse locations selected were the Hyslop Agronomy Farm, Corvallis, Oregon (1000 mm of rainfall) and Sherman Experimental Station, Moro, Oregon (250 mm of rainfall). The effectiveness of early generation selection for the measured characteristics was evaluated by growing F_3 lines identified as the earliest 1% and the

highest yielding 1% of F_2 individuals in each cross. These were grown along with the parents, F_1's, BC_1's, BC_2's and F_2's under space-planted conditions at Hyslop Agronomy Farm. A study with the same populations was conducted by vernalizing and planting in the spring to gain further information on earliness.

Analyses of variance were conducted for all characteristics measured. Frequency distributions for days to heading of F_1, F_2, backcross generations and parents were examined. From the data collected, estimates of F_1-midparent deviations, degree of dominance, heritability in the narrow sense and genetic advance under selection were determined for each cross. The data were further analyzed by parent-progeny regression, correlation and path-coefficient analyses, polynomial and multiple regressions.

Partially dominant major genes, varying in number between one to five depending on the particular cross, appeared to influence heading date. Modifying factors also seemed to affect the date of heading. The gene action involved in the inheritance of earliness was primarily additive indicating that selection for earliness would be effective as early as the F_2 generation under both high and low rainfall conditions. Estimates of additive and nonadditive gene action suggested both were equally important in determining the yield components. Higher heritability estimates for the components of yield indicated that there was more genetic variability associated with the yield components than yield *per se*. Occurrence of additive genetic variation by location interaction implied that selection should be practiced simultaneously under different environments if wide adaptability of potential lines is desired. Since pronounced additive effect by year interactions occurred for the yield components, delayed selection for these traits may not be productive.

Positive correlations were obtained between yield and the number of days to heading when all generations were combined. However, in the F_2 generations, it appeared possible to select for the desired earliness with high yields as indicated by the low association between these two traits.

The path-coefficient analyses suggested that tiller number had the highest direct effect on grain yield. However, because of a negative association between tiller number and kernel weight, selection pressures would have to be balanced between these two components. In most cases, linear relationships existed between grain yield and seven measured traits, respectively. The result of regression analyses also showed that grain yield may be described best as a linear function of its components.

Inheritance and Association of Earliness and Grain Yield in Four Winter x Spring Wheat Crosses (*Triticum aestivum* L. em Thell.)

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Typed by Opal Grossnicklaus for Ahmet Ertug Firat

IN DEDICATION TO

my wife and my mother

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INTRODUCTION

Despite progress made in increasing cereal production, a world shortage of cereals will become more acute due to rapid increases in population. With only a limited amount of land remaining to be brought under cultivation, it is apparent that these additional increases must be obtained by increasing the amount of grain produced per hectare.

Many of the major wheat producing areas of the world are located in rainfed regions where the lack of moisture and frequent droughts are major limiting factors to increased production. In such regions, early maturity would be a desirable characteristic as a drought avoiding mechanism. Other advantages of early maturity would include avoiding such hazards as certain insect and disease problems and the hot winds which are frequently observed late in the growing season in some north African countries. Also cultivars which are earlier in maturity would be better adapted to multiple cropping systems. Therefore developing early maturing cultivars has been a major objective in many wheat breeding programs. Concerns have been expressed, however, as to how far breeders can go in selecting for earliness without sacrificing grain yield.

If earlier maturity is to be combined with satisfactory yield levels, then the plant breeder must have a wide range of genetic variability for these desirable characteristics. One approach to creating such genetic variability in wheat would be to utilize crosses between day-length insensitive spring cultivars and high yielding winter types. This approach of systematically transferring genetic material between winter and spring cultivars is proving successful for a number of agronomic characteristics in creating additional usable genetic variation.

It was the objective of this study to obtain information from selected crosses involving winter and spring wheat cultivars regarding: (1) the nature of inheritance of earliness, yield and yield-related characteristics; (2) the feasibility of selection in early generations for these traits, and; (3) the possible associations and inter-relationships among these traits as they might influence the amount of genetic gain which can be achieved in developing early and high yielding cultivars.

LITERATURE REVIEW

Significance of Earliness

Earliness in cereal grains is generally measured as the number of days to heading or anthesis or as physiological maturity which is determined by the moisture content of the grain. The type of earliness required will vary depending on the specific set of environmental conditions and cropping systems found for a given region. Where late frost occurs, as in the Klamath Basin of Oregon, it is desirable to have a prolonged vegetative period with a short period from heading to maturity. This is in contrast to the Willamette Valley of Oregon, where early heading followed by a long grain filling duration results in higher yields. Since earliness is a major objective in many breeding programs there has been a great deal of work conducted to gain a greater understanding of this characteristic.

Factors Related to Earliness

Several environmental factors are important in influencing the date of heading or maturity. The two most important factors involved are day-length or photoperiod and temperature or vernalization requirement.

Wheat cultivars differ in their response to both photoperiod and vernalization requirements with regard to the initiation of the reproductive stage of growth. There are those genotypes which require relatively long days and extended periods of low temperatures for vernalization. Others are day-length insensitive and require very little or no vernalization. In general, winter type wheats require both long days and a cold period for vernalization as prerequisites for the shoot meristem to shift from vegetative to floral differentiation. Spring wheat cultivars may also vary in their response to photoperiod; however, most require some vernalization before floral initiation will be induced.

Both photoperiodic and vernalization requirements are under genetic control and can be altered through selection. It is also apparent that there may be an interaction between temperature, photoperiod and genotype.

As defined in the text by Salisbury and Ross (1969), if flowering occurs at any daylength but more rapidly at long days, the plant is a quantitative or facultative long-day plant. In an absolute or qualitative long day plant, no flowering will occur when the days are shorter than a particular number of hours. For instance, in most winter wheat cultivars the period must be more than 12 hours. This is called the critical daylength. Critical night duration which is the period of darkness is an important factor in short day plants.

Jahnson (1953) and Gries _et al_. (1956) studied photoperiodic responses in winter and spring wheats. They observed an accelerating effect of increased daylength on time to maturity. Riddell *et al*. (1958), Riddell and Gries (1958a and 1958b) reported that greenhouse-grown spring wheat may be accelerated in its development by breaking the dark period by a brief period of illumination. Therefore, the light-to-darkness ratio was an important factor. The spring wheat cultivar, Chinese spring, was earlier under short-day, cool temperature conditions; whereas, the other spring wheat cultivar, White Federation 38, was earlier in a long-day, warm temperature environment. The development of winter wheat was accelerated by vernalization treatments of longer than 20 days.

Pinthus (1963) studied the inheritance of heading date in crosses between early by late cultivars of spring wheat. The parents did not show any response to vernalization when planted the end of April; thus, the time of spike initiation was determined solely by the response to daylength. He observed that early spike initiation was dominant to late. Also, a short period from initiation to heading was dominant. Spike initiation and the period from initiation to heading were found to be linked.

Levy and Peterson (1972) investigated whether a vernalization response existing among a diverse group of wheats which differed widely in maturity, origin and photoperiod response. They used spring, winter, semi-winter and durum wheat cultivars from Mexico, India, Chile, Colombia, Turkey, Italy, Canada, California, North

Dakota, Oklahoma and Russia. All spring cultivars, a semi-winter and a winter cultivar headed sooner if vernalized. The response in spring cultivars was small (2 or 3 days) with the exception of Pitic 62, which headed in 42.2 days when not vernalized and 26.2 days when vernalized. They concluded that response to vernalization of spring types appeared unrelated to earliness of maturity under field conditions. Without exception, all cultivars headed earlier with increasing photoperiods. Responses to vernalization and long day-lengths were quantitative, except in the winter cultivar, which had an absolute cold requirement at least 28 days and a quantitative response for additional cold period up to 56 days. This suggested that photo-period alone rather than vernalization appeared to be the primary factor controlling maturity in spring wheats.

In crosses between photoperiod-sensitive and insensitive spring cultivars Keim et al. (1973) provided evidence of a two-gene inheritance system with dominant epistasis present for insensitivity. Contrasting results were found by Klaimi and Qualset (1973) where F_1 and F_2 data indicated that daylength insensitivity was not always dominant over sensitivity and that two different major loci were responsible for this reaction. In both studies, genes with minor effects also influenced the photoperiodic response in a quantitative manner.

Environmental factors such as temperature, light intensity, humidity, soil moisture, soil nutrients, pesticides or herbicides all may influence plant growth and development. High temperature was found to favor rapid post-initiation as reported by Riddell and Gries (1958a). Under conditions of moist soil, high relative humidity and cloudy skies, the maturing period tends to be longer (Peterson, 1965). Delayed maturity also has been observed with increasing nitrogen levels in the soil (Bolton, 1977). Wiedman (1970) reported that some herbicides and pesticides such as 2, 4-D and DDT delayed maturity in wheat if used in optimum concentrations.

The delaying effects of certain cultural practices such as seeding dates and seeding rates on time of heading were reported by several investigators. Late planting dates may result in a delayed maturity (Pehlivanturk, 1976), and low seeding rates tended to stimulate vegetative growth and retard heading date (Guler, 1975).

Inheritance of Earliness

Several workers using different techniques have studied inheritance of earliness in spring, winter and spring x winter wheat crosses. These studies have produced conflicting results as to the nature of inheritance, number of segregating genes involved and heritability estimates. However, since heritability estimates depend on the method used, the generations and populations utulized, and the environmental conditions encountered during the experiments, different estimates would be expected. The results do suggest that a degree of dominance does exist in the inheritance pattern for earliness.

Stephens (1927) studied the inheritance of earliness in six spring wheat cultivars. His results indicated that the mean values of F_1 and F_2 populations were intermediate but skewed toward the early parent. The F_3 families showed all degrees of earliness within the limits of the parental cultivars. The data suggested that earliness was determined by the action of a number of independent multiple factors having cumulative effects.

Using a ten-parent diallel cross, Crumpacker and Allard (1962) investigated heading date involving reciprocal F_1 and F_2 populations. They found earliness to be either dominant or recessive depending on the cross. Few genes were found to be involved which had major effects. The remaining genetic variation was controlled by minor genes displaying little or no dominance. Relatively high heritability estimates (55, 67, and 74 percent) were obtained in three successive years. A similar study was conducted by Walton (1971), where additive genetic variance formed the major part of the total genetic variance present for days to heading, days to anthesis and days to grain filling. Dominance effects were also evident at the three stages of development.

Allard and Harding (1963) using two wheat cultivars, Ramona and Baart 46, suggested that the most of the variation in heading was governed by one gene pair in early generations. The later generations, F_4, F_6, and F_7, differed from the earlier generations with respect to the expected distributions with some families being much earlier than the early parent and others were much later than the late parent. They concluded that there was the masking effect in the early generations by the major gene on at least three, and probably many more genes.

Partial dominance for earliness in heading date was reported by Anwar and Chowdry (1969). Results from this study indicated that in four spring wheat crosses earliness was quantitatively inherited with the narrow-sense heritability values ranging from 23 to 37 percent. In contrast, Bhatt (1972) noted a minimum of one major factor being responsible for producing variation in heading date of two spring wheat crosses. Gene action estimates were primarily additive with narrow-sense heritability estimates ranging from 48 to 64 percent. Higher heritability values, some over 90 percent, were reported by Gandhi et al. (1964) in crosses involving spring wheats and Sidwell (1975) for segregating populations of winter wheat.

Fonseca and Patterson (1968) estimated heritabilities in the narrow-sense from the regression of F_1 and F_2 means on mid-parent values in a seven-parent diallel cross in winter wheat grown under different planting designs. The estimates were 87 and 78 percent in hilled planting for F_1's in successive years, and 82 and 80 in hilled and drilled plantings of F_2 populations, respectively.

Amaya et al. (1971) conducted an experiment to estimate genetic effects on heading date in durum cultivars which originated from Russia, Italy, and the USA. Means of the backcross populations were between the F_1 and recurrent parent mean values. Additive genetic effects were found to be important in the expression of heading date. Epistatic effects were signified in some crosses when analyzed under individual environments, but these effects were not detected when the data were combined over locations and years. Randomly selected F_3 lines for heading date significantly exceeded both parents in some crosses.

Edwards et al. and Ketata et al. (1976) found a significant deviation of the F_1 from mid-parent values indicating a sizeable amount of nonadditive gene action for heading date. However, the narrow-sense heritability values were also very high. Duplicate epistasis was detected suggesting problems would be encountered in selecting for earlier maturity in these crosses. Ketata et al. (1976) showed that heading date was controlled by additive and dominance effects implying more effective selection could be achieved in later generations.

A relatively low heritability (34 percent) was found by Abo-Alenein et al. (1967) for heading date in a spring x winter barley cross. Mean values for the F_1 and F_2 were skewed toward the late parent indicating partial dominance. Transgressive segregation beyond the late parent was also observed. These data suggested that at least two major factors, and perhaps some modifying factors were influencing heading date.

It would appear that earliness is influenced by both environmental and genetic factors. The nature of inheritance appears to be a function of the parental lines used in the crosses with the heritability estimates being greatly influenced by the environment and method of computing the values.

Components of Yield

The primary objective of most wheat breeding programs is to improve the grain yielding capacity. This improvement is dependent upon the amount of genetic variability available and the selection procedure applied. Kronstad and Foote (1964) warned that breeding for increased yielding ability by directly selecting for yield *per se* may limit future progress because of the complex nature of the trait. In recent years a great deal of interest has been paid to the components of yield as they are assumed to be less complex in their inheritance and less influenced by environmental variation.

Yield in small grains was described as a rectangular parallelepiped with edges X (the number of heads per unit area), Y (the number of kernels per head), and Z (the average kernel weight) by Grafius

(1956, 1964). Grain yield (W), the volume of this rectangular parallelepiped, is the product of the three components (XYZ). He emphasized that there was no way in which yield can be changed without changing one or more of the components. On the other hand, changes in X, Y, or Z may tend to counter balance each other in a homeostasis effect for yield. Hence, he concluded that all changes in the components need not be expressed in changes in yield, but all changes in yield must be accompanied by changes in one or more of the components. The geometrical concept of yield in small grain suggests that the greatest rate of change in volume is achieved by changes in the shortest edge. A question may exist whether it is better to select for one edge alone, or two, or three edges simultaneously in order to gain the greatest gain in volume or yield. Grafius and Wiebe (1959) also discussed expected genetic gain in yield in small grain and suggested that it would be better to concentrate on improving one edge alone when the expected genetic gain for the other two was low, but if these were high, it might be better to select for two, or even three edges at one time. Adams (1967) worked on yield component compensation in several crop species and found that increasing one yield component will not necessarily increase yield.

Heritability estimates for yield components in relation to the estimates for yield as an indication of genetic potential becomes very important when utilizing yield component breeding. Several workers have used different techniques for estimating the degree of heritability. Warner (1952) has provided a comprehensive review of the various methods of determining heritability.

Many investigators have found higher heritability estimates for the components of yield than for grain yield per se in wheat (Kronstad and Foote, 1964; Gandhi et al., 1964; Fonseca and Patterson, 1968; Ketata et al., 1976; Alexander, 1976).

In winter wheat crosses, a large range in narrow sense heritability estimates for grain yield has been reported. Intermediate values (0.26 to 0.34) were reported by Kronstad and Foote (1964), and Sidwell (1975); low values (-0.15 to 0.16) by Jahnson et al. (1966), Alexander (1976), and Ketata et al. (1976); high values (0.61 to 1.39) by Abi-Antoun (1977); low to high values (-0.16 to 0.68) by Daaloul (1974). In spring wheat crosses Anwar and Chowdry (1969) noted low to medium (0.12 to 0.41) heritability estimates.

Fonseca and Patterson (1968) calculated narrow sense heritability estimates from a seven-parent diallel using regression of F_1 or F_2 means on the mid-parent. The magnitude of their estimates ranged from 0.34 to 0.80 for spikes/930 cm^2, 0.47 to 0.89 for kernels/spike, 0.15 to 0.55 for kernel weight, and 0.17 to 0.49 for grain yield depending on the generation, year and type of planting designs, but the relative ranking did not change among the components with grain yield having the lowest heritability values in all cases.

Heritability estimates obtained for winter wheat by the regression of the F_1 on midparent in standard units was noted by Daaloul (1974) for the number of tillers to be medium (0.26 to 0.48), for kernel weight as medium to high (0144 to 0.90), for the number of kernels per spike as high (0.84 to 0.91) when the material was grown at three locations.

Sidwell (1975) reported that heritability estimates based on Warner's method, the single-rep selection method, and the regression method were relatively high (0.26 to 0.65) for kernel weight, while heritability estimates for the other two components were low to intermediate (0.05 to 0.39). Heritability estimates for grain yield ranged from 0.29 to 0.34. The study also indicated that nonadditive gene action was more pronounced than additive gene action for grain yield, tiller number, and kernels/spike; while additive and nonadditive gene action were about equally important for kernel weight.

Heritability in the narrow sense using Warner's method was estimated in a winter wheat cross for yield and its components by Ketata _et al_. (1976). Narrow sense heritability estimates for tiller number, kernels/spike, kernel weight, and grain yield were 0.36, 0.15, 0.65, and 0.16, respectively. Moreover, additive effects were the main source of genetic variation for kernel weight indicating that early generation selection for higher kernel weight should be effective in this material. Bhatt (1972) also reported high heritability estimates

(0.56 and 0.69) for kernel weight in two spring wheat crosses.

Three winter wheat populations were analyzed to provide information on heritabilities based on Warner's method by Alexander (1976). The result indicated medium values (0.26 to 0.42) for tiller number, low to medium values (0.01 to 0.38) for kernels per spike, low to high values (-0.02 to 0.54) for kernel weight, and low estimates (-0.15 to 0.09) for grain yield.

Heritability estimates greater than the theoretical limit as measured by Warner's method or parent-progeny regression were reported for yield and other agronomic traits by Daaloul (1972); Ketata et al. (1976) and Abi-Antoun (1977). They attributed this unrealistic situation to sampling errors, differential responses of the F_2 vs. the backcrosses to the environment, non-allelic interaction, and existence of non-genetic factors which resulted in an upward bias of the heritability estimates.

Association and Interrelationships among Agronomic Traits

Improvement of complex characters such as yield may be accomplished through the component approach to breeding. This method in general assumes strong associations between yield and a number of characters making up yield (Edwards et al., 1976). The existence of negative correlations among the yield components were attributed by Rasmusson and Cannel (1970) to a linkage of genes controlling the components. However, an alternative explanation based on an oscillatory response of components due to the sequential nature of component development and a limitation of environmental resources was proposed by Adams and Grafius (1971).

When using correlation coefficients to study possible relationship, it is of prime importance to recognize the nature of the population under consideration if the appropriate selection procedure is to be determined (Dewey and Lu, 1959). The separation of correlation coefficients into direct and indirect effects by path-coefficient analysis provides an effective means of understanding the associations and permits a critical examination of the specific forces acting to produce a given correlation. Thus a measure of the relative importance of each causal factor for each yield component can be obtained. Furthermore, it is apparent that many of the characteristics are correlated because of a mutual association, positive or negative, with other characters. As more variables are considered in the correlation table, these indirect associations become more complex, less obvious, and somewhat perplexing (Dewey and Lu, 1959).

Association among agronomic traits in wheat has been studied extensively, and contradictory results have been obtained. Earliness has been reported to be both negatively and positively associated with grain yield by Alim (1949); Gandhi _et al_. (1964), and Fonseca and Patterson (1968). Although, the magnitude of the correlation coefficients, however, were relatively low: +0.336, -0.131, and -0.288, respectively. In the latter study, early genotypes tended to have fewer tillers and higher kernel weights, but fewer kernels per head, and the direct effect of earliness on yield was very low (b' = +0.0012).

Positive correlations of different magnitudes between yield and yield components were found by several investigators (Gandhi et al., 1964; Fonseca and Patterson, 1968; Daaloul, 1974; Sidwell, 1975; and Abi-Antoun, 1977). The same investigators indicated that negative associations were observed among some yield components. Depending upon the populations and locations, certain yield components were more pronounced in having significantly higher associations and direct effects on yield. Sidwell (1975) found that tiller number had the largest correlation coefficient (r=0.68) and direct (b' = 0.84) influence on grain yield in a hard red winter wheat cultivar. Abi-Antoun (1977) reported that under non-competitive condition yield correlated significantly with fertility having high direct influence (r=0.93; b' = 0.85) and that there was a considerable lack of association between yield and tiller number (r=0.39 to r=0.31), and between yield and seed size (r=-0.25 to 4=0.38) under different environments for winter wheat.

It is apparent that if a plant breeder is to use the component approach to increasing grain yield that some evaluation of the relative direct and indirect association among the components must be identified for specific environments and different populations.

MATERIALS AND METHODS

Four winter wheat cultivars, Hyslop, Yamhill, Bezostaia 1 and Sprague, and one spring wheat cultivar, Inia 66, were utilized to study earliness and its relation to grain yield in winter x spring crosses conducted over two years in Oregon. The three soft white winter wheat cultivars, Hyslop, Yamhill and Sprague, are grown commercially in the Pacific Northwest. Bezostaia 1 is a hard red cultivar developed in Russia, and is being grown in Eastern Europe and some Near East countries. The spring cultivar, Inia 66, is very early, light insensitive and was developed in Mexico. These cultivars were selected on the basis of their relative earliness and contrasting ways of achieving grain yield. Detailed descriptions of parental cultivars are presented in Appendix Table 1.

The four winter wheat cultivars were each crossed reciprocally with the spring cultivar, Inia 66, to produce the F_1 generation. The F_2 generation, including reciprocals, was obtained from selfing the F_1 plants. One reciprocal of the F_2 population was missed in Sprague x Inia 66 cross because of limited F_1 seed. The remaining F_1 plants were then backcrossed to both their respective winter and spring parents to produce the first generation backcrosses, BC_1 and BC_2, respectively in the greenhouse. Three selected F_3 families in each cross were developed by selecting the earliest (E) 1% and the highest yielding (Y) 1% of selfed individuals from the F_2 population.

The parental lines, F_1's, F_2's, and the two first generation backcrosses, BC_1 and BC_2, of each cross were seeded at Hyslop Agronomy Farm, Corvallis, Oregon on October 13, 1975 and Sherman Experimental Station, Moro, Oregon on October 16, 1975.

The selected F_3 families, F_3 (E) and F_3 (Y), were included in the experimental material along with the other noted populations from each cross during the 1976-77 growing season. This material was planted at Hyslop Agronomy Farm, Corvallis, Oregon on October 11, 1976. The Bezostaia 1 x Inia 66, and Sprague x Inia 66 crosses could not be backcrossed to the spring side, thus, were missing from the experimental populations. Reciprocal crosses in F_1's and F_2's were not kept separate during the second year since consistent reciprocal differences were not observed during the first year. A parallel study using the same populations was also performed by vernalizing the same experimental materials and planting in the spring of 1977 at the Horticulture Farm, Corvallis, Oregon. In this parallel study, seeds were watered and artificially vernalized at 1 to 4^{o}C in the dark for a period of two months. The vernalized seeds of all generations were removed in trays and placed outside prior to transplanting. The seedlings were then transplanted from trays to the field on April 3, 1977.

The two locations selected, Hyslop Agronomy Farm near Corvallis, Oregon and Sherman Experimental Station located at Moro, Oregon represent two distinct environments with respect to soil and climatic conditions.

The soil type at Hyslop Agronomy Farm is a Woodburn silt loam. A preplant treatment of ammonium nitrate (34% N) was applied at the rate of 100 kg/ha; in addition, at the tillering stage the plots were top-dressed with 100 kg/ha urea (46% N). The precipitation at Corvallis was 953.1 mm and 479.1 mm during the 1975-76 and the 1976-77 growing seasons, respectively. The climatic pattern provides a very wet environment with mild winter temperatures for fall planted cereals.

Sherman Experimental Station, Moro, is a dryland location with wide temperature extremes. The soil type is classified as a Walla Walla silt loam which consists of a deep well drained and medium textured soil. A total of 226.0 mm of rainfall was recorded at this site during the growing season in 1975-76. Monthly distributions of precipitation and temperatures for both Corvallis and Moro are presented in Appendix Table 2. At Moro, 50 kg/ha of nitrogen in the form of ammonium nitrate (34% N) was applied prior to planting during the seedbed preparation. No additional fertilizer was used at this site.

The soil type at the Horticulture Farm, Corvallis, is a Chehalis silt loam. At this experimental site, 266 kg/ha nitrogen in the form of ammonium sulfate (21% N) was added to the soil before planting. The plots were irrigated throughout the growing season to avoid moisture stress.

At each location, the experimental materials resulting from four winter x spring wheat crosses were grown under space planted conditions in a randomized complete block design with three blocks. The land upon which the experiments were conducted had been in a summer-fallow rotation. To avoid possible phytotoxicity and delaying effects of the herbicides on maturity, weed control was done by hand.

In the 1975-76 growing season at both locations, Hyslop and Moro, individual plots consisted of one row for the parents, F_1's and BC's, and five rows for F_2's. The rows were 4 m long. In the 1976-77 growing season at Hyslop and the Horticulture Farm, nursery plots were composed of one row for the parents, F_1's, and F_3's, two rows for each BC, and three rows for each F_2 population. The row length was 2 m. The rows were spaced 30 cm apart and seeds were sown by hand to ensure accuracy in spacing of 20 cm within the row in all experiments. A semi-dwarf barley line (FB. 73-186) was planted around the experiments to avoid any border effect. Also, missing plants or where poor plant development occurred due to adverse environmental factors, seedlings of the barley line were transplanted to maintain uniformity of stand. All measurements for the following eight characters were collected on an individual plant basis:

Grain yield: total weight in grams of the clean seed from each plant was obtained.

Days to heading: number of days from April 11 to the date when the first spike fully emerged from flag-leaf sheath were recorded for each plant.

Days to maturity: Physiological maturity was considered to be the date when the first peduncle had ripened (yellow); i. e., the water content of the grain had decreased or no more reserve material had translocated from the stem and leaves. April 11 was also used as the starting date for the number of days to maturity.

Maturity duration: post anthesis duration was determined from the difference between days to maturity and days to heading.

Tiller number: number of seed-bearing heads were counted at harvest.

Unproductive tiller number: number of sterile or short semi-sterile tillers were counted just before harvest.

Kernel weight: the weight in grams of 100 randomly selected kernels was obtained.

Fertility: number of kernels per spike was calculated as:

$$\text{Fertility} = \frac{\text{Grain yield per plant (g)} \times 100}{\text{100 kernel wgt. (g)} \times \text{No. of tillers}}$$

Analysis of variance including all generations and crosses was used for each character over the years and locations to detect whether differences existed among entries (Snedecor and Cochran, 1967).

Entries were portioned into among and within crosses or generations including parents. Adjacent ranked mean values and planned comparisons were made for each character at each location and year utilizing LSD test of significance (Steel and Torrie, 1960).

Frequency distributions of heading date including parents and each generation were developed for each cross. Observed genetic ratios were examined for goodness of fit by using chi-square analysis (Briggs and Knowles, 1967).

The data for all characters from the three blocks were pooled to compute means, variances, heritability estimates and genetic advances under selection for each cross.

Pooled sample variance, an estimate of the population variance, was calculated by the following formula to eliminate variation among the blocks (Petersen, 1975):

$$s_p^2 = \frac{(n_1-1)\, s_1^2 + (n_2-1)\, s_2^2 + (n_3-1)\, s_3^2}{n_1 + n_2 + n_3 - 3}$$

where s_1^2, s_2^2, s_3^2, and n_1, n_2, n_3 are sample variances and number of samples within blocks, respectively.

Degree of dominance was estimated by using the formula suggested by Griffing (1949):

$$d = \frac{\overline{F}_1 - MP}{\overline{P}_1 - MP} \quad \text{where:}$$

d = degree of dominance

$\overline{F}_1$ = the mean of F_1 population

MP = mid-parent value

$\overline{P}_1$ = the mean of winter parent.

Heritability in the narrow sense, h^2_{ns}, was estimated for each character by Warner's method (Warner, 1952) as:

$$h^2_{ns} = [2V_{F_2} - (V_{BC_1} + V_{BC_2})]/V_{F_2}$$

where V_{F_2}, V_{BC_1}, and V_{BC_2} are the variances of the F_2, the backcross of the F_1 with the winter parent, and the backcross of the F_1 with the spring parent, respectively. The standard error of h^2_{ns}, SE, was computed as the square root of the variance of h^2_{ns}, $V(h^2_{ns})$ (Ketata et al., 1976).

$$V(h^2_{ns}) = \frac{2\left\{[(V_{BC_1} + V_{BC_2})^2/df_{F_2}] + (V_{BC_1}{}^2/df_{BC_1}) + (V_{BC_2}{}^2/df_{BC_2})\right\}}{V_{F_2}{}^2}$$

where df_{F_2}, df_{BC_1}, and df_{BC_2} refer to the degrees of freedom associated with V_{F_2}, V_{BC_1}, and V_{BC_2}, respectively. Significance of h^2_{ns} was also tested using the following test statistic (Ketata et al. (1976):

$$F = \frac{2V_{F_2}}{V_{BC_1} + V_{BC_2}}$$, with n_1 and n_2 degrees of freedom where

$n_1 = df_{F_2}$, and

$$n_2 = (V_{BC_1} + V_{BC_2})^2 / [(V_{BC_1}^2 / df_{BC_1}) + (V_{BC_2}^2 / df_{BC_2})].$$

Genetic gain under selection (G.S.) was predicted by substituting the narrow sense heritability value, h^2_{ns}, the phenotypic standard deviation in F_2 population, σ_p, and the selection differential in standard unit which is constant for certain selection pressure, k, to the equation:

$$G.S. = (k)\ (\sigma_p)\ (h^2_{ns})$$

which was explained by Allard (1960). Actual genetic advance was also determined by subtracting the F_2 mean from the corresponding selected F_3 family mean. Actual and expected genetic advances were expressed as a percentage of the mean.

Segregating minimum number loci involved in a trait, n, was estimated to support examination of the F_2 distribution. The formula:

$$n = \frac{(\overline{P}_1 - \overline{P}_2)^2}{8\ (V_{F_2} - V_{F_1})}$$

was suggested by Wright (1968). In this formula $\overline{P}_1$, $\overline{P}_2$, V_{F_2}, and

V_{F_1} refer to means of winter parent, spring parent, variances of F_2, and F_1 generations, respectively.

In addition to Warner's method, heritability estimates in the narrow sense were also obtained by using parent-progeny regression and standard unit procedures. F_1, F_2, or F_3 plot means were regressed on mid-parent values (Frey and Horner, 1957; Falconer, 1960). In this calculation, the plot means were obtained from the average of the reciprocals where they existed.

Simple phenotypic correlations among characters were computed from the plot means for parents, F_1's and F_2's individually, parents and F_1's together, and all generations together. The correlations were further partitioned into direct and indirect effects to determine interrelationships among agronomic traits. This path-coefficient analysis was described by Dewey and Lu (1959).

The final tests utilized were regression analyses (Draper and Smith, 1966; Neter and Wasserman, 1974). Polynomials were used to obtain regression equations of sucessively higher orders which describe yield per plant (y) as a function of one of the seven measured traits (x), individually. If the fitted equation was of a second order polynomial, the value of x (independent variable), at which y (dependent variable = grain yield per plant) was a maximum or minimum, was found as:

$$x_m = -b_1/2b_{11}$$

where b_1 and b_{11} are regression coefficients of the first order and second order terms, respectively.

In another regression analysis, the seven measured agronomic traits were partitioned into two classes, identified as earliness-related traits (heading, maturity and maturity duration), and yield-related traits (tiller, unproductive tiller, kernel weight, and fertility). Equations were fitted under extra sum of squares principle to describe grain yield per plant containing the earliness and yield components alone or together to judge what proportion of variation in grain yield was accounted for by each class.

Multiple regression analysis using stepwise regression procedure was also performed to select the best equation which describes the grain yield.

RESULTS AND DISCUSSION

Analysis of Variance

The results and discussion presented in this section were obtained by measuring eight agronomic traits involving the parents, F_1's and selected segregating populations. These experimental populations were grown for two years at the Hyslop Agronomy Farm, Corvallis (1976, 1977) and one year at the Sherman Experimental Station, Moro (1976). Data for heading date only were obtained in 1977 from a spring planting of the material grown on the Horticulture Farm.

Observed mean squares from the analysis of variance for eight measured traits involving the parents and all generations of the four crosses at three locations are presented in Tables 1 through 6. It may be noted from the tables that among all entries (treatments) highly significant differences were found for all measured traits at all sites and for both years at Hyslop. Since significant differences were observed among treatments, the data were further partitioned into among and within crosses or generations variances.

When parents and each winter x spring cross were considered as a group, there were highly significant differences among groups for each trait at each site with the exception of grain yield per plant at Moro (Tables 1, 2, and 3). Highly significant differences were

Table 1. Summary of observed mean squares from analysis of variance for eight measured characters involving parents and F_1, BC_1, BC_2, and F_2 generations of wheat cultivars grown on the Hyslop Agronomy Farm in 1976.

		Observed Mean Squares							
Source of Variation	D.F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Blocks	2	187.89**	25.68**	1.13	31.54**	29.19**	0.04	0.235**	39.58
Treatments	27	151.87**	139.75**	73.29**	23.25**	5.53**	0.69**	0.380**	214.83**
Among Groups	4	194.03**	375.42**	198.96**	64.23**	12.10**	1.53**	1.358**	632.22**
Within Groups	23	144.54**	98.76**	51.43**	16.12**	4.39*	0.55**	0.210**	142.24**
Within Parents	4	246.96**	334.85**	171.69**	37.15**	5.90*	0.60**	0.509**	304.63**
Within P_1xP_5 [1/]	5	224.55**	33.88**	10.59**	9.77**	10.62**	0.26	0.171**	63.77**
Within P_2xP_5	5	182.64**	77.56**	54.94**	4.82	2.25	0.49**	0.172**	254.51**
Within P_3xP_5	5	33.59	13.56**	7.03**	2.17	0.67	0.49**	0.073	74.03**
Within P_4xP_5	4	33.16	76.79**	33.36**	34.61**	2.40	0.99**	0.178**	22.87
Error	54	28.77	1.32	1.73	2.08	2.13	0.13	0.041	15.38
Total	83								

*Significant at the 5% level.

**Significant at the 1% level.

[1/] P_1 = Hyslop, P_2 = Yamhill, P_3 = Bezostaia I, P_4 = Sprague, P_5 = Inia 66.

Table 2. Summary of observed mean squares from analysis of variance for eight measured characters involving parents and F_1, BC_1, BC_2, and F_2 generations of wheat cultivars grown on the Sherman Experimental Station in 1976.

Source of Variation	D.F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
		Observed Mean Squares							
Blocks	2	246.00*	37.64**	15.18*	6.85	89.17**	0.23	0.066	35.40
Treatments	27	147.06**	75.96**	36.02**	13.36**	61.07**	1.04**	0.282**	89.01**
Among Groups	4	131.14	168.30**	72.68**	31.16**	68.20**	2.26**	0.648**	291.12**
Within Groups	23	149.83**	59.90**	29.64**	10.26**	59.83**	0.82*	0.219**	53.86**
Within Parents	4	273.76**	208.89**	84.61**	29.91**	181.26**	0.80	0.939**	196.54**
Within P_1xP_5 1/	5	223.47**	27.59**	12.00**	6.67	49.18**	0.50	0.057	23.82
Within P_2xP_5	5	96.77	51.17**	35.40**	12.09*	26.85	0.36	0.026	22.12
Within P_3xP_5	5	71.67	11.54	9.85*	2.39	7.57	1.14*	0.046	29.82
Within P_4xP_5	4	97.87	22.67**	14.28**	2.67	58.26**	1.42*	0.155**	18.44
Error	54	53.20	5.79	3.09	4.05	13.14	0.45	0.036	14.62
Total	83								

*Significant at the 5% level.

**Significant at the 1% level.

1/ P_1 = Hyslop, P_2 = Yamhill, P_3 = Bezostaia I, P_4 = Sprague, P_5 = Inia 66.

Table 3. Summary of observed mean squares from analysis of variance for eight measured characters involving parents and F_1, BC_1, BC_2, F_2, and F_3 generations of wheat cultivars grown on the Hyslop Agronomy and Horticulture Farms in 1977.

		Observed Mean Squares								
		Hyslop Agronomy Farm								Horticulture Farm
Source of Variation	D. F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading 1/
Blocks	2	59.90	13.03**	26.91**	3.49	0.54	3.63**	0.062	232.62**	7.28*
Treatments	42	235.55**	225.28**	64.36**	63.16**	18.36**	1.85**	0.427**	174.50**	136.43**
Among Groups	4	764.70**	676.48**	216.56**	146.60**	38.95**	1.42**	1.318**	891.34**	350.92**
Within Groups	38	179.85**	177.79**	48.34**	54.38**	16.19**	1.90**	0.333**	88.52**	113.85**
Within Parents	4	688.22**	513.45**	127.98**	144.92**	50.37**	4.94**	1.444**	184.68**	382.72**
Within $P_1 x P_5$ 2/	9	180.17**	300.43**	84.20**	80.91**	15.58**	1.18**	0.074*	73.30**	191.46**
Within $P_2 x P_5$	9	90.28**	100.82**	28.85**	32.44**	6.01**	1.61**	0.113**	70.01**	55.87**
Within $P_3 x P_5$	8	60.05*	62.51**	6.17**	43.68**	7.78**	2.78**	0.286**	76.89**	30.55**
Within $P_4 x P_5$	8	145.87**	73.84**	32.27**	14.63**	19.66**	0.62	0.365**	90.00**	40.64**
Error	84	22.34	2.13	1.28	1.82	1.84	0.52	0.033	16.24	1.72
Total	128									

*Significant at the 5% level.

**Significant at the 1% level.

1/ Vernalized and spring planted.

2/ P_1 = Hyslop, P_2 = Yamhill, P_3 = Bezostaia I, P_4 = Sprague, P_5 = Inia 66.

also detected within groups for each trait at all locations indicating that generations within each of the four crosses differed significantly at the 1% level from each other.

Differences within parents were fairly consistent at the 1% level for the expression of grain yield per plant, heading and maturity dates, maturity duration, tiller number, unproductive tiller number, kernel weight, and fertility. Tiller number and unproductive tiller number were the two exceptions. The former was only significant at the 5% level under low rainfall conditions of Moro (Table 2), and the latter was nonsignificant in the first year; although, highly significant in the second year at Hyslop (Tables 1 and 3).

When the four winter x spring wheat crosses were examined separately, different responses were obtained depending on the trait between locations and years (Tables 1, 2, and 3). Significant differences for most traits were noted; however, there were several exceptions. No difference was observed for days to heading at Moro for the cross $P_3 \times P_5$ (Table 2). This lack of significance within $P_3 \times P_5$ for days to heading was likely the result of the relative similarity of the parents for this trait and perhaps late moisture stress. Although highly significant differences for fertility were noted for most crosses for years and locations, $P_4 \times P_5$ was the exception as no significant differences were detected at Moro (Table 2). This failure to detect significant differences for some traits among generations within each individual cross might be attributed to experimental error or genotype by location and genotype by year interactions.

When the total variation among treatments for the experimental population was partitioned into the observed mean squares among and within generations, highly significant differences among generations were observed for all measured traits at Hyslop (Tables 4, 5, and 6). Also significant differences among generations for all traits were found for both years and locations, with the exception of kernel weight at Moro. Highly significant differences within generations were consistent for all traits over locations and years with the exception of grain yield at Moro where the differences were significant at the 5% level.

Significant differences among genotypes within each generation, F_1, BC_1, BC_2, F_2, and F_3, considering traits and sites were not consistent. The lack of significant difference was more pronounced under low rainfall conditions at Moro. Further, failure to detect significant differences between locations were more evident than that encountered over years.

Of particular interest was the greater differences noted when the F_1's were crossed to the winter parent rather than the spring cultivar for most of the traits measured (Tables 4, 5, and 6).

In Tables 8, 9, and 10 the mean values for the parents and each generation involving the four crosses and eight measured

Table 4. Summary of observed mean squares from analysis of variance for eight measured characters involving four winter x spring wheat crosses grown on the Hyslop Agronomy Farm in 1976.

		Observed Mean Squares							
Source of Variation	D. F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Blocks	2	187.89**	25.68**	1.13	31.54**	29.19**	0.04	0.235**	39.58
Treatments	27	151.87**	139.75**	73.29**	23.25**	5.53**	0.69**	0.380**	214.83**
Among Generations	4	280.16**	471.92**	170.88**	84.89**	8.23**	2.19**	0.385**	322.24**
Within Generations	23	129.56**	81.98**	56.32**	12.53**	5.06**	0.43**	0.379**	196.15**
Within Parents	4	246.96**	334.85**	171.69**	37.15**	5.90*	0.60**	0.509**	304.63**
Within F_1's	7	68.91*	14.44**	39.90**	12.03**	2.50	0.72**	0.316**	128.91**
Within BC_1's 1/	3	455.68**	76.15**	62.30**	5.11	15.03**	0.61**	0.583**	619.25**
Within BC_2's 2/	3	15.54	3.99*	4.51	0.829	3.65	0.22	0.291**	49.44*
Within F_2's	6	16.00	34.11**	21.47**	6.26*	3.21	0.03	0.308**	64.08**
Error	54	28.77	1.32	1.73	2.08	2.13	0.18	0.041	15.38
Total	83								

*Significant at the 5% level.

**Significant at the 1% level.

1/ $BC_1 = F_1$ x winter parent.

2/ $BC_2 = F_1$ x spring parent.

Table 5. Summary of observed mean squares from analysis of variance for eight measured characters involving four winter x spring wheat crosses grown on the Sherman Experimental Station in 1976.

		Observed Mean Squares							
Source of Variation	D.F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Blocks	2	246.00*	37.64**	15.18*	6.85	89.17**	0.23	0.066	35.40
Treatments	27	147.06**	75.96**	36.02**	13.36**	61.07**	1.04**	0.282**	89.01**
Among Generations	4	447.61**	162.47**	69.18**	36.70**	136.98**	1.02*	0.055	95.36**
Within Generations	23	94.79*	60.92**	30.25**	9.30**	47.87**	1.04**	0.322**	87.91**
Within Parents	4	273.76**	208.89**	84.61**	29.91**	181.26**	0.80	0.[illegible]39**	196.54**
Within F_1's	7	75.26	27.05**	26.96**	2.35	24.23	0.33	0.097*	77.91**
Within BC_1's 1/	3	113.98	58.08**	17.07**	15.47*	18.87	3.66**	0.431**	94.60**
Within BC_2's 2/	3	35.11	12.14	5.79	2.76	6.80	0.58	0.132*	59.38*
Within F_2's	6	18.51	27.58**	16.68**	3.86	21.55	0.94*	0.212**	38.06*
Error	54	53.20	5.79	3.09	4.05	13.14	0.45	0.036	14.62
Total	83								

*Significant at the 5% level.

**Significant at the 1% level.

1/ $BC_1 = F_1$ x winter parent.

2/ $BC_2 = F_1$ x spring parent.

Table 6. Summary of observed mean squares from analysis of variance for eight measured characters involving four winter x spring wheat crosses grown on the Hyslop Agronomy and Horticulture Farms in 1977.

		Observed Mean Squares Hyslop Agronomy Farm								Horticulture Farm
Source of Variation	D. F.	Yield	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading[1/]
Blocks	2	59.90	13.03**	26.91**	3.49	0.54	3.63**	0.062	232.62**	7.28**
Treatments	42	235.55**	225.28**	64.36**	63.16**	18.36**	1.85**	0.427**	174.50**	136.43**
Among Generations	6	320.16**	657.43**	193.35**	154.23**	29.75**	2.92**	0.253**	245.57**	347.37**
Within Generations	36	221.45**	153.26**	42.86**	47.98**	16.46**	1.67**	0.456**	162.66**	101.27**
Within Parents	4	688.22**	513.45**	127.98**	144.92**	50.37**	4.94**	1.444**	184.68**	382.72**
Within F_1's	3	85.83*	57.38**	11.61**	18.07**	1.67	2.20**	0.251**	164.49**	18.43**
Within BC_1's[2/]	3	69.39*	74.35**	39.40**	10.88**	16.51**	0.37	0.641**	137.70**	39.81**
Within BC_2's[3/]	1	2.16	49.88**	0.38	41.61**	0.96	0.03	0.104	21.66	26.04**
Within F_2's	3	114.33**	14.61**	1.18	8.90**	4.41	0.29	0.159**	139.57**	22.91**
Within F_3(E)'s[4/]	11	199.55**	75.40**	15.32**	37.04**	18.04**	0.74	0.301**	221.31**	26.63**
Within F_3(Y)'s[5/]	11	201.22**	195.01**	64.15**	53.19**	11.27**	2.16**	0.370**	121.41**	141.14**
Error	84	22.34	2.13	1.28	1.82	1.84	0.32	0.033	16.24	1.72
Total	128									

*Significant at the 5% level.

**Significant at the 1% level.

1/ Vernalized and spring planted.

2/ $BC_1 = F_1$ x winter parent.

3/ $BC_2 = F_1$ x spring parent.

4/ F_3 families selected for earliness.

5/ F_3 families selected for yield.

Table 7. Mean values for eight measured characters involving parents and F_1, BC_1, BC_2, and F_2 generations of wheat cultivars grown on the Hyslop Agronomy Farm in 1976.

Parents and Generations		Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
P	Hyslop (P_1)	34.9	44.6	90.3	45.9	12.4	0.15	4.72	57.7
	Yamhill (P_2)	40.1	50.5	97.0	46.4	10.8	0.24	5.19	70.9
	Bezostaia I (P_3)	28.3	37.9	84.4	46.6	9.3	0.17	5.00	58.8
	Sprague (P_4)	19.6	47.7	94.5	46.8	9.9	0.63	4.10	48.9
	Inia 66 (P_5)	19.8	24.0	78.4	54.2	8.9	1.20	4.82	44.9
F_1	P_1xP_5	35.9	29.9	81.7	51.7	10.5	0.54	5.05	64.5
	P_5xP_1	27.9	29.4	80.7	51.3	8.5	0.53	5 09	62.6
	P_2xP_5	33.3	31.7	85.6	54.0	8.8	0.73	5.27	71.8
	P_5xP_2	35.3	34.0	87.7	53.7	9.0	1.07	5.36	70.1
	P_3xP_5	30.0	28.0	79.7	51.7	9.4	1.17	5.28	61.2
	P_5xP_3	26.2	27.7	79.5	51.8	8.3	0.64	5.08	62.1
	P_4xP_5	28.1	30.7	87.5	57.1	10.8	1.86	4.67	53.8
	P_5xP_4	22.0	32.7	87.2	54.6	9.0	1.52	4.42	53.8
BC_1	$P_1(P_1xP_5)$	47.7	35.8	85.3	49.7	13.4	0.13	5.30	66.9
	$P_2(P_2xP_5)$	40.7	43.0	93.7	50.6	9.3	1.15	5.27	82.4
	$P_3(P_3xP_5)$	31.8	31.4	83.1	51.7	8.9	0.80	5.02	69.8
	$P_4(P_4xP_5)$	19.2	39.8	88.4	48.6	8.7	1.01	4.35	47.7
BC_2	$(P_1xP_5)P_5$	25.5	27.0	81.6	54.2	8.2	0.77	5.16	58.7
	$(P_2xP_5)P_5$	20.1	27.6	80.5	53.0	6.9	0.54	4.91	56.0
	$(P_3xP_5)P_5$	23.8	24.9	78.6	53.7	8.3	1.05	4.99	57.1
	$(P_4xP_5)P_5$	22.8	26.2	80.1	53.9	9.6	1.13	4.44	49.5

Table 7. (Continued)

Parents and Generations		Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
F_2	P_1xP_5	27.7	34.6	83.6	49.1	10.4	0.05	4.76	55.1
	P_5xP_1	26.2	30.1	80.9	50.7	9.7	0.10	4.68	56.8
	P_2xP_5	25.5	33.8	85.5	51.7	8.1	0.27	4.87	63.3
	P_5xP_2	24.3	33.0	85.5	52.6	7.9	0.18	4.83	62.4
	P_3xP_5	27.2	28.2	80.7	52.5	9.3	0.16	4.93	59.0
	P_5xP_3	23.3	26.7	79.9	53.1	8.7	0.29	4.82	55.9
	P_5xP_4	21.1	35.4	86.3	50.4	10.4	0.34	3.99	49.7
Coefficient of Variation (%)		19.1	3.5	1.6	2.8	15.5	54.0	4.1	6.6
$LSD_{.05}$		8.8	1.9	2.2	2.4	2.4	0.58	0.33	6.4
$LSD_{.01}$		11.7	2.5	2.9	3.1	3.2	0.77	0.44	8.6

Table 8. Mean values for eight measured characters involving parents and F_1, BC_1, BC_2, and F_2 generations of wheat cultivars grown on the Sherman Experimental Station in 1976.

Parents and Generations		Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
P	Hyslop (P_1)	26.6	58.4	96.6	38.2	17.5	0.96	3.68	41.5
	Yamhill (P_2)	33.7	63.7	101.6	37.8	17.0	0.43	3.97	47.9
	Bezostaia I (P_3)	25.5	51.5	93.1	41.5	13.3	0.45	4.41	43.0
	Sprague (P_4)	25.7	59.1	97.1	38.0	27.8	1.68	3.02	29.7
	Inia 66 (P_5)	7.9	42.3	87.3	45.0	6.3	1.11	4.30	30.3
F_1	P_1xP_5	32.9	49.2	92.3	43.0	19.1	1.42	4.08	40.9
	P_5xP_1	20.8	52.4	95.6	43.2	14.0	1.17	4.09	37.1
	P_2xP_5	21.6	55.0	98.6	43.7	13.5	1.03	3.77	39.6
	P_5xP_2	23.7	53.2	96.3	43.2	14.3	1.02	4.01	40.2
	P_3xP_5	22.8	46.6	90.8	44.0	13.0	0.88	4.21	39.4
	P_5xP_3	17.6	47.6	89.6	42.0	10.6	0.71	4.19	42.0
	P_4xP_5	16.4	48.6	92.8	44.2	14.5	1.02	3.76	29.1
	P_5xP_4	21.5	48.3	93.3	44.9	18.6	1.78	3.86	29.4
BC_1	$P_1(P_1xP_5)$	33.5	55.8	96.1	40.3	19.0	0.99	3.80	42.3
	$P_2(P_2xP_5)$	24.8	60.9	99.2	38.3	13.3	0.26	3.87	46.8
	$P_3(P_3xP_5)$	29.7	50.3	93.4	43.1	14.1	1.41	4.38	47.2
	$P_4(P_4xP_5)$	19.2	54.2	97.0	42.8	15.4	2.88	3.46	35.1
BC_2	$(P_1xP_5)P_5$	10.8	48.6	91.1	42.5	8.3	1.49	3.86	34.5
	$(P_2xP_5)P_5$	9.3	48.0	89.7	41.9	6.1	1.17	3.83	40.0
	$(P_3xP_5)P_5$	15.7	44.2	88.3	44.1	9.8	2.19	4.23	38.0
	$(P_4xP_5)P_5$	7.8	47.9	91.3	43.4	8.0	1.43	3.76	29.8

Table 8. (Continued)

Parents and Generations		Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
F_2	P_1xP_5	20.8	51.5	93.5	42.0	13.6	0.51	3.86	39.0
	P_5xP_1	26.8	47.6	92.4	44.8	16.0	1.62	4.09	40.1
	P_2xP_5	19.3	53.6	95.4	41.9	12.0	0.53	3.83	40.7
	P_5xP_2	22.6	54.4	97.5	43.4	12.8	0.85	3.99	41.3
	P_3xP_5	20.3	47.2	90.4	43.2	12.0	0.46	4.06	40.9
	P_5xP_3	20.5	47.6	92.0	44.5	11.8	1.09	4.04	41.0
	P_5xP_4	21.5	51.8	94.9	42.8	19.0	1.84	3.19	31.3
Coefficient of Variation (%)		34.0	4.7	1.9	4.7	26.0	57.7	4.8	9.9
$LSD_{.05}$		11.9	3.9	2.9	3.3	5.9	1.09	0.31	6.3
$LSD_{.01}$		15.9	5.2	3.8	4.4	7.9	1.46	0.41	8.3

Table 9. Mean values for eight measured characters involving parents and F_1, BC_1, BC_2, F_2, and F_3 generations of wheat cultivars grown on the Hyslop Agronomy and Horticulture Farms in 1977.

Parents and Generations			Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading[1/] (from Apr. 11)
			Hyslop Agronomy Farm								Horticulture Farm
P	Hyslop	(P_1)	57.3	43.3	90.2	46.9	19.8	0.07	4.66	61.9	67.1
	Yamhill	(P_2)	41.4	50.7	93.5	42.8	12.8	0.11	5.46	58.6	70.1
	Bezostaia I	(P_3)	28.1	37.7	83.9	46.1	10.5	0.09	5.17	51.1	57.0
	Sprague	(P_4)	21.7	47.5	92.3	44.8	14.2	1.15	3.63	41.8	64.2
	Inia 66	(P_5)	22.4	17.6	77.9	60.3	9.3	3.04	4.73	50.3	41.8
F_1	P_1xP_5		41.2	24.3	79.1	54 8	12.7	1.07	5.05	63.7	52.8
	P_2xP_5		43.2	32.0	82.2	50.2	11.7	1.72	5.39	68.4	52.9
	P_3xP_5		38.3	21.8	76.6	55.8	11.0	2.15	5.28	66.4	47.6
	P_4xP_5		31.0	27.2	80.7	53.5	12.4	0.18	4.74	51.8	51.7
BC_1	$P_1(P_1xP_5)$		40.5	39.9	84.8	44.9	16.5	0.09	4.61	51.8	62.4
	$P_2(P_2xP_5)$		40.2	41.7	87.2	45.6	12.2	0.37	5.06	62.0	61.5
	$P_3(P_3xP_5)$		35.2	30.5	79.5	48.9	12.0	0.65	5.06	56.9	54.3
	$P_4(P_4xP_5)$		30.4	39.2	87.1	47.8	15.8	0.90	4.09	46.2	59.7
BC_2	$(P_1xP_5)P_5$		28.6	18.1	78.0	59.9	10.9	2.04	4.84	53.3	46.4
	$(P_2xP_5)P_5$		29.8	23.9	78.5	54.6	10.1	2.17	5.11	57.1	50.6
F_2	P_1xP_5		43.9	26.6	79.7	53.1	15.5	0.40	4.78	60.6	55.1
	P_2xP_5		37.9	31.5	81.2	49.7	12.6	0.30	5.04	57.6	56.6
	P_3xP_5		37.5	27.2	80.6	53.4	14.4	0.84	4.71	54.4	52.1
	P_4xP_5		28.9	28.8	80.3	51.5	13.8	0.93	4.48	44.8	50.5

Table 9. (Continued)

			Hyslop Agronomy Farm							Horticulture Farm
Parents and Generations		Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading (from Apr. 11)
F_3	(E-1)[2/] P_1xP_5	46.3	26.1	79.3	53.2	16.9	0.25	4.86	56.0	52.6
	(E-2) P_1xP_5	35.8	23.2	77.4	54.2	13.8	0.08	4.73	55.2	49.4
	(E-3) P_1xP_5	31.9	21.4	79.2	57.8	13.4	1.[illegible]	4.74	49.9	50.3
	(E-1) P_2xP_5	38.6	27.3	81.4	54.1	12.4	1.15	4.81	62.0	52.9
	(E-2) P_2xP_5	37.3	31.8	81.9	50.1	11.9	1.26	5.14	59.0	55.3
	(E-3) P_2xP_5	31.4	35.6	83.0	47.4	12.4	0.48	4.92	50.0	54.3
	(E-1) P_3xP_5	27.0	19.8	76.8	57.0	10.6	1.69	5.29	47.5	47.0
	(E-2) P_3xP_5	29.4	17.6	77.2	59.6	9.8	0.75	5.21	57.7	45.8
	(E-3) P_3xP_5	27.5	24.2	78.5	54.3	10.5	0.78	4.45	56.4	49.1
	(E-1) P_4xP_5	31.9	27.3	79.3	51.9	17.0	0.95	4.75	39.0	51.1
	(E-2) P_4xP_5	16.6	26.6	76.3	49.8	9.8	1.37	4.23	37.7	47.4
	(E-3) P_4xP_5	19.2	23.0	77.1	54.2	11.3	1.50	4.49	37.8	51.6

Table 9. (Continued)

Parents and Generations	Yield (per plant)	Days to Heading (from Apr. 11)	Days to Maturity (from Apr. 11)	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading (from Apr. 11)
	Hyslop Agronomy Farm								Horticulture Farm
F_3 (Y-1)[3/] P_1xP_5	53.6	45.0	90.9	45.5	18.1	0.33	4.71	62.1	69.3
(Y-2) P_1xP_5	46.6	36.8	86.2	49.4	14.9	0.44	4.98	61.5	61.2
(Y-3) P_1xP_5	48.5	44.6	90.5	45.9	17.2	0.29	4.53	61.8	68.1
(Y-1) P_2xP_5	40.6	41.3	89.3	48.0	13.1	0.12	4.84	63.8	63.8
(Y-2) P_2xP_5	44.8	35.5	82.2	46.7	14.1	0.32	5.17	60.8	60.1
(Y-3) P_2xP_5	47.3	38.9	83.8	44.9	15.4	0.07	5.35	58.4	59.6
(Y-1) P_3xP_5	37.8	22.9	80.8	57.9	13.0	0.38	5.05	57.8	51.3
(Y-2) P_3xP_5	31.4	22.8	78.2	55.4	12.2	3.18	4.78	53.7	50.5
(Y-3) P_3xP_5	34.3	30.9	79.3	48.4	14.0	0.27	4.61	52.8	54.7
(Y-1) P_4xP_5	39.1	30.2	81.9	51.7	14.6	0.22	5.12	51.6	53.2
(Y-2) P_4xP_5	33.1	32.1	82.5	50.4	17.2	0.62	4.04	47.8	55.2
(Y-3) P_4xP_5	25.9	23.1	77.9	54.7	12.6	0.60	4.62	43.8	48.3
Coefficient of Variation (%)	13.2	4.8	1.4	2.6	10.1	85.9	3.8	7.4	2.4
$LSD_{.05}$	7.7	2.4	1.8	2.2	2.2	1.17	0.30	6.5	2.1
$LSD_{.01}$	10.2	3.1	2.4	2.9	2.9	1.55	0.39	8.7	2.8

1/ Vernalized and spring planted.

2/ F_3 families selected for earliness.

3/ F_3 families selected for yield.

characters are presented for each experimental site.

Inia 66, the spring cultivar, was significantly different for at least one trait when contrasted with the winter parents, Hyslop, Yamhill, Bezostaia 1, and Sprague. Performances of parental lines for each trait depended on the cultivar and location. At the Hyslop site, the cultivar Hyslop was higher for grain yield and fertility in 1977 and number of tillers per plant for both years; Yamhill for grain yield and fertility in 1976, and for lateness of heading and maturity and 100 kernel weight in both years; Inia 66 for earliness of heading and maturity, maturity duration and unproductive tiller number (Tables 7 and 9). For Moro, it can be observed that Hyslop was higher in tiller number; Yamhill had the highest yield per plant, was later in heading and maturity and higher for fertility; Bezostaia 1 was the highest for 100 kernel weight; Sprague ranked first for unproductive tiller number; Inia 66 was earlier for heading and maturity and had the longest maturity duration (Table 8).

When reciprocal crosses were compared at either location or between years, highly significant differences were found in certain cases such as the F_1 of the $P_1 \times P_5$ cross for grain yield, the F_1 of the $P_2 \times P_5$ cross and the F_2 of the $P_1 \times P_5$ cross for heading date at Hyslop (Table 7). However, no reciprocal differences were observed when the respective F_1 and F_2 mean values were compared, indicating that maternal inheritance was not involved for any of the traits measured. Due to the lack of consistent differences between generations and locations for these crosses it is felt that sampling error or possible genotype x environment interactions were responsible for the few differences noted and not maternal inheritance.

In most cases, mean values of BC_1's, when the winter cultivars were used as the recurrent parent, exceeded their corresponding parent and F_1 means in yield and yield components at the Hyslop and Moro sites in 1976 (Tables 7 and 8). The apparent superiority of BC_1's over the parents and F_1's could be attributed to inadequate sample size of the backcross population. This advantage of the BC_1's over the F_1 and highest parent also may be the result of some hybrid vigor plus the favorable combination or accumulation of yield genes.

The earliest cross with regard to heading and maturity dates was $P_3 \times P_5$, while $P_2 \times P_5$ was the latest cross at both experimental sites. In general, the mean values of the progeny reflected the relative heading or maturity of their respective winter parent with crosses involving P_3 being the earliest and those with P_4 the latest.

Within the BC_1's, highly significant differences were observed for days to heading and maturity at all sites. Genotypes within BC_2 differed for heading date at the 5% and 1% levels at the Hyslop site in both 1976 and 1977. No significant differences were found at the Moro site. However, very large differences for both days to heading and maturity were detected between BC_1's and BC_2's. At the Hyslop site in 1976 the mean value of the backcross to winter parent, $P_2 (P_2 \times P_5)$, for heading date was 43.0 days; whereas, the value of the backcross to the spring parent in the same cross $(P_2 \times P_5)P_5$, was 27.6 days. Similar results were obtained in the other crosses at both the Hyslop and Moro sites.

The differences in heading date between BC_1's and BC_2's can be further illustrated in Figures 1 to 4 for each of the four crosses. These results suggest that earliness can be fixed by backcrossing to an early parent.

In all four winter x spring wheat crosses, including parents, early genotypes for days to heading also tended to be earlier for days to maturity at both sites. Maturity duration, days between physiological maturity and heading dates, was much longer in early genotypes than late genotypes. This duration was increased under high rainfall environment at Hyslop. Under low rainfall conditions at the Moro site, maturity duration was shorter because of the influences of drought on the maturity date. The expression of duration of the grain filling period was also changed a few days during the second year at the Hyslop site; however, the differences were not as pronounced as between high and low rainfall conditions (Tables 7, 8, and 9).

Coefficients of variation were calculated for each analysis of variance (Tables 7, 8, and 9). In general, higher C.V. values were found at the Moro site than those observed at Hyslop. Usually the highest C.V. was noted for the unproductive tiller number followed by grain yield and tiller number at both locations. Coefficient of variation values were calculated to be 19.1, 34.0, and 13.2 percent for yield per plant; 54.0, 57.7, and 85.9 percent for unproductive tiller number at Hyslop, 1976; Moro, 1976; and Hyslop, 1977, respectively. Close agreement of high C.V. values for the same traits over years and locations indicated that the environment influenced these two traits more than did sampling error. The lowest C.V. values were observed for days to maturity at all sites.

Another aspect of this study was to investigate the response of heading date to different growing season associated with longer day-length. Thus, the same set of material of 1977 experiment was artificially vernalized, and transplanted to the field at the Horticulture Farm on April 3rd. After induction of the growing points from vegetative to floral, experimental plants were exposed to long days which were 12 hours 58 minutes at transplanting time in Corvallis. Significant differences among populations, among and within crosses and generations, were observed (Tables 3 and 6). When plot means of fall and spring planted materials were correlated, correlation coefficients were found to be 0.973**; 0.953**; and 0.935**, between parents; parents and F_1's; and for all treatments together, respectively (Appendix Table 3). Correlation coefficient between the two F_2 populations was low, 0.339, and nonsignificant implying existence of variability in response to season, photoperiod or vernalization. Furthermore, when compared to the fall planted experiment, there existed a reversal in the ranking of means within parents and crosses (Table 9). When planted in the fall, two winter parents, Hyslop and Sprague, ranked third and fourth days to heading for earliness at the Hyslop and Moro locations in both years. The difference between these two winter parents was highly significant at the 1% level when adjacent means were ranked using LSD test. Their crosses with Inia 66, ($P_1 \times P_5$ and $P_4 \times P_5$) followed a similar pattern in each generation. The two crosses including their winter parents responded differently to long days after vernalization when planted in the spring. Sprague became earlier than Hyslop with the difference being highly significant. The same reversal occurred in the F_1, F_2, and F_3 populations. A possible explanation of this change between response of Hyslop and Sprague including their crosses is that perhaps Hyslop has the ability to initiate floral induction more efficiently at short photoperiods than does Sprague. Another possibility might be that Sprague and crosses with Inia 66 were accelerated to a greater degree by longer photoperiods than was Hyslop and its progeny. Such an explanation would agree with the findings of Gries et al. (1956). Regarding a possible vernalization effect, Levy and Peterson (1972) found that the winter wheat cultivar, Triumph, had an absolute cold requirement of at least 28 days before floral induction and a quantitative response for additional cold up to 56 days. If the vernalization requirements for the four winter parents and their winter x spring crosses was exceeded by vernalizing the period of this study, the different response of earliness might result from a different quantitative response by these two winter parents for additional cold period after the critical period had been reached. However, the results of vernalization experiment presented in this study suggested that more detailed experiments will be required to investigate the response of winter x spring wheat crosses to day-length and vernalization.

In summary, the following conclusions were drawn from the analyses of variance: (1) The parents differed widely in eight measured characters particularly in terms of earliness of heading and maturity; (2) variability in generations and crosses was sufficient to prompt further investigation of inheritance of eight agronomic traits in these four winter x spring wheat crosses; (3) the greater variability was observed when the F_1's were backcrossed to the winter parents; (4) maternal inheritance was not involved in the genetic control of earliness, grain yield and the components of yield; (5) a reversal of earliness between two winter cultivars, Hyslop and Sprague, and their crosses occurred between fall and spring plantings.

Inheritance and Genetic Advance

Progress in wheat breeding depends on effective selection of individual plants. Hence, selection procedures play an important role in the effectiveness of selection. More emphasis is now being given to improving the components of yield to increase the yielding capacity of the plants. Considering earliness of heading or maturity is a desirable character especially in certain environments, it is of equal importance to evaluate how these traits influence such factors as grain yield and the yield-related traits. If a knowledge of the nature of inheritance and association of these agronomic characters is known then predictions of the genetic advance under selection might be made and particularly in early generations. Thus, the major aspect of the present study was to obtain information concerning the inheritance of earliness and yield components, and determine the feasibility of selecting for these characteristics in early generations.

The frequency distributions for days to heading of the F_1, the BC_1 and BC_2, and F_2 generations along with both parental populations for the four crosses grown on the Hyslop Agronomy Farm are shown in Figures 1 to 4.

From the frequency distributions of the cross Hyslop (P_1) x Inia 66 (P_5) in Figure 1, it is apparent that Hyslop was much later than Inia 66 for days to heading. The F_1 population is skewed toward earliness being midway between Inia 66 and the midparent value. This suggests that the genes conditioning earliness are partially dominant. Inia 66, and F_1 and BC_2 individuals had completed

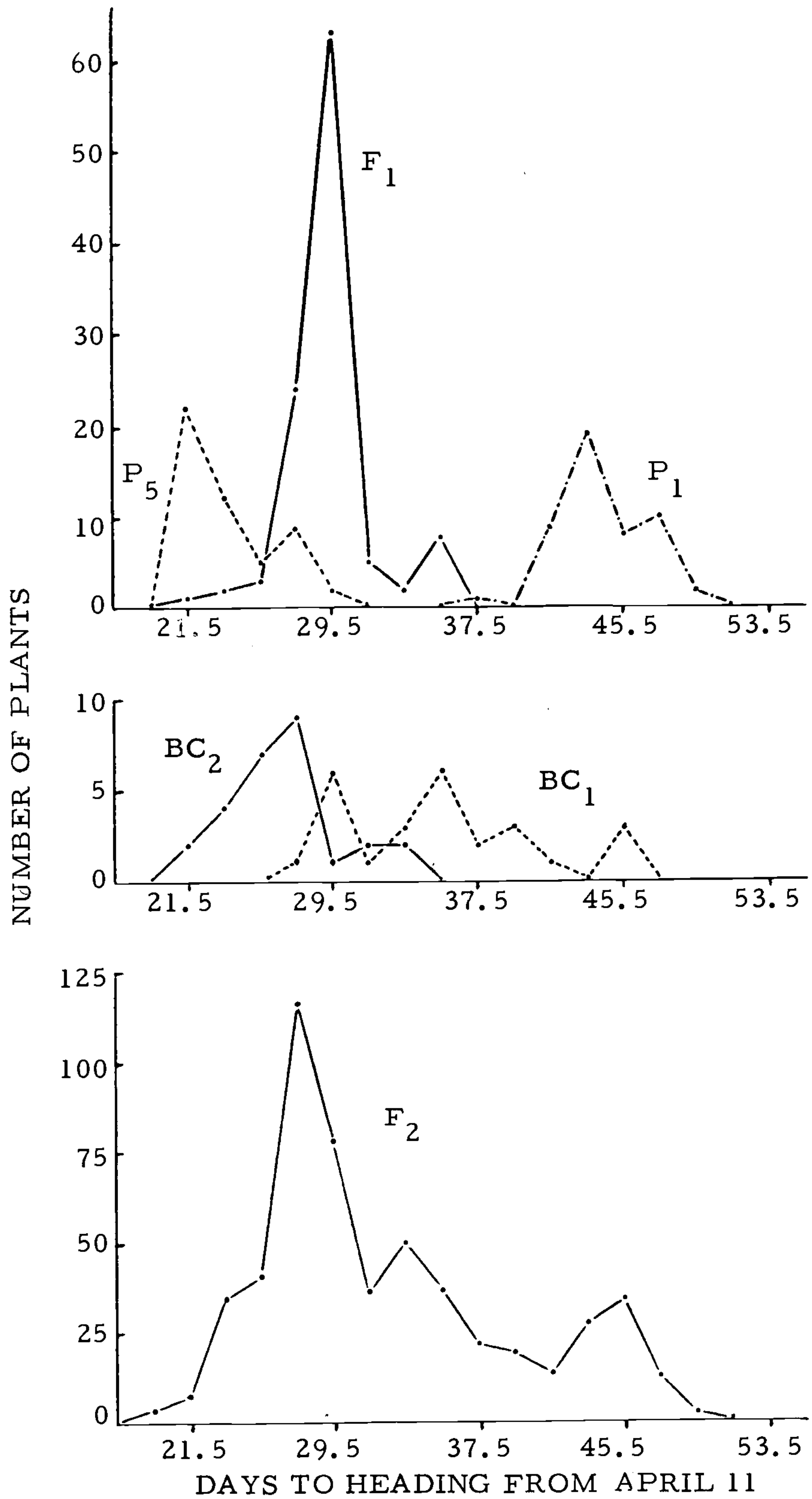

Figure 1. Frequency distributions for parents, F_1, BC_1, BC_2, and F_2 from the cross Hyslop (P_1) and Inia 66 (P_5).

heading before Hyslop had begun to head. The F_2 population also showed a skewness distribution toward the early parent with both parental extremes being recovered. Furthermore, transgressive segregation toward early heading was evident; however, this was not the case for lateness. A segregation ratio of 3:1 (early:late) was observed in the F_2, suggesting that the variation in heading date is governed by one major partially dominant gene. The observed ratios were 400:130. The chi-square value (0.06) was acceptable with a probability of 0.90-0.75. According to the F_2 data with one gene segregation, the BC_1 generation would be expected to be 1:1 segregation ratio (early:late). The observed ratio was 17:10 which fits the theoretical 1:1 ratio with a chi-square value 1.81 and with acceptable probability of 0.25-0.10. The minimum number of genes estimated to govern earliness of heading in this cross using Wright's formula (1968) was 1.5 showing only slight disagreement with estimated value from the F_2 distribution.

The BC_1, BC_2, and F_2 of the cross Yamhill (P_2) x Inia 66 (P_5) showed nondiscrete classes and closely resembled normal distributions (Figure 2). The F_2 population distribution covered the entire range of the early parent but not the late parent. There were no indications of transgressive segregation in either direction. The means of the F_1 and F_2 were skewed toward earliness suggesting that partially dominant genes for early heading were present. The

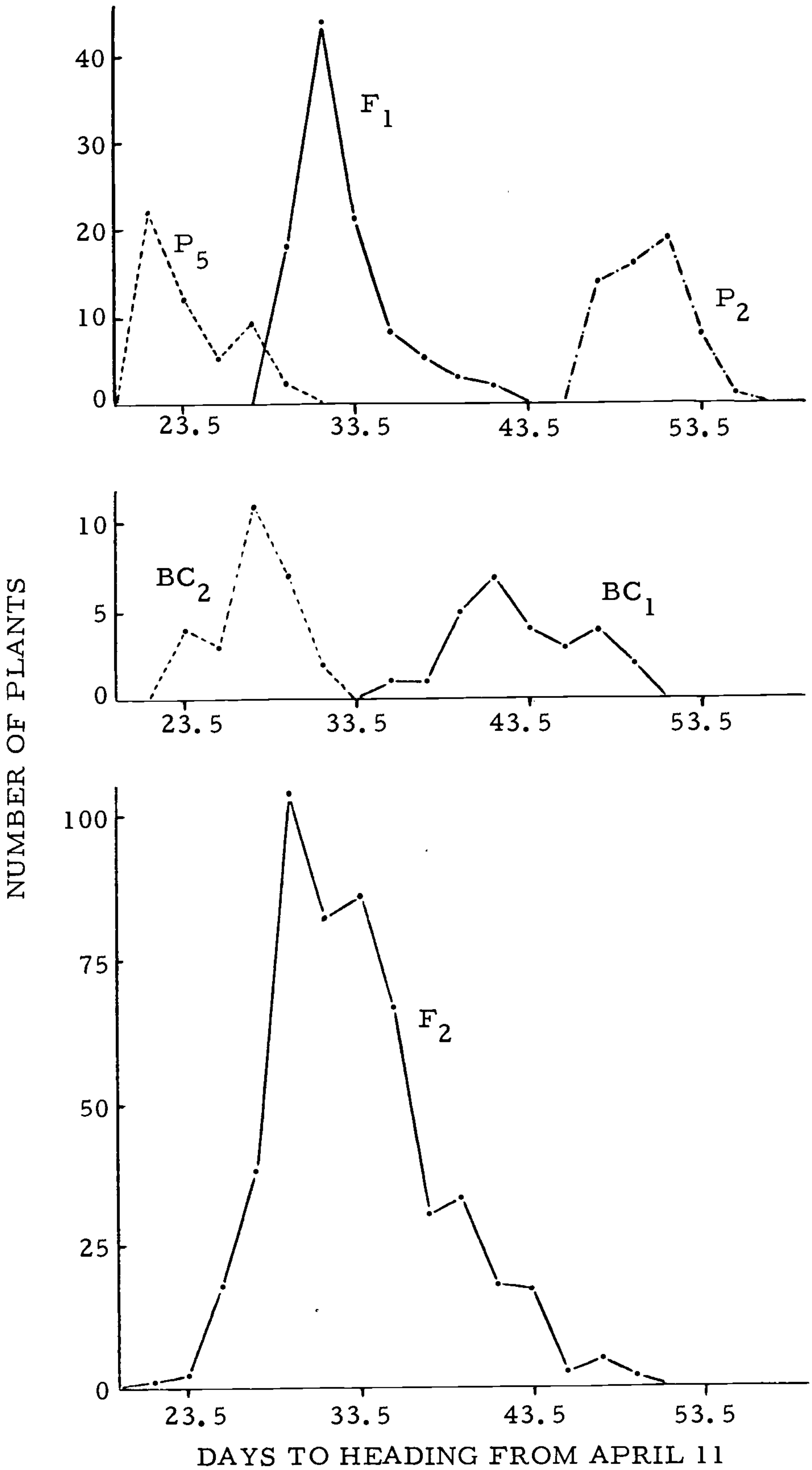

Figure 2. Frequency distributions for parents, F_1, BC_1, BC_2, and F_2 from the cross Yamhill (P_2) and Inia 66 (P_5).

estimated minimum gene number for the expression of earliness of heading was 5.2 in this cross. Since only one of the parental types was recovered in 256 individuals, is additional evidence that more than four allelic pairs are responsible for the expression of this trait (Allard, 1960). Hence, the estimated number of gene pairs by Wright's formula (5.2) may be a good estimate to explain the variation with perhaps some modifying factors also being present in this cross.

The cross Bezostaia 1 (P_3) x Inia 66 (P_5) produced a bimodal distribution skewed toward earliness in the F_2 (Figure 3). The inheritance pattern in this cross may be complicated by modifying genes; thus, no discrete classes were observed. Transgressive segregation was apparent in the F_2 population for both early and late days to heading. The F_1 hybrid was slightly later than the early parent indicating partial dominance for earliness. It was estimated using Wright's formula that a minimum of 1.8 loci were responsible for this trait. Since parental types were recovered in about 500 individuals observed would further support this conclusion.

The F_2 distribution was trimodal having three maximas in the cross Sprague (P_4) x Inia 66 (P_5). Again as in previous crosses the skewness was toward Inia 66 in both the F_1 and F_2 populations. Since neither parental extreme was recovered in the F_2 distribution of 256 individuals suggest that at least four allelic pairs were

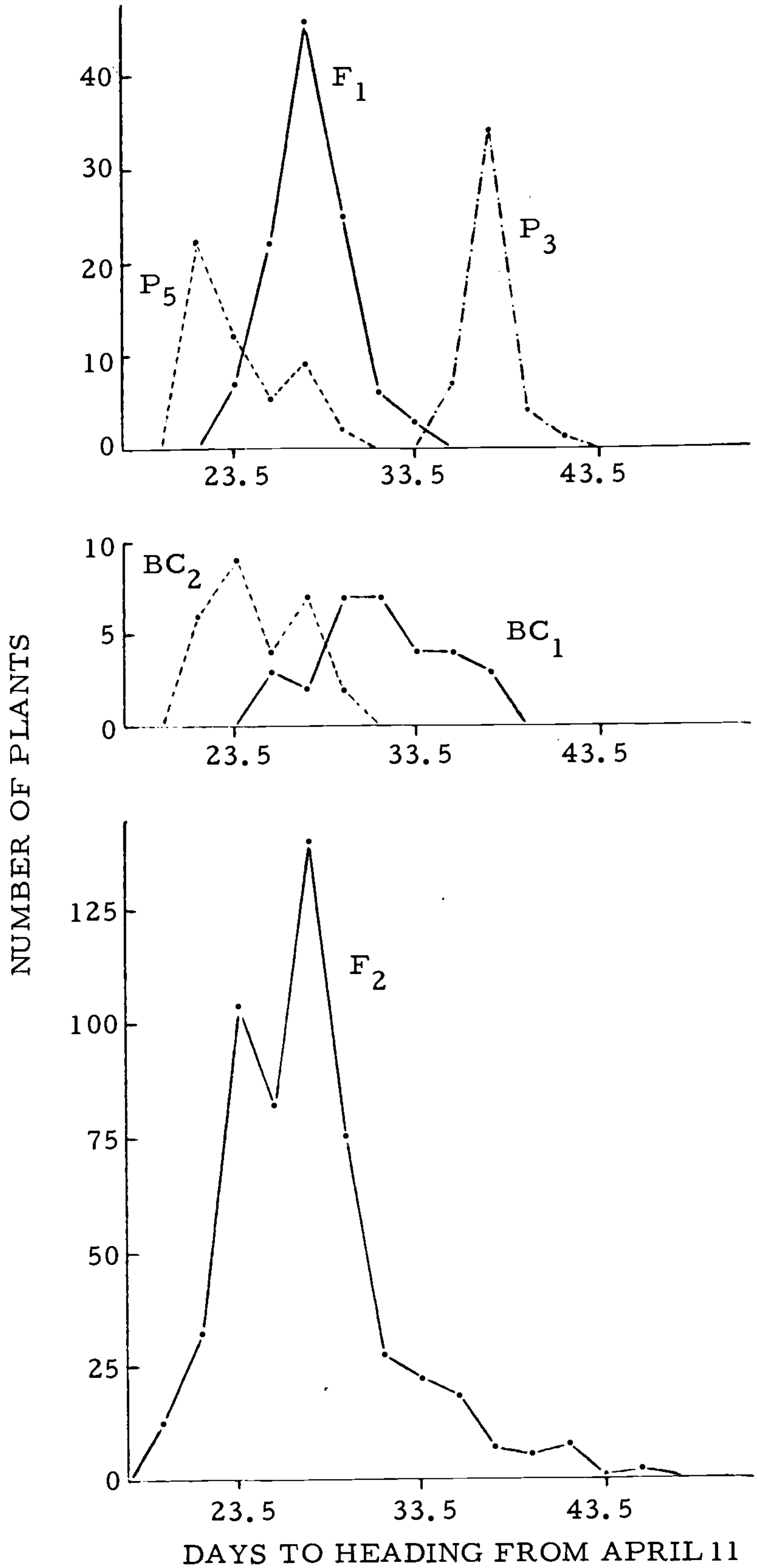

Figure 3. Frequency distributions for parents, F_1, BC_1, BC_2, and F_2 from the cross Bezostaia I (P_3) and Inia 66 (P_5).

involved. By Wright's formula, minimum number of segregating loci were predicted to be 4.8 which supported to the former estimate.

In summary, the frequency distributions of the F_2, backcrosses, F_1, and parental populations for heading date in four winter x spring wheat crosses suggested the following: (1) the estimated minimum number of major genes responsible for the expression of heading date were few varying between one to five, which is in agreement with the findings of Allard and Harding (1963); Anwar and Chowdry (1969); (2) the remaining unexplained genetic variations in segregating generations were postulated to be due to modifying factors; (3) a certain degree of dominance for earliness of heading agrees with findings obtained in previous studies, and (4) transgressive segregating for heading date was noted for all crosses except the cross Sprague (P_4) and Inia 66 (P_5).

Estimates of population means, phenotypic variances, F_1-mid-parent deviations, degree of dominance, narrow sense heritability estimates, and expected genetic advance for each of eight measured characters in the four crosses are presented in Tables 10, 11, and 12. The mean estimates obtained differed in each cross, location and year. Phenotypic variances were pooled among blocks to remove replication effects. These variances were usually greater for segregating generations than for nonsegregating generations. However, generation variances were less for the F_2's than for the parents or

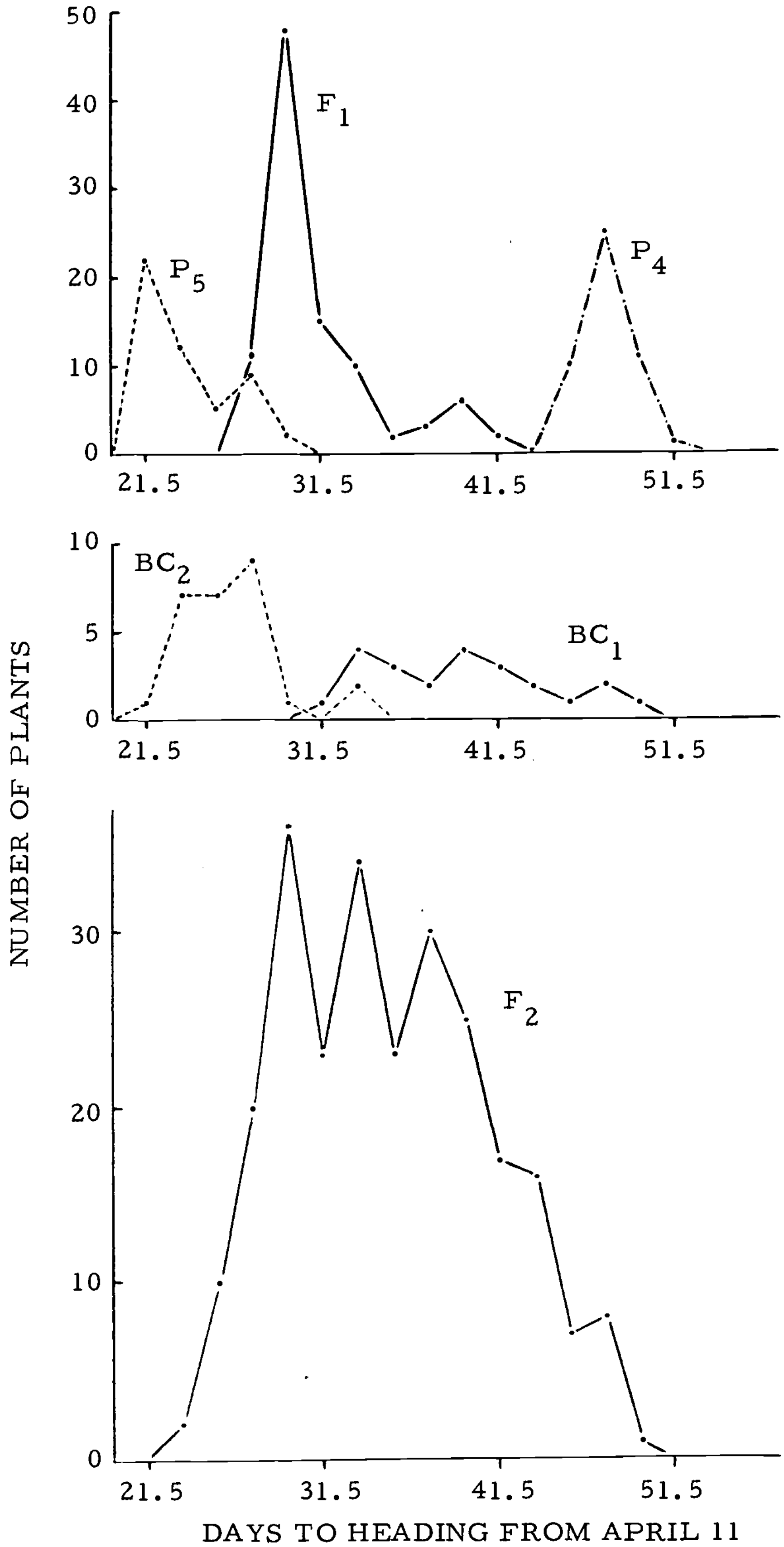

Figure 4. Frequency distributions for parents, F_1, BC_1, BC_2 and F_2 from the cross Sprague (P_4) and Inia 66 (P_5).

Table 10. Estimates of generation means, pooled variances among-blocks, F_1-midparent deviations ($\overline{F_1}$-MP), degree of dominance (d), heritability in the narrow sense (h^2_{ns}), and expected genetic advance (G. S.) for eight agronomic characters in four winter x spring wheat crosses grown on the Hyslop Agronomy Farm in 1976.

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_1}$ (Hyslop)	34.9[1/]	44.6	90.3	45.9	12.4	0.15	4.72	57.7
	238.74	3.31	6.37	1.39	19.42	0.216	0.107	89.04
$\overline{P_5}$ (Inia 66)	19.8	24.0	78.4	54.2	8.9	1.20	4.82	44.9
	71.68	5.88	2.32	2.12	6.99	2.472	0.097	89.86
$\overline{F_1}$	31.9	29.7	81.2	51.5	9.5	0.54	5.07	63.6
	283.70	6.21	6.45	2.67	14 34	1.049	0.201	159.24
$\overline{F_2}$	27.0	32.4	82.3	49.9	10.1	0.08	4.72	56.0
	168.58	40.70	23.02	4.74	13.76	0.113	0.224	176.26
$\overline{BC_1}$	47.7	35.8	85.3	49.7	13.4	0.13	5.30	66.9
	262.70	26.36	30.06	3.52	10.03	0.180	0.212	124.14
$\overline{BC_2}$	25.5	27.0	81.6	54.2	8.2	0.77	5.16	58.7
	133.91	9.91	11.36	1.06	7.16	1.136	0.146	141.22
$\overline{F_1}$-MP	4.5**	-4.6**	-3.2**	1.4**	-1.2**	-0.14	0.30**	12.3**
d [2/]	0.60	-0.45	-0.54	0.33	-0.71	0.26	-6.00	1.92
h^2_{ns} ±SE	-0.35±0.29	1.11**±0.21	0.20±0.42	1.03**±0.23	0.75**±0.27	-9.65±3.13	0.42±0.35	0.49±0.33
G. S. [3/] (%)	0.0	52.0	3.0	11.5	72.7	0.0	11.0	30.7

Table 10. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_2}$ (Yamhill)	40.1	50.5	97.0	46.4	10.8	0.24	5.19	70.9
	435.68	2.47	0.69	1.19	29.71	0.328	0.211	108.47
$\overline{P_5}$ (Inia 66)	19.8	24.0	78.4	54.2	8.9	1.20	4.82	44.9
	71.68	5.88	2.32	2.12	6.99	2.472	0.097	89.86
$\overline{F_1}$	34.3	32.9	86.7	53.9	8.9	0.90	5.32	71.0
	368.78	4.08	8.33	3.17	15.90	2.257	0.153	133.31
$\overline{F_2}$	24.9	33.4	85.5	52.2	8.0	0.23	4.85	62.9
	192.14	21.02	17.78	3.88	10.96	0.414	0.260	212.91
$\overline{BC_1}$	40.7	43.0	93.7	50.6	9.3	1.15	5.27	82.4
	331.40	9.11	6.42	2.47	11.40	1.824	0.152	126.72
$\overline{BC_2}$	20.1	27.6	80.5	53.0	6.9	0.54	4.91	56.0
	124.26	5.09	6.03	2.74	7.21	1.321	0.211	211.22
$\overline{F_1}$-MP	1.9	-5.0**	-1.0**	3.6**	-1.0**	0.18	0.31**	13.1**
d	0.19	-0.38	-0.11	-0.92	-1.11	-0.38	1.72	1.01
h^2_{ns} ±SE	-0.37±0.55	1.32**±0.15	1.30**±0.11	0.22**±0.29	0.30±0.37	-5.60±1.65	0.60*±0.30	0.41±0.35
G. S. (%)	0.0	36.2	13.0	2.1	32.5	0.0	16.7	25.1

Table 10. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_3}$ (Bezostaia I)	28.3	37.9	84.4	46.6	9.3	0.17	5.00	58.8
	146.09	2.37	3.78	0.76	6.90	0.24	0.119	128.01
$\overline{P_5}$ (Inia 66)	19.8	24.0	78.4	54.2	8.9	1.20	4.82	44.9
	71.68	5.88	2.32	2.12	6.99	2.472	0.097	89.86
$\overline{F_1}$	28.1	27.9	79.6	51.8	8.9	0.91	5.18	61.7
	132.68	5.54	2.70	2.55	10.10	1.451	0.178	116.26
$\overline{F_2}$	25.3	27.5	80.3	52.8	9.0	0.23	4.88	57.5
	134.98	18.39	9.82	3.30	11.72	0.488	0.221	151.50
$\overline{BC_1}$	31.8	31.4	83.1	51.7	8.9	0.80	5.02	69.8
	205.42	11.10	8.79	1.44	9.00	2.304	0.161	229.31
$\overline{BC_2}$	23.8	24.9	78.6	53.7	8.3	1.05	4.99	57.1
	68.96	5.29	2.51	1.26	6.49	2.380	0.103	147.31
$\overline{F_1}$-MP	4.0**	-3.1**	-1.8**	1.4**	-0.2	0.22*	0.27**	9.8**
d	0.95	-0.45	-0.60	-0.37	-1.00	-0.42	3.00	1.42
h^2_{ns} ±SE	-0.03±0.46	1.11**±0.22	0.85**±0.26	1.18**±0.17	0.68*±0.27	-7.45±1.99	0.81**±0.25	-0.49±0.52
G. S. (%)	0.0	41.2	8.7	9.1	67.8	0.0	20.7	0.0

Table 10. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_4}$ (Sprague)	19.6	47.7	94.5	46.8	9.9	0.63	4.10	48.9
	61.33	1.29	2.74	0.87	14.33	1.148	0.177	87.84
$\overline{P_5}$ (Inia 66	19.8	24.0	78.4	54.2	8.9	1.20	4.82	44.9
	71.68	5.88	2.32	2.12	6.99	2.472	0.097	89.86
$\overline{F_1}$	25.1	31.7	87.4	55.9	9.9	1.69	4.55	53.8
	160.80	16.58	4.80	5.81	13.97	5.163	0.170	97.59
$\overline{F_2}$	21.1	35.4	86.3	50.4	10.4	0.34	3.99	49.7
	145.83	31.95	16.74	3.63	20.14	0.731	0.378	133.43
$\overline{BC_1}$	19.2	39.8	88.4	48.6	8.7	1.01	4.35	47.7
	137.67	25.80	19.95	4.09	10.16	2.449	0.364	175.78
$\overline{BC_2}$	22.8	26.2	80.1	53.9	9.6	1.13	4.44	49.5
	170.48	7.49	6.83	4.25	6.51	2.423	0.636	199.78
$\overline{F_1}$-MP	5.4**	-4.2**	0.9**	5.4**	0.5	0.77**	0.09*	6.9**
d	-54.00	-0.36	0.11	-1.46	1.00	-2.66	-0.25	3.45
h^2_{ns} ±SE	-0.11±0.52	0.96±0.28**	0.40±0.42	-0.30±0.53	1.17±0.21**	-4.66±1.65	-0.65±0.66	-0.81±0.70
G. S. (%)	0.0	40.4	5.0	0.0	>100	0.0	0.0	0.0

*, **Significant at P = 0.05 and 0.01, respectively.

1/ The values in the upper and lower lines refer to means and pooled variances among-blocks for each generation respectively.

2/ d = 0 no dominance, d = 1 complete dominance, d > 1 over dominance.

3/ Genetic advance (G. S.) represents the expected increase in the F_3 above the F_2 mean when the best 1% of the F_2 plants are selected.

Table 11. Estimates of generation means, pooled variances among blocks, F_1-midparent deviations ($\overline{F_1}$-MP), degree of dominance (d), heritability in the narrow sense (h^2_{ns}), and expected genetic advance (G. S.) for eight agronomic characters in four winter x spring wheat crosses grown on the Sherman Experimental Station in 1976.

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_1}$ (Hyslop)	26.6[1/]	58.4	96.6	38.2	17.5	0.96	3.68	41.5
	78.15	10.79	3.71	5.53	32.38	1.126	0.081	34.81
$\overline{P_5}$ (Inia 66)	7.9	42.3	87.3	45.0	6.3	1.11	4.30	30.3
	4.28	22.79	2.75	18.54	1.50	0.667	0.119	182.29
$\overline{F_1}$	26.9	50.8	94.0	43.1	16.6	1.30	4.09	39.0
	102.05	25.80	9.93	15.61	37.20	2.627	0.097	47.51
$\overline{F_2}$	23.8	49.6	93.0	43.4	14.8	1.07	3.98	39.6
	151.38	45.33	15.51	30.87	43.37	1.862	0.172	95.22
$\overline{BC_1}$	33.5	55.8	96.1	40.3	19.0	0.99	3.80	42.3
	326.50	39.81	17.91	18.22	62.56	1.496	0.104	80.76
$\overline{BC_2}$	10.8	48.6	91.1	42.5	8.3	1.49	3.86	34.5
	10.54	22.73	8.35	22.30	7.44	3.840	0.325	34.78
$\overline{F_1}$-MP	9.6**	0.4	2.0**	1.5**	4.7**	0.26	0.10*	3.1**
d [2/]	1.03	0.05	0.43	-0.44	0.84	-3.25	-0.32	0.55
h^2_{ns} ±SE	-0.23±0.78	0.62*±0.21	0.31±0.45	0.69*±0.13	0.39±0.25	-0.87±0.91	-0.49±0.81	0.79*±0.33
G. S.[3/] (%)	0.0	22.2	3.4	23.3	27.0	0.0	0.0	51.5

Table 11. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P_2}$ (Yamhill)	33.7	63.7	101.6	37.8	17.0	0.43	3.97	47.9
	174.82	3.57	4.18	5.42	26.87	0.322	0.114	85.36
$\overline{P_5}$ (Inia 66)	7.9	42.3	87.3	45.0	6.3	1.11	4.30	30.3
	4.28	22.79	2.75	18.54	1.50	0.667	0.119	182.29
$\overline{F_1}$	22.7	54.1	97.5	43.5	13.9	1.03	3.89	39.9
	198.27	17.56	4.80	13.94	42.47	1.566	0.124	79.61
$\overline{F_2}$	21.0	54.0	96.5	42.7	12.4	0.69	3.91	41.0
	184.23	28.70	13.60	11.13	37.51	1.190	0.209	110.59
$\overline{BC_1}$	24.8	60.9	99.2	38.3	13.3	0.26	3.87	46.8
	160.44	12.71	2.17	6.22	28.01	0.252	0.125	107.85
$\overline{BC_2}$	9.3	48.0	89.7	41.9	6.1	1.17	3.83	40.0
	146.35	25.40	12.97	6.55	5.88	2.417	0.365	101.28
$\overline{F_1}$-MP	1.9	1.1*	3.0**	2.1**	2.2**	0.26*	-0.25**	0.8
d	0.15	0.10	0.42	-0.58	0.42	-0.76	1.47	0.09
h^2_{ns} ±SE	0.33±0.57	0.67*±0.48	0.89**±0.35	0.85*±0.42	1.10**±0.29	-0.24±1.19	-0.34±1.04	0.11±0.65
G.S. (%)	56.2	17.6	9.0	17.6	>100	0.0	0.0	7.6

Table 11. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P}_3$ (Bezostaia I)	25.5	51.5	93.1	41.5	13.3	0.45	4.41	43.0
	69.79	12.04	3.59	5.02	13.09	0.417	0.073	41.84
$\overline{P}_5$ (Inia 66)	7.9	42.3	87.3	45.0	6.3	1.11	4.30	30.3
	4.28	22.79	2.75	18.54	1.50	0.667	0.119	182.29
$\overline{F}_1$	20.2	47.1	90.2	43.0	11.8	0.80	4.20	40.7
	123.23	37.77	14.68	22.24	24.17	0.875	0.166	63.63
$\overline{F}_2$	20.4	47.4	91.2	43.9	11.9	0.78	4.05	41.0
	188.27	40.64	17.34	25.74	28.60	1.278	0.215	82.46
$\overline{BC}_1$	29.7	50.3	93.4	43.1	14.1	1.41	4.38	47.2
	135.76	20.98	14.13	8.21	20.42	1.738	0.157	71.23
$\overline{BC}_2$	15.7	44.2	88.3	44.1	9.8	2.19	4.23	38.0
	172.94	23.84	7.59	5.29	33.20	4.954	0.110	85.51
$\overline{F}_1$-MP	3.5*	0.2	0.0	-0.3	2.0**	0.02	-0.16**	4.0**
d	0.40	0.04	0.00	0.17	0.57	-0.06	-3.20	0.63
h^2_{ns} ±SE	0.36±0.51	0.90**±0.33	0.75*±0.34	1.48**±0.14	0.13±0.61	-3.24±1.92	0.76±0.30	0.10±0.59
G.S. (%)	63.7	31.9	9.0	30.5	15.1	0.0	23.0	5.4

Table 11. (Continued)

Generation or Parameter	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
$\overline{P}_4$ (Sprague)	25.7 128.61	59.1 14.09	97.1 5.35	38.0 8.22	27.8 100.93	1.68 3.778	3.02 0.050	29.7 29.50
$\overline{P}_5$ (Inia 66)	7.9 4.28	42.3 22.79	87.3 2.75	45.0 18.54	6.3 1.50	1.11 0.667	4.30 0.119	30.3 182.29
$\overline{F}_1$	19.0 74.50	48.5 28.96	93.1 14.39	44.6 22.77	16.6 34.22	1.40 2.229	3.81 0.180	29.3 38.32
$\overline{F}_2$	21.5 188.27	51.8 36.35	94.9 14.21	42.8 25 03	19.0 91.69	1.84 3.382	3.19 0.357	31.3 101.59
$\overline{BC}_1$	19.2 158.73	54.2 28.82	97.0 8.82	42.8 24.07	15.4 58.99	2.88 9.959	3.46 0.256	35.1 47.18
$\overline{BC}_2$	7.8 124.08	47.9 32.61	91.3 9.92	43.4 17.32	8.0 21.45	1.43 2.630	3.76 0.312	29.8 75.15
$\overline{F}_1$-MP	2.2*	-2.2**	0.9**	3.1	-0.5	0.00	0.15**	-0.7
d	0.25	-0.26	0.18	0.89	-0.05	0.00	-0.23	2.33
h^2_{ns} ±SE	0.50±0.48	0.31±0.52	0.68±0.41	0.35±0.51	1.12**±0.29	-1.72±4.94	0.41±0.52	0.80*±0.40
G.S. (%)	84.2	9.5	7.2	10.7	>100	0.0	20.4	68.1

*, **Significant at P = 0.05 and 0.01, respectively.

1/ The values in the upper and lower lines refer to means and pooled variances among-blocks for each generation, respectively.

2/ d= 0 no dominance, d=1 complete dominance, d >1 over dominance.

3/ Genetic advance, (G.S.) represents the expected increase in the F_3 above the F_2 mean when the best 1% of the F_2 plants are selected.

Table 12. Estimates of generation means, pooled variances among-blocks, F_1-midparent deviations ($\overline{F_1}$-MP), degree of dominance (d), heritability in the narrow sense (h^2_{ns}), actual and expected genetic advances (G. S.) for eight agronomic characters in four winter x spring wheat crosses grown on the Hyslop Agronomy and Horticulture Farms in 1977.

Generation or Parameter	Hyslop Agronomy Farm								Horticulture Farm
	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to heading[1/]
$\overline{P_1}$ (Hyslop)	57.3[2/]	43.3	90.2	46.9	19.8	0.07	4.66	61.9	67.1
	245.59	1.03	0.69	0.72	19.36	0.072	0.058	58.79	6.91
$\overline{P_5}$ (Inia 66)	22.4	17.6	77.9	60.3	9.3	3.04	4.73	50.3	41.8
	41.60	5.26	1.41	6.47	3.39	5.407	0.129	114.69	10.49
$\overline{F_1}$	41.2	24.3	79.1	54.8	12.7	1.07	5.05	63.7	52.8
	132.03	5.85	2.32	6.93	6.69	3.781	0.071	68.51	4.45
$\overline{F_2}$	43.9	26.6	79.7	53.1	15.5	0.40	4.78	60.6	55.1
	251.72	41.84	11.62	18.01	15.69	1.257	0.201	121.98	17.98
$\overline{BC_1}$	40.5	39.9	84.8	44.9	16.5	0.09	4.61	51.8	62.4
	275.98	22.46	12.12	7.59	28.10	0.119	0.162	140.07	10.19
$\overline{BC_2}$	28.6	18.1	78.0	59.9	10.9	2.04	4.84	53.3	46.4
	101.33	19.73	5.39	16.64	6.50	5.135	0.178	123.57	11.69
$\overline{F_3}$ (E)[3/]	38.0	23.6	78.6	55.0	16.9	0.44	4.78	53.7	50.8
	146.82	12.85	5.92	9.03	7.50	0.696	0.135	98.77	14.72
$\overline{F_3}$ (Y)[4/]	49.6	42.1	89.2	47.1	18.1	0.24	4.74	61.8	66.2
	230.40	2.37	2.86	2.23	11.39	0.406	0.119	90.54	4.76
$\overline{F_1}$-MP	3.1	-6.2**	-5.0**	1.2**	-1.9**	-0.49	0.35**	7.6**	-1.7**
d [5/]	0.16	-0.48	-0.82	-0.18	-0.37	0.33	-8.75	1.31	-0.13
h^2_{ns} ±SE	0.50±0.33	0.99**±0.22	0.49±0.33	0.65*±0.30	-0.21±0.51	-2.18±1.05	-0.31±0.13	-0.16±0.46	0.78**±0.23
G. S. % (Actual)[6/]	13.0	11.3	1.4	--	--	--	--	--	7.8
G. S. % (Expected)	47.6	63.5	5.5	13.6	0.0	0.0	7.7	7.7	15.8

Table 12. (Continued)

Generation or Parameter	Hyslop Agronomy Farm: Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Horticulture Farm: Days to Heading
$\overline{P}_2$ (Yamhill)	41.4	50.7	93.5	42.8	12.8	0.11	5.46	58.6	70.1
	164.39	1.72	0.60	1.21	6.95	0.116	0.181	113.83	1.29
$\overline{P}_5$ (Inia 66)	22.4	17.6	77.9	60.3	9.3	3.04	4.73	50.3	41.8
	41.60	5.26	1.41	6.47	3.39	5.407	0.129	114.69	10.49
$\overline{F}_1$	43.2	32.0	82.2	50.2	11.7	1.72	4.39	68.4	52.9
	167.88	3.70	6.10	5.11	8.43	3.061	0.084	45.57	4.45
$\overline{F}_2$	37.9	31.5	81.2	49.7	12.6	0.30	5.04	57.6	56.6
	201.65	19.29	8.42	10.11	8.60	0.561	0.189	208.00	23.22
$\overline{BC}_1$	40.2	41.7	87.2	45.6	12.2	0.37	5.06	62.0	61.5
	361.46	10.15	9.24	4.37	11.67	0.666	0.223	244.50	14.45
$\overline{BC}_2$	29.8	23.9	78.5	54.6	10.1	2.17	5.11	57.1	50.6
	119.63	18.02	5.50	15.08	6.82	7.458	0.201	158.44	20.54
$\overline{F}_3$(E)	35.8	31.6	82.1	50.5	12.2	0.96	4.96	57.0	54.2
	206.48	9.82	6.38	11.24	9.85	2.365	0.225	171.22	5.79
$\overline{F}_3$(Y)	44.2	38.6	85.1	46.5	14.2	0.17	5.12	61.0	61.2
	226.13	5.05	5.62	4.93	12.37	0.163	0.124	139.83	8.84
$\overline{F}_1$-MP	11.3**	-2.2**	-3.5**	-1.4**	0.6	0.14	0.29**	13.9**	-3.1**
d	1.19	-0.13	-0.45	0.16	0.35	-0.10	0.81	3.39	-0.22
h^2_{ns} ±SE	-0.39±0.54	0.54±0.32	0.25±0.38	0.08±0.44	-0.15±0.47	-12.48±12.51	-0.24±0.23	0.06±0.18	0.49±0.30
G. S. % (Actual)	16.6	-0.3	-1.1	--	--	--	--	--	4.2
G. S. % (Expected)	0.0	20.0	2.3	1.4	0.0	0.0	0.0	4.0	11.0

Table 12. (Continued)

Generation or Parameter	Hyslop Agronomy Farm: Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Horticulture Farm: Days to Heading
$\overline{P}_3$ (Bezostaia I)	28.1	37.7	83.9	46.1	10.5	0.09	5.17	51.1	57.0
	49.51	4.63	0.63	3.58	3.91	0.079	0.033	35.57	2.41
$\overline{P}_5$ (Inia 66)	22.4	17.6	77.9	60.3	9.3	3.04	4.73	50.3	41.8
	41.60	5.26	1.41	6.47	3.39	5.407	0.129	114.69	10.49
$\overline{F}_1$	38.3	21.8	77.6	55.8	11.0	2.15	5.28	66.4	47.6
	61.63	8.84	4.96	10.31	5.80	5.820	0.048	43.96	15.04
$\overline{F}_2$	37.5	27.2	80.6	53.4	74.4	0.84	4.71	54.4	52.1
	161.56	27.34	7.38	19.57	14.31	2.258	0.180	139.27	30.98
$\overline{BC}_1$	35.2	30.5	79.5	48.9	12.0	0.65	5.06	56.9	54.3
	146.70	14.94	7.38	10.81	7.51	1.301	0.133	99.36	12.82
$\overline{F}_3$ (E)	28.0	20.5	77.5	57.0	10.3	1.07	4.98	53.9	47.3
	131.67	9.07	6.64	12.20	11.96	2.098	0.141	112.09	7.52
$\overline{F}_3$ (Y)	34.5	25.5	79.4	53.9	13.1	1.28	4.81	54.8	52.2
	106.75	10.20	3.70	8.73	9.83	2.710	0.091	81.43	10.02
$\overline{F}_1$-MP	13.0**	-5.9**	-3.3**	2.6**	1.1*	0.58	0.33**	15.7**	1.8**
d	4.64	-0.59	-1.10	0.37	1.83	-0.39	1.50	39.25	-0.24
G. S. % (Actual)	-8.0	24.6	3.9	--	--	--	-	--	9.2

Table 12. (Continued)

Generation or Parameter	Hyslop Agronomy Farm								Horticulture Farm
	Yield (per plant)	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility	Days to Heading
$\overline{P}_4$ (Sprague)	21.7	47.5	92.3	44.8	14.2	1.15	3.63	41.8	64.2
	60.98	1.27	0.69	1.87	14.30	1.559	0.060	46.55	3.04
$\overline{P}_5$ (Inia 66)	22.4	17.6	77.9	60.3	9.3	3.04	4.73	50.3	41.8
	41.60	5.26	1.41	6.47	3.39	5.407	0.129	114.69	10.49
$\overline{F}_1$	31.0	27.2	80.7	53.5	12.4	0.18	4.74	51.8	51.7
	158.13	1.92	3.21	2.93	7.38	0.302	0.215	142.18	11.34
$\overline{F}_2$	28.9	28.8	80.3	51.5	13.8	0.93	4.48	44.8	50.5
	180.23	41.44	13.19	22.93	16.36	2.325	0.338	131.32	20.67
$\overline{BC}_1$	30.4	39.2	87.1	47.8	15.8	0.90	4.09	46.2	59.7
	143.11	6.61	6.70	7.52	19.08	1.606	0.336	135.92	7.18
$\overline{F}_3$ (E)	22.6	25.6	77.6	52.0	12.7	1.27	4.49	38.2	50.0
	104.88	24.49	5.41	16.46	16.31	2.362	0.153	93.78	15.15
$\overline{F}_3$ (Y)	32.7	28.5	80.8	52.3	14.8	0.48	4.59	47.7	52.2
	101.05	14.03	6.07	9.20	11.94	1.131	0.187	41.30	5.61
$\overline{F}_1$-MP	8.9**	-5.4**	-4.4**	0.9**	0.6	-1.92**	0.56**	5.7**	-1.3*
d	-22.25	-0.36	-0.61	-0.12	0.25	2.02	-1.02	-1.33	-0.12
G. S. % (Actual)	13.1	11.1	3.4	--	--	--	--	--	1.0

*, **Significant at P = 0.05 and 0.01, respectively.

1/ Vernalized and spring planted.

2/ The values in the upper and lower lines refer to means and pooled varinaces among-blocks for each generation, respectively.

3/4/ F_3 (E) and F_3(Y) refer to F_3 families selected for earliness and yield, respectively.

5/ d = 0 no dominance, d = 1 complete dominance, d > 1 over dominance.

6/ Actual and expected genetic advances represent the 1% selection intensity.

F_1's indicating that much of the variation was due to environmental effects in some traits. Also, in some instances, the phenotypic variances of the backcross generations were greater than their respective F_2 generation variances. This large unexpected environmental variance could be ascribed to larger sampling error or more likely to unequal environmental variances resulting from different genotype x environment interactions.

The F_1's frequently deviated significantly from their corresponding midparent values ($\overline{F}_1$-MP) for all eight agronomic traits. The amount of deviation depends on the crosses and site. Significant F_1-midparent deviations indicated a considerable amount of non-additive gene action in the expression of all traits measured. However, the F_1 was never significantly better than the earliest parent indicating that nonadditive gene action was of minor importance for days to heading and maturity and maturity duration. Grain yield, the components of yield, and unproductive tiller number, appeared to be largely controlled by nonadditive gene action depending on the cross and location. As with days to heading, the magnitude and sign of F_1-midparent deviations depends on the parents being considered. Positive and negative signs indicate the deviations from the midparent are towards the winter or spring parents, respectively. The F_1 mean values for yield and the yield components were above the low parents except in the P_4 x P_5 cross for fertility. This was also true in the $P_2 \times P_5$ and $P_3 \times P_5$ for 100 kernel weight at Moro (Table 11).

Degree of dominance was computed by dividing the F_1-midparent deviation by the corresponding winter parent-midparent deviation (Griffing, 1949). Negative values indicate the direction of dominance toward the spring parent (Tables 10, 11, and 12).

The values obtained for the degree of dominance differed widely in this study depending on the cross and site. For grain yield per plant at the Hyslop site, the degree of dominance toward the higher yielding parents ranged from 0.16 to 0.95 in the crosses $P_1 \times P_5$ in 1976 and 1977 and for $P_2 \times P_5$, and $P_3 \times P_5$ in 1976. Overdominance ($d > 1.00$) existed in the crosses $P_4 \times P_5$ in 1976 and 1977; $P_2 \times P_5$ and $P_3 \times P_5$ in 1977. Overdominance for grain yield was found at the Moro site in the cross $P_1 \times P_5$, but partial dominance was involved in the remaining crosses. Degree of the dominance values were also noted for the yield components. The values varied depending on the cross and with location and over years, suggesting possible nonadditive x location and nonadditive x year interactions. Similar findings were reported by Amaya et al. (1972), and Daaloul (1974).

Tiller number ranged from -0.05 to 0.84 at the Moro site suggesting partial dominance (Table 11). For two successive years at Hyslop the degree of dominance values obtained showed that partial dominance, complete dominance and overdominance were all involved in the expression of tiller number (Tables 10 and 12). Kernel weight also appeared to be controlled by partially dominant or overdominant genes under both locations. For fertility, however, nonadditive gene action was not expressed at the Moro site in contrast to the Hyslop site. For this trait, the values larger than 1.00 were obtained in all four crosses showing overdominance at Hyslop; whereas, at Moro, only in one cross, $P_4 \times P_5$, was the value more than 1.00. The other values were low and ranged from 0.09 to 0.63 (Table 11).

Gene action estimates for days to heading are supported by the results obtained in the F_2 population at Hyslop. This evidence of partially dominant gene action toward the early parent in each cross is in agreement with Anwar and Chowdry (1969); and Ketata et al. (1976). Under low rainfall conditions at Moro, the degree of dominance favored the late parent in the three crosses; however, the magnitudes were very low: 0.05, 0.10, 0.04, and -0.26 in the $P_1 \times P_5$, $P_2 \times P_5$, $P_3 \times P_5$, and $P_4 \times P_5$ crosses, respectively (Table 11). These results suggest that only very small part of the total genetic variability is associated with nonadditive gene effects for earliness is in agreement with Anwar and Chowdry (1969), and Bhatt (1972).

Similar results were obtained for the trait days to maturity with only one exception. The exception was the overdominant gene action for days to maturity observed in the cross $P_3 \times P_5$ in 1977 at Hyslop (Table 12). The mean values of parents were very close which might have influenced this estimate.

The results from F_1-midparent deviations and degree of dominance indicated that: (1) nonadditive gene action for earliness of heading and maturity was of minor importance under both conditions; (2) for grain yield and the components of yield nonadditive gene action may be as important as additive gene action at both experimental sites. Yield and the components of yield were controlled by varying degrees of dominance and even overdominance; (3) nonadditive x location and nonadditive x year interactions were pronounced for most of the traits studied.

Narrow sense heritability estimates for eight agronomic traits were derived from Warner's method (1952) and the parent-progeny regressions (Falconer, 1960) and are presented in Tables 10 through 14. In addition to those values, heritability values in the standard unit were obtained by simple correlation (Frey and Horner, 1957). This method, the author stated,

> has advantages over other methods where comparisons were made over years and locations since this procedure has an approximate ceiling of 100 percent in all instances irrespective of the postulated environmental scaling effects.

Coefficient of determination (R^2) values are also given in Tables 13 and 14. The R^2 value can be thought of as narrow sense heritability

Table 13. Parent-progeny regression (b), correlation (r) and coefficients and coefficients of determination (R^2) by mean values of F_1 and F_2 on mid-parental values for the two experiments at the Hyslop Agronomy Farm, and the Sherman Experimental Station in 1976.

Agronomic Trait	F_1 b	F_1 r	F_1 R^2	F_2 b	F_2 r	F_2 R^2
			Hyslop Agronomy Farm			
Yield	0.343	0.531	0.282	0.297*	0.602*	0.362*
Days to Heading	0.815**	0.951**	0.903**	1.061**	0.873**	0.763**
Days to Maturity	1.237**	0.879**	0.772**	0.894**	0.864**	0.747**
Maturity Duration	2.713*	0.700*	0.491*	1.444	0.553	0.306
Tiller	0.552	0.533	0.284	0.386	0.439	0.193
Unproductive Tiller	2.960**	0.735**	0.540**	0.522	0.488	0.238
100 Kernel Weight	1.211**	0.781**	0.610**	1.424**	0.864*	0.746**
Fertility	0.739	0.562	0.316	0.574	0.574	0.330
			Sherman Experimental Station			
Yield	0.380	0.243	0.059	0.279	0.399	0.159
Days to Heading	0.871**	0.734**	0.539**	0.770**	0.767**	0.588**
Days to Maturity	1.355**	0.831**	0.691**	1.236**	0.885**	0.783**
Maturity Duration	0.133	0.114	0.013	-0.042	-0.058	0.003
Tiller	0.507	0.448	0.201	0.699**	0.817**	0.668**
Unproductive Tiller	0.738	0.467	0.218	1.225**	0.785**	0.616**
100 Kernel Weight	0.437*	0.622*	0.386*	0.931**	0.764**	0.583**
Fertility	1.116**	0.812**	0.659**	0.975**	0.875**	0.765**

*Significant at the 5% level.

**Significant at the 1% level.

Table 14. Parent-progeny regression (b), correlation (r) coefficients and coefficients of determination (R^2) by mean values of F_1, F_2, and F_3 on mid-parental values for the two experiments at the Hyslop Agronomy and Horticulture Farms in 1977.

	F_1			F_2			$F_3(E)$ 1/			$F_3(Y)$ 2/		
Agronomic Trait	b	r	R^2	b	r	R^2	b	r	R^2	b	r	R^2
					Hyslop Agronomy Farm							
Yield	0.419	0.470	0.221	0.628**	0.801**	0.641**	--	--	-	0.949**	0.949**	0.900**
Days to Heading	1.483**	0.914**	0.835**	0.686*	0.668*	0.446*	1.568**	0.905**	0.820**	--	--	--
Days to Maturity	0.894**	0.819**	0.670**	0.204	0.250	0.063	0.608*	0.582*	0.339*	--	--	--
Maturity Duration	1.991**	0.790**	0.624**	1.275*	0.673*	0.453*	1.911*	0.656*	0.431*			
Tiller	0.201	0.254	0.065	0.320	0.494	0.244	--	--	--	0.615**	0.829**	0.688**
Unproductive Tiller	0.593	0.424	0.180	0.203	0.547	0.299	0.283	0.443	0.196	0.024	0.041	0.002
100 Kernel Weight	0.669**	0.853**	0.728**	0.502**	0.833**	0.694**	--	--	--	0.463**	0.813**	0.660**
Fertility	0.984**	0.714**	0.509**	1.114**	0.836**	0.700**	--	--	--	1.078**	0.890**	0.792**
					Horticulture Farm							
Days to Heading 3/	0.814**	0.894**	0.800**	0.716*	0.669*	0.447*	0.890**	0.841**	0.707**	--	--	--

*Significant at the 5% level.

**Significant at the 1% level.

1/ F_3 families selected for earliness.

2/ F_3 families selected for yield.

3/ Vernalized and spring planted experiment.

estimate, if genotypic variance of the parental lines are associated with the phenotypic variance of their progeny (Thomas and Kernkamp, 1954). Narrow sense estimates of heritability measures only the additive portion of the total genetic variance; thus, when a given trait is associated with largely additive gene action, selection for the trait is likely to be more effective, particularly in early generations with self pollinating species.

In the present study heritability estimates greater than 1.00 were observed for certain traits when Warner's and the parent-progeny regression methods were used. This could be attributed to possible sampling errors and/or unequal environmental influences on the various generations. It should be noted that in the regression method, estimates are for all four crosses combined. Also differential responses of intra-allelic and nonallelic interactions in each cross may have increased heritability estimates as measured by the parent-progeny regression. Also negative heritability estimates were found in some cases where the variances associated with the backcrosses were relatively large in comparison to their corresponding F_2 variance. This implies that nonadditive gene action was involved in the expression of the trait.

Narrow sense heritability estimates for heading date were high in each cross at both locations (Tables 10, 11, and 12). This is in agreement with Crumpacker and Allard (1962); Gandhi et al. (1964); Sidwell (1975); Fonseca and Patterson (1968); Edwards et al. (1976); and Ketata et al. (1976). Since heading date is governed by primarily additive gene action selection should be effective in all four crosses. Heritability estimates for this trait derived by the regression and the standard unit methods confirmed the results obtained by Warner's method (Tables 13 and 14).

Narrow sense estimates of heritability determined by Warner's method ranged from medium to high for the trait days to maturity (0.20 to 1.30), and from low to high for maturity duration (-0.30 to 1.48) depending on the cross and location. When determined by either the regression method or the standard unit, the estimates were usually high and significant except that for days to maturity obtained by the regression and correlation of F_2 on mid-parental values at Hyslop 1977 ($b=0.20$; $r=0.25$; and $R^2=0.06$) as seen in Tables 13 and 14. It should be noted that, the regression and the standard unit methods covered all four winter x spring wheat crosses; whereas, by Warner's method, the results are for individual crosses.

Heritability values for grain yield were uniformly low and negative, which should be interpreted as being zero for each cross at Hyslop site in 1976 (Table 10). At Moro in 1976 (Table 11), the only negative value observed was in the cross $P_1 \times P_5$ while in the remaining crosses positive values ranging from 0.33 to 0.50 were found; however, large standard errors were associated with grain yield. Large standard errors for the heritability estimates could be ascribed to the large backcross variances and their small degrees of freedom. The estimates determined by the regression and correlation were larger than those determined by Warner's method for grain yield (Tables 13 and 14). High estimates were more pronounced when calculated by the regression of F_3 selected families for yield on midparental values. Heritability estimates in the narrow sense ranging from low to high (-0.15 to 1.39) were also found by Kronstad and Foote (1964); Jahnson et al. (1966); Anwar and Chowdry (1969); Daaloul (1972 and 1974); Alexander (1976); Ketata et al. (1976); and Abi-Antoun (1977).

Narrow sense estimates of heritability as measured by Warner's method for the yield components, namely tiller number, kernel weight and fertility, varied widely from low to high (-0.81 to 1.17) in the four crosses under the two distinct environments (Tables 10, 11, and 12). It is noteworthy that in each cross at least one or more components of yield had a higher heritability estimate than yield *per se*. Moreover, pronounced interactions between additive gene action and location and over years were observed for the yield components; e.g., heritability levels for tiller number were found to be 0.75 and -0.21 in 1976 and 1977, respectively, at Hyslop site in the cross $P_1 \times P_5$. An example of additive gene action by location interaction for fertility was noted in the cross $P_1 \times P_5$ where the levels of heritability were -0.81 at Moro and 0.80 at Hyslop in 1976. The regression and standard unit methods also gave medium to high (F_1 on midparent; b=0.201 to b=1.211) heritability values for the components of yield (Tables 13 and 14). Although relatively high values were obtained for grain yield as determined by regression and correlation, the values were lower than those for at least one or more yield components. The estimates for the yield components, in general, agreed with other investigators previously cited.

Negative heritability values for unproductive tiller number were obtained for crosses and at both locations when measured by Warner's method. Large disagreements were found between heritability estimates obtained by regression or correlation and Warner's methods (Tables 10 through 14). The regression and the standard unit methods gave considerably higher values except when F_3 selected familes for grain yield were regressed or correlated on midparental values. Then the values were very low, being $b = 0.02$; $r = 0.04$; and $R^2 = 0.00$.

Genetic gains (G. S.) were computed based on heritability estimates in the narrow sense assuming the top 1% of individuals were selected for each character, cross and location (Tables 10, 11, and 12). Genetic advance (G. S.) was expressed as a percentage of mean, of the F_3 over the F_2. Where negative heritability estimates were encountered, zero values for G. S. were assigned and no increase of F_3 mean over F_2 mean would be expected. The expected advance was then compared with actual genetic advance, which was the difference between the F_3 and F_2 population means for grain yield, heading and maturity dates (Table 12).

The genetic advance in grain yield per plant obtained at the Hyslop site in 1977 indicated that no increase in F_3 mean over F_2 mean would be expected in any of the four crosses (Table 10). Whereas, at the Moro site, except for the cross $P_1 \times P_5$, the predicted gains in the crosses $P_2 \times P_5$, $P_3 \times P_5$, and $P_4 \times P_5$ were quite large being 56.2, 63.7, and 84.2%, respectively, for grain yield per plant. These higher predicted gain values could be due to large F_2 variances; although, intermediate heritability values were obtained for these crosses (Table 11).

High expected gains in heading date were observed, ranging from 40.4 to 52.0 and from 9.5 to 31.9% at Hyslop and Moro, respectively, in 1976. The predicted improvements in maturity date were observed to be lower than observed for heading date in all four crosses at both locations (Tables 10, 11, and 12).

Genetic advances calculated for the yield components varied from more than 100% to zero values at both locations. However, where the genetic advance was not expected in one of the three yield components, the other one or two components appeared to have very high G.S. values, e.g., at the Hyslop site in 1976, the predicted gain for fertility was 0% in the cross $P_3 \times P_5$; whereas, the values for tiller number and 100 kernel weight were 67.8 and 20.7%, respectively. The percentages of expected gain for the yield components ranged from 32.5 to more than 100 for tiller number; from 0.0 to 20.7% for 100 kernel weight; from 0.0 to 30.7% for fertility at Hyslop in 1976. Corresponding values for Moro were from 15.1 to over 100% for tiller number, from 0.0 to 23.0% for 100 kernel weight; and from 5.4 to 68.1% for fertility depending on the cross.

Since unproductive tiller number was due mainly to environmental factors such as late spring frost, moisture stress and cool weather during the fertilization period no genetic gain would be expected for the trait.

The actual versus expected genetic gains obtained through selection (1% intensity) are presented in Table 12 for grain yield per plant, heading date and maturity date in the crosses P_1 x P_5 and P_2 x P_5. The expected gain for grain yield in the P_1 x P_5 cross was larger than that actually obtained, 13.0 and 47.6% for actual and expected gains, respectively. The selected F_3 families, however, averaged more than their respective F_1 and F_2 population means and were close to the best parent. In the cross P_2 x P_5, no increase was expected. However, the mean yield of the F_3 families exceeded the F_2 mean by 16.6%. Furthermore, the F_3 selected family mean was higher than means of the best parent and the F_1. The disagreement between the actual and expected gains in case of grain yield could be attributed to the large F_2 variance and sampling error rather than reliability of the method. However, in both cases the heritability values were associated with very large standard errors which may account for this discrepancy.

For heading date, the expected gains were greater than those actually obtained in the both $P_1 \times P_5$ and $P_2 \times P_5$ crosses indicating overestimations of the heritability value. However, this would be expected since the mean values of selected F_3 families were smaller than their corresponding F_1 means. By contrast in the other three crosses, the F_2 population mean was 0.1 and 0.4 days earlier than the F_3 and F_1 populations, respectively, in the cross $P_2 \times P_5$ indicating more pronounced nonadditive gene effects than with the other three crosses. Frequency distributions of F_3 families selected for earliness involving the four crosses are presented in Figures 5 through 8. It can be seen from the figures that the majority of the F_3 plants reached the heading stage before the mean dates of their corresponding F_1 and F_2 population, even though the selection had been made for earliness of maturity in the F_2 population. The actual gains for heading date obtained were 24.6% in the $P_3 \times P_5$ and 11.1% in the $P_4 \times P_5$.

Similar results were obtained for days to maturity for the actual versus expected genetic advance. The discrepancies between expected and actual gains were relatively small for days to maturity.

In summary, based on F_1-midparent deviations, degree of dominance, heritability estimates and genetic advance, both additive and nonadditive genetic effects were involved in the expression of all

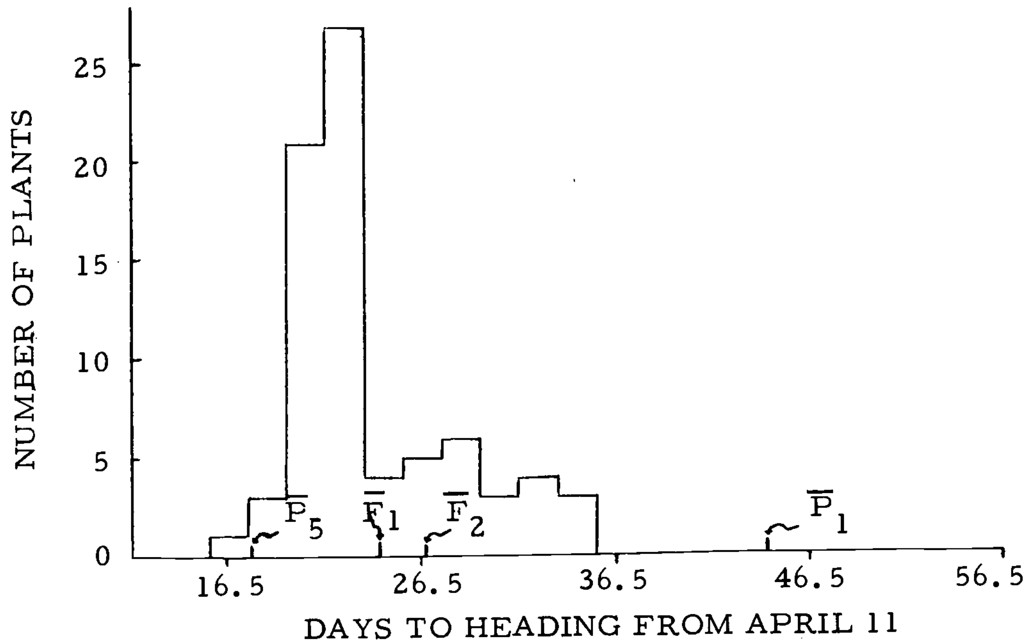

Figure 5. Frequency distribution of F_3 families selected for earliness from the cross Hyslop (P_1) and Inia 66 (P_5) with the parents, F_1, and F_2 mean values.

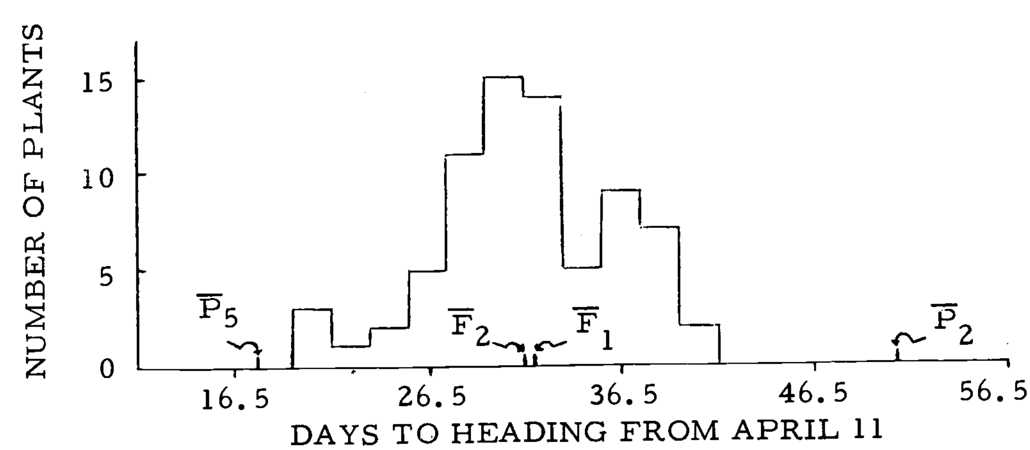

Figure 6. Frequency distribution of F_3 families selected for earliness from the cross Yamhill (P_2) and Inia 66 (P_5) with the parents, F_1, and F_2 mean values.

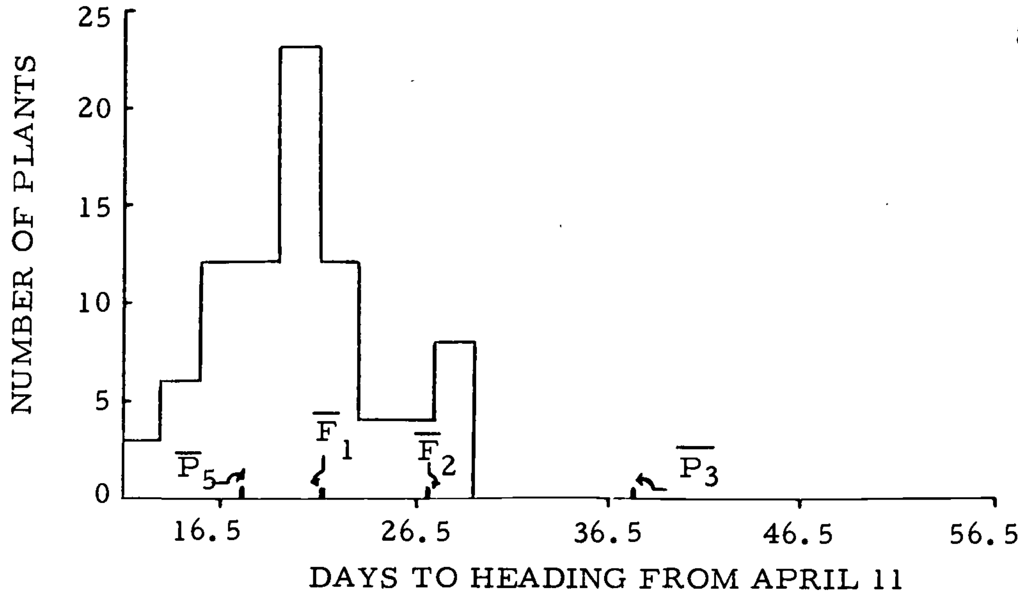

Figure 7. Frequency distribution of F_3 families selected for earliness from the cross Bezostaia I (P_3) and Inia 66 (P_5) with the parents, F_1, and F_2 mean values.

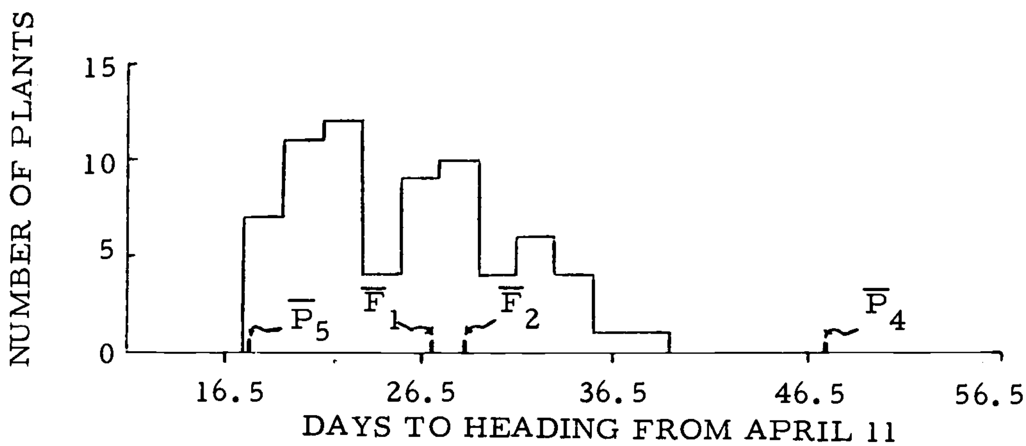

Figure 8. Frequency distribution of F_3 families selected for earliness from the cross Sprague (P_4) and Inia 66 (P_5) with the parents, F_1, and F_2 mean values.

the characters but the estimates differed in magnitude depending on the trait, location, and year. The gene action involved in earliness was primarily additive indicating that selection for earliness would be effective as early as the F_2 generation under both high and low rainfall conditions. Low narrow sense heritability levels obtained for yield _per se_ suggested that selection directly for yield would not be effective. The F_3 families selected for yield exhibited some actual advance over the F_2 and the best parent in most of the crosses. This might be due to presence of appreciable amount of additive epistasis. Amaya _et al_. (1972) stated that even if significant amounts of heterosis are observed in wheat hybrids, it may be possible to select inbred lines similar in yield to the F_1's. Additive and nonadditive gene action were equally important for yield components since very high narrow sense heritability estimates were observed as well as a high degree of dominance. Higher heritability estimates for the components of yield indicated that there was more genetic variability associated with the yield components than yield _per se_. High heritability values for each of the yield components were not consistent at both locations for each cross. Each component appeared to be promising in terms of having high heritability estimates in different crosses. In all four winter x spring wheat crosses, selection for increased grain yield should emphasize tiller number, fertility and kernel weight. Occurrence of additive genetic variation by location interactions implied that selection should be practiced simultaneously under as many different environments as possible if wide adaptability of potential lines is desired. Because of pronounced additive effect by year interactions involving the yield components, delayed selection for these traits may not be productive. The results of this study were obtained under spaced conditions such as is used in the pedigree system of breeding. Thus, it is suggested that selection should be practiced as early as the F_2 populations emphasizing on the yield components to increase the yielding ability and earliness as well. A large number of lines in the F_3 and later generations will be necessary to insure effectiveness of selection where nonadditive genetic effects are more important than additive effects in the expression of any trait. Also due to the large environment x additive gene effect interactions segregation populations should be grown at different locations. It might also be necessary to make selections under specific environmental conditions if progress is to be made in developing the best adapted cultivars for a given location.

Association and Interrelationships among Agronomic Traits

Knowledge of the relationships among agronomic traits is helpful in evaluation of experimental material in a breeding program since selection for a character sometimes results in a response in another character due to linkage or some biological relationships. Concerns have been expressed that perhaps there may be a negative association between earliness and grain yield. Thus, one of the main objectives of this study to evaluate possible association between these two traits along with the components of yield.

To measure possible relationships between agronomic traits evaluated in this study, correlation coefficients were computed among all measured traits for the parents, F_1's, BC's, F_2's, and F_3's (Tables 15 to 17). Correlation values were also determined for each of the parent, F_1 and F_2, generations separately (Appendix Tables 4 through 15). The correlations were further partitioned into direct and indirect effects through the path-coefficient analysis and presented in Tables 18 to 20, and Appendix Tables 16 to 18 for each location.

Intermediate (r=0.343 to r=0.480) and positive correlation coefficients were obtained between grain yield and days to heading or maturity at both locations when all the genotypes were included in the matrices (Tables 15, 16, and 17). It was observed that later genotypes performed better even under low rainfall conditions than the early ones. These results, especially under dryland conditions, were somewhat unexpected because of moisture stress late in the growing season. The reason for these associations was the large positive relationship between the characters measured in this study

Table 15. Correlation coefficients of eight measured characters for the parent, F_1, BC_1, BC_2, and F_2 populations grown on the Hyslop Agronomy Farm in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.343**	0.328**	-0.227*	0.723**	0.062	0.488**	0.720**
Days to Heading		0.910**	-0.738**	0.369**	0.204	-0.161	0.230*
Days to Maturity			-0.395**	0.288**	0.032	-0.105	0.303**
Maturity Duration				-0.353**	0.515**	0.188	-0.013
Tiller					-0.060	-0.110	0.109
Unproductive Tiller						0.048	-0.036
100 Kernel Weight							0.659**

*Significant at the 5% level.

**Significant at the 1% level.

1/ D.F. = 82.

Table 16. Correlation coefficients of eight measured characters for the parent, F_1, BC_1, BC_2, and F_2 populations grown on the Sherman Experimental Station in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.402**	0.480**	-0.143	0.806**	0.133	0.090	0.564**
Days to Heading		0.895**	-0.772**	0.447**	-0.187	-0.428**	0.239**
Days to Maturity			-0.410**	0.491**	-0.024	-0.350**	0.245*
Maturity Duration				-0.227*	0.337**	0.387**	-0.129
Tiller					0.288**	-0.347**	0.056
Unproductive Tiller						-0.130	-0.211
100 Kernel Weight							0.398**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 82.

Table 17. Correlation coefficients of eight measured characters for the parent, F_1, BC_1, BC_2, F_2, and F_3 populations grown on the Hyslop Agronomy Farm in 1977.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.442**	0.478**	-0.338**	0.670**	-0.324**	0.369**	0.746**
Days to Heading		0.923**	-0.925**	0.481**	-0.418**	-0.119*	0.184*
Days to Maturity			-0.710**	0.486**	-0.301**	-0.130	0.268**
Maturity Duration				-0.402**	0.467**	0.085	-0.070
Tiller					-0.405**	-0.259**	0.078
Unproductive Tiller						-0.018	-0.025
100 Kernel Weight							0.530**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 127.

and the parent populations used (Appendix Table 10). Correlation coefficients with grain yield were r = 0.708 and 0.811 for days to heading and maturity, respectively, under low rainfall at Moro.

In comparing correlation coefficients for the F_2 populations alone, small, negative associations were found between yield and days to heading or maturity (r=-0.085 at Moro; r=-0.205 at Hyslop). This suggests that some selection for earliness can be done without reducing grain yield under both high and low rainfall conditions (Appendix Tables 4, 8, and 12). Consistent negative associations for maturity duration with grain yield involving all genotypes together and the nonsegregating generations separately were obtained. This relationship was positive in the F_2 generations being high (r=0.616) at Moro, and intermediate (r=0.380) at Hyslop (Appendix Tables 8 and 12); that is, in the F_2 populations, the extended filling period tended to produce much higher grain yield. The longer filling period permitted the plants to produce more fertile spike and heavier seed. Positive correlations were also found between 100 kernel weight and fertility in the F_2 populations. Consistently high and positive association existed between days to heading and days to maturity indicating that variation in heading date was reflected in almost the same pattern of variation in physiological maturity. This suggested that simultaneous improvement of both traits would be feasible.

Comparing the relationships grain yield and the yield components under both high and low rainfall conditions, it was evident that there was an association between yield and its components. Tiller number and fertility had higher correlation coefficients with yield than 100 kernel weight. This was particularly true under low rainfall conditions at Moro where kernel weight contributed less to yield than the other two components (Table 16). Almost no correlation between yield and 100 kernel weight was found at this site (r=0.090). The last stage of plant growth, kernel weight, is considered to be very sensitive to the effects of moisture stress; especially when plants have many tillers and seed has been formed. At both experimental sites, negative relationships between number of tillers per plant and 100 kernel weight were observed. The cause of this negative association was due to the fact that the plants which had many tillers produced lighter seed than those with fewer tillers. This suggests that simultaneous progress for both of these characters would be difficult to accomplish, especially where moisture is the limiting factor. However, the existence of negative correlation among the yield components was explained as an oscillatory response of components due to the sequential nature of components development and a limitation of environmental resources by Adams and Grafius (1971). The correlation coefficients, though, significant only at Hyslop 1977, showed that early genotypes tended to produce more unproductive tillers. This trait was negatively associated with grain yield under high rainfall conditions (Table 17). Under dryland conditions unproductive tiller number was positively associated with grain yield. The reason for this small but positive relationship was that unproductive tiller number was positively associated with grain yield. The reason for this small but positive relationship was that unproductive tiller number was positively correlated with productive tiller number which was in turn positively correlated with productive tiller number which was in turn positively correlated with grain yield.

Path-coefficient analysis provides a better understanding of association between the agronomic traits and yield by partitioning the correlation coefficients into direct and indirect effects obtained from the parents and all generations as shown in Tables 18 to 20.

The path-coefficient analysis calculated from data obtained at the Hyslop site in 1976 and 1977 indicated that tiller number and fertility had the largest direct influences on grain yield (Tables 18 and 20). In both years, the direct effect of kernel weight was relatively low (0.257 and 0.247) with a small negative indirect effect of this character via tiller number and days to maturity. Days to heading and maturity were of opposite signs in terms of the direct effects when the two experimental years are compared. The association of these factors with grain yield were consistent being positive and ranged from 0.328 to 0.478. These traits affected grain yield indirectly through number of tillers, fertility and maturity duration.

Table 18. Path-coefficient analyses of direct and indirect effects of seven traits on grain yield per plant involving parents and F_1, BC_1, BC_2, and F_2 generations grown on the Hyslop Agronomy Farm in 1976.

Relationships of Yield and:	Association with Yield (r)	Direct Effect (b')	Indirect Effects Via ($b'_{yj} \times r_{ij}$) Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Days to Heading	0.343	0.255	--	-0.165	-0.071	0.255	0.002	-0.041	0.109
Days to Maturity	0.328	-0.181	0.232	--	-0.038	0.199	-0.000	-0.027	0.143
Maturity Duration	-0.227	0.096	-0.188	0.071	--	-0.244	-0.004	0.048	-0.006
Tiller	0.723	0.691	0.094	-0.052	-0.034	--	0.001	-0.028	0.051
Unproductive Tiller	-0.063	-0.008	-0.052	-0.006	0.049	0.041	--	0.012	-0.017
100 Kernel Weight	0.488	0.257	-0.041	0.019	0.018	-0.076	-0.000	--	0.311
Fertility	0.720	0.472	0.059	-0.055	-0.001	0.075	0.000	0.169	--

$R^2, [\sum_{i=1}^{7} (r_{yi} \times b'_{yi})], = 0.972$

Table 19. Path-coefficient analyses of direct and indirect effects of seven traits on grain yield per plant involving parents and F_1, BC_1, BC_2, and F_2 generations grown on the Sherman Experimental Station in 1976.

Relationships of Yield and:	Asssociation with Yield (r)	Direct Effect (b')	Indirect Effects Via ($b'_{yj} \times r_{ij}$) Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Days to Heading	0.402	-1.126	--	0.755	0.388	0.374	0.002	-0.092	0.102
Days to Maturity	0.480	0.844	-1.008	--	0.206	0.410	0.000	-0.076	0.105
Maturity Duration	-0.143	-0.503	0.869	-0.346	--	-0.190	-0.003	0.084	-0.055
Tiller	0.806	0.836	-0.503	0.414	0.114	--	-0.003	-0.075	0.024
Unproductive Tiller	0.133	-0.010	0.211	-0.020	-0.170	0.241	--	-0.028	-0.090
100 Kernel Weight	0.090	0.216	0.482	-0.295	-0.195	-0.290	0.001	--	0.170
Fertility	0.564	0.427	-0.269	0.207	0.065	0.047	0.002	0.086	--

R^2, $[\sum_{i=1}^{7} (r_{yi} \times b'_{yi})]$, = 0.957

Table 20. Path-coefficient analyses of direct and indirect effects of seven traits on grain yield per plant involving parents and F_1, BC_1, BC_2, F_2, and F_3 generations grown on the Hyslop Agronomy Farm in 1977.

Relationships of Yield and:	Association with Yield (r)	Direct Effect (b')	Indirect Effects Via (b'_{yj} xr_{ij})						
			Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Days to Heading	0.442	-0.428	--	0.213	0.254	0.321	0.007	-0.029	0.104
Days to Maturity	0.478	0.231	-0.395	--	0.195	0.324	0.005	-0.032	0.150
Maturity Duration	-0.338	-0.275	0.396	0.164	--	-0.268	-0.007	0.021	-0.039
Tiller	0.670	0.667	-0.206	0.112	0.111	--	0.006	-0.064	0.044
Unproductive Tiller	-0.324	-0.016	0.179	0.070	-0.128	0.270	--	-0.004	-0.014
100 Kernel Weight	0.369	0.247	0.051	-0.030	-0.023	-0.173	0.000	--	0.297
Fertility	0.746	0.560	-0.079	0.062	0.019	0.052	0.000	0.131	--

$R^2, [\sum_{i=1}^{7} (r_{yi} x b'_{yi})], = 0.976$

Path-coefficient analysis values calculated for the Moro site were different than for Hyslop in case of earliness (Table 19). Although, the correlation coefficient between days to heading and grain yield was medium and positive (r=0.402), the direct effect of this trait on grain yield was very high and negative (b'=-1.126) under dryland conditions (Table 19). This implies that decreasing days to heading will increase grain yield provided that the indirect effects via other traits are held constant. In fact, at the Moro site, the indirect effects on grain yield via days to maturity, maturity duration, tiller number, and fertility were 0.755, 0.388, 0.374, and 0.102, respectively. An important point here is that earliness resulted in decreased tiller number and fertility and thus may reduce grain yield.

Among the yield components, tiller number showed the highest direct effect on grain yield. This trait also exhibited negative indirect effects and especially for days to heading and kernel weight at both experimental sites. However, the indirect effects of tiller number via the other components were very low with the exceptions of days to heading and maturity, maturity duration and kernel weight at the Moro site. Fertility had a high direct effect on grain yield and also indirectly through kernel weight at high rainfall site in both years. At the low rainfall site days to heading and days to maturity also were indirectly influenced by fertility and hence grain yield. Kernel weight had a low direct effect on grain yield but a positive indirect effect on grain yield through fertility for both years and locations. A negatively indirect effect for kernel weight via tiller number at both locations was noted. It was further observed that kernel weight had an indirect effect on grain yield being positive via days to heading and negative via days to maturity and maturity duration at the low rainfall site.

Similar associations were found for the yield components when just the parents and F_1 populations were considered (Appendix Tables 16, 17, and 18).

Based on the correlation and path-coefficient analyses, the following conclusions were made: (1) positive correlations were obtained between yield and days to heading when compared over all generations. However, in the F_2 generations, it seems possible to combine the desired earliness with high yields as indicated by the low association between these two traits at both experimental sites; (2) with regards to the yield components, tiller number had the highest direct influence on grain yield. However, because of a negative association between number of tillers and kernel weight, selection practices should be balanced between these two traits.

Regression Analyses

Regression analyses were used to obtain information about the nature of the relationship between yield and the other morphologic traits. This should provide information regarding the best predictors of grain yield. Also such analysis may provide an indication of the relative importance of yield-related characters and their relationship to earliness. Grain yield was selected as the response variable (dependent) and heading, maturity, maturity duration, unproductive tiller number and the yield components (tiller number, kernel weight and fertility) as the explanatory (independent) variables. The parents and all the generations in four winter x spring crosses at each location were utilized in this analysis. Data were examined to determine if a functional relationship exists between grain yield per plant and each of the measured agronomic traits. Data were fitted to polynomials of successively higher order with the equations concerning grain yield at each location presented in Tables 21, 22, and 23. At the Hyslop site, the equations indicated that there were significant linear relationships between yield and each of all agronomic traits in both years except unproductive tiller number in 1976 (Tables 21 and 23). In addition the second order terms had no real effects in respect to the independent variables at the Hyslop site in the first year of experiment. The significant simple regression coefficients of the first order term implies the amount of increase or decrease in unit change of the independent variable on grain yield (y) per plant (Tables 21, 22, and 23). In the second year (1977), however, the data suggested that the

Table 21. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, and F_2 generations grown on the Hyslop Agronomy Farm in 1976.

Variable	First and Second Order Equations	R_L^2 and R_Q^2	$R_Q^2 - R_L^2$	x_{max} and x_{min}
x_1, Days to Heading	$\hat{y} = 14.03^{**} + 0.427^{**}\, x_1$	0.1177**		
x_1^2, Sq. Days to Heading	$\hat{y} = 5.60 + 1.553\, x_1 - 0.015\, x_1^2$	0.1270	0.0093	
x_2, Days to Maturity	$\hat{y} = -19.16 + 0.559^{**}\, x_2$	0.1076**		
x_2^2, Sq. Days to Maturity	$\hat{y} = -75.73 + 1.871 - 0.008\, x_2^2$	0.1083	0.0007	
x_3, Maturity Duration	$\hat{y} = 60.10^{**} - 0.621^{*}\, x_3$	0.0513*		
x_3^2, Sq. Maturity Duration	$\hat{y} = 60.15 - 0.623\, x_3 + 0.00\, x_3^2$	0.0513	0.0000	
x_4, Tiller	$\hat{y} = 1.25 + 3.125^{**}\, x_4$	0.5228**		
x_4^2, Sq. Tiller	$\hat{y} = 6.06 + 1.659\, x_4 + 0.070\, x_4^2$	0.5254	0.0026	
x_5, Unproductive Tiller	$\hat{y} = 28.78^{**} - 0.964\, x_5$	0.0039		
x_5^2, Sq. Unproductive Tiller	$\hat{y} = 29.65^{**} - 4.315\, x_5 + 1.813\, x_5^2$	0.0091	0.0052	
x_6, 100 Kernel Weight	$\hat{y} = 23.20^{*} + 10.542^{**}\, x_6$	0.2383**		
x_6^2, Sq. 100 Kernel Weight	$\hat{y} = -58.72 + 25.374\, x_6 - 1.538\, x_6^2$	0.2399	0.0016	
x_7, Fertility	$\hat{y} = -12.60^{**} + 0.683^{**}\, x_7$	0.5188**		
x_7^2, Sq. Fertility	$\hat{y} = 18.54 + 0.882\, x_7 - 0.002\, x_7^2$	0.5193	0.0005	

*, **Significant at P = 0.05 and 0.01, respectively.

Table 22. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, and F_2 generations grown on the Sherman Experimental Station in 1976.

Variable	First and Second Order Equations	R^2_L and R^2_Q	$R^2_Q - R^2_L$	x_{max} and x_{min}
x_1, Days to Heading	$\hat{y} = -14.45 + 0.698^{*}\ x_1$	0.1618**		
x_2^2, Sq. Days to Heading	$\hat{y} = -76.00 + 3.074\ x_1 - 0.023\ x_1^2$	0.1698	0.0080	
x_2, Days to Maturity	$\hat{y} = -91.46^{**} + 1.203^{**}\ x_2$	0.2308**		
x_2^2, Sq. Days to Maturity	$\hat{y} = -105.25 + 1.496\ x_2 - 0.002\ x_2^2$	0.2308	0.0000	
x_3, Maturity Duration	$\hat{y} = 42.78^{*} - 0.504\ x_3$	0.0205		
x_3^2, Sq. Maturity Duration	$\hat{y} = -6.45 + 1.846\ x_3 - 0.028\ x_3^2$	0.0212	0.0007	
x_4, Tiller	$\hat{y} = 2.27 + 1.371^{**}\ x_4$	0.6502**		
x_4^2, Sq. Tiller	$\hat{y} = -4.77 + 2.371^{**}\ x_4 - 0.043^{*}\ x_4^2$	0.6748*	0.0246	$x_{max} = 27.6$
x_5, Unproductive Tiller	$\hat{y} = 19.59^{**} + 1.574\ x_5$	0.0177		
x_5^2, Sq. Unproductive Tiller	$\hat{y} = 19.76^{**} + 1.259\ x_5 + 0.096\ x_5^2$	0.0178	0.0001	
x_6, 100 Kernel Weight	$\hat{y} = 11.68 + 2.483\ x_6$	0.0081		
x_6^2, Sq. 100 Kernel Weight	$\hat{y} = 40.72 - 12.903\ x_6 + 2.020\ x_6^2$	0.0095	0.0014	
x_7, Fertility	$\hat{y} = -11.13^{*} + 0.845^{**}\ x_7$	0.3176**		
x_7^2, Sq. Fertility	$\hat{y} = 33.85 - 1.592\ x_7 + 0.032\ x_7^2$	0.3428	0.0252	

*, **Significant at P= 0.05 and 0.01, respectively.

Table 23. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, F_2, and F_3 generations grown on the Hyslop Agronomy Farm in 1977.

Variable	First and Second Order Equations	R_L^2 and R_Q^2	$R_Q^2 - R_L^2$	x_{max} or x_{min}
x_1, Days to Heading	$\hat{y} = 20.66^{**} + 0.490^{**} x_1$	0.1950**		
x_1^2, Sq. Days to Heading	$\hat{y} = 4.96 + 1.528^{*} x_1 - 0.016 x_1^2$	0.2112	0.0162	
x_2, Days to Maturity	$\hat{y} = -44.18^{**} + 0.974^{**} x_2$	0.2286**		
x_2^2, Sq. Days to Maturity	$\hat{y} = -699.36^{**} + 16.638^{**} x_2 - 0.093^{**} x_2^2$	0.2801**	0.0515	$x_{max} = 89.5$
x_3, Maturity Duration	$\hat{y} = 71.30^{**} - 0.694^{**} x_3$	0.1140**		
x_3^2, Sq. Maturity Duration	$\hat{y} = 34.46 + 0.741 x_3 - 0.014 x_3^2$	0.1151	0.0011	
x_4, Tiller	$\hat{y} = 3.58 + 2.401^{**} x_4$	0.4493**		
x_4^2, Sq. Tiller	$\hat{y} = -3.02 + 3.361^{*} x_4 - 0.034 x_4^2$	0.4507	0.0014	
x_5, Unproductive Tiller	$\hat{y} = 38.28^{**} - 3.117^{**} x_5$	0.1050**		
x_5^2, Sq. Unproductive Tiller	$\hat{y} = 40.05^{**} - 7.603^{**} x_5 + 1.168^{*} x_5^2$	0.1472*	0.0422	$x_{min} = 3.25$
x_6, 100 Kernel Weight	$\hat{y} = -6.86 - 8.820^{**} x_6$	0.1365**		
x_6^2, Sq. 100 Kernel Weight	$\hat{y} = -0.01 + 63.774^{*} x_6 - 5.839 x_6^2$	0.1583	0.0218	
x_7, Fertility	$\hat{y} = -10.62^{**} + 0.850^{**} x_7$	0.5559**		
x_7^2, Sq. Fertility	$\hat{y} = -20.96 + 1.250^{*} x_7 - 0.004 x_7^2$	0.5572	0.0013	

*, **Significant at P = 0.05 and 0.01, respectively.

statistical relation was curvilinear for days to maturity and unproductive tiller number (Table 23). The curvilinear relationship between grain yield and maturity date implies that as days to maturity increases, the yield increases up to the 89.5 days and then begins to decline. The maximum grain yield was obtained when unproductive tiller number was zero. The mean yield was minimized when there were 3.25 unproductive tillers per plant indicating that unproductive tillers decrease yield. In both years the largest amount of variation in yield was accounted for by variation in tiller number and fertility.

Since there were no relationships noted at the Moro site for maturity duration, unproductive tiller number and kernel weight (Table 22), no first-order or second order equations can be used to describe the data.

Grain yield was found to be a quadratic function of tiller number with about 67% of the variation being accounted for by fitting to a second order equation. With maximum grain yield the averaged tiller number was 27.6 tillers per plant.

When the independent variables were partitioned into two classes, earliness-related traits and yield-related traits, the equations for each location indicated that most of the variation in grain yield was explained for by the variation in yield-related traits (Table 24). Earliness-related traits (days to heading, maturity,

Table 24. Equations relating relating yield (y) per plant, earliness (x_1-x_3) and yield (x_4-x_7) related traits for parents and F_1, BC_1, BC_2, F_2, and F_3 generations grown on the Hyslop Agronomy Farm and the Sherman Experimental Station in 1976 and 1977.

Variable Added[1/]	Regression Equation	R_e^2 and R_f^2 [2/]	R_y^2 [3/]
	1977, Hyslop Agronomy Farm		
x_1, x_2, x_3	$\hat{y} = -47.83 + 1.611\,x_1 - 0.607\,x_2 + 1.634\,x_3$	0.231**	
x_4, x_5, x_6, x_7	$\hat{y} = -54.33 - 0.474\,x_1 + 0.470\,x_2 = 0.566\,x_3 + 2.390\,x_4 - 0.153\,x_5 + 5.904\,x_6 + 0.638\,x_7$	0.976**	0.745**
	1976, Hyslop Agronomy Farm[4/]		
x_1, x_2, x_3	$\hat{y} = 4.59 + 0.822\,x_1 - 0.345\,x_2 + 0.497\,x_3$	0.119*	
x_4, x_5, x_6, x_7	$\hat{y} = -51.56 + 0.318\,x_1 - 0.309\,x_2 + 0.263\,x_3 + 2.986\,x_4 - 0.123\,x_5 + 5.553\,x_6 + 0.448\,x_7$	0.972**	0.853**
	1976, Sherman Experimental Station[4/]		
x_1, x_2, x_3	$\hat{y} = -110.26 - 3.044\,x_1 + 4.328\,x_2 - 2.779\,x_3$	0.237**	
x_4, x_5, x_6, x_7	$\hat{y} = -69.07 - 1.953\,x_1 + 2.113\,x_2 - 1.768\,x_3 + 1.421\,x_4 - 0.113\,x_5 + 5.954\,x_6 + 0.640\,x_7$	0.957**	0.720**

*, **Significant at P = 0.05 and 0.01, respectively.

1/ x_1 = Days to Heading, x_2 = days to maturity, x_3 = maturity duration, x_4 = tiller, x_5 = unproductive tiller, x_6 = 100 kernel weight, x_7 = fertility.

2/ R_e^2, accounts for by the earliness-related traits; R_f, for full model.

3/ R_y^2, accounts for by the yield-related traits.

4/ For parents and F_1, BC_1, BC_2, and F_2 generations only.

and maturity duration) accounted for only about 23, 12, and 24% of the variation as noted by the R^2 values for grain yield at Hyslop 1976, Hyslop 1977, and Moro 1976, respectively. Whereas, yield related-traits (tiller number, unproductive tiller number, kernel weight, and fertility) accounted for about 75, 85, and 72% of the variation in grain yield at the corresponding locations.

Multiple regression analysis was used to determine the best predictors of grain yield under both high and low rainfall conditions (Tables 25, 26, and 27). The best regression equation to describe grain yield at Hyslop in 1976 included the independent variables of tiller number, fertility, and kernel weight in order of their respective importance. These accounted for a total of 97% of the variation in grain yield per plant. At Hyslop site in 1977, yield was described as a linear function of the same variables except days to heading was included in the equation which accounted for a total of about 98% of the variation in grain yield.

Under dryland conditions the yield components, tiller number, kernel weight, and fertility, also made up the linear regression equation which best described yield per plant (Table 26). About 95% of the variation in yield was accounted for by these components. However, the contribution of kernel weight to the coefficient of determination was low, being only about 3%. A similar situation was also observed in the path-coefficient analysis with kernel weight

Table 25. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, and F_2 generations grown on the Hyslop Agronomy Farm in 1976.

Variable Order	Regression Equation	R_L^2	S^2	$R_L^2 - R_{L-1}^2$ 1/
x_4, Tiller	$\hat{y} = -1.25 + 3.125^{**}(x_4)$	0.5228**	35.092	0.5228
x_7, Fertility	$\hat{y} = -35.07^{**} + 2.818^{**}(x_4) + 0.615^{**}(x_7)$	0.9388**	4.555	0.3860
x_6, 100 Kernel Weight	$\hat{y} = -53.50^{**} + 3.016^{**}(x_4) + 5.359^{**}(x_6)$ $+ 0.455^{**}(x_7)$	0.9716**	2.140	0.0328
x_3, Maturity Duration	$\hat{y} = -50.14^{**} - 0.068(x_3) + 2.982^{**}(x_4)$ $+ 5.490^{**}(x_6) + 0.452^{**}(x_7)$	0.9721**	2.128	0.0005
x_5, Unproductive Tiller	$\hat{y} = -50.49^{**} - 0.060(x_3) + 2.985^{**}(x_4)$ $-0.074(x_5) + 5.488^{**}(x_6) + 0.452^{**}(x_7)$	0.9721**	2.154	0.0000
x_1, Days to Heading	$\hat{y} = -51.81^{**} + 0.011(x_1) - 0.042(x_3)$ $+ 2.984^{**}(x_4) - 0.010(x_5) + 5.543^{**}(x_6)$ $+ 0.449^{**}(x_7)$	0.9722**	2.180	0.0001
x_2, Days to Maturity	$\hat{y} = -51.56^{**} + 0.318(x_1) - 0.309(x_2)$ $+ 0.263(x_3) + 2.986^{**}(x_4) - 0.123(x_5)$ $+ 5.553^{**}(x_6) + 0.448^{**}(x_7)$	0.9722**	2.203	0.0000
The best equation:	$\hat{y} = -53.50^{**} + 3.016^{**}(x_4) + 5.359^{**}(x_6)$ $+ 0.455^{**}(x_7)$	0.9716**	2.140	

*, **Significant at P = 0.05 and 0.01, respectively.

1/ $R_L^2 - R_{L-1}^2$, the proportion of variation in y accounted for by the last variable added.

Table 26. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, and F_2 generations grown on the Sherman Experimental Station in 1976.

Variable Order	Regression Equation	R^2_L	S^2	$R^2_L - R^2_{L-1}$ 1/
x_4, Tiller	$\hat{y} = 2.27 + 1.371^{**}(x_4)$	0.6542**	31.293	0.6542
x_7, Fertility	$\hat{y} = -27.06^{**} + 1.322^{**}(x_4) + 0.780^{**}(x_7)$	0.9198**	7.263	0.2656
x_6, 100 Kernel Weight	$\hat{y} = -47.12^{**} + 1.458^{**}(x_4) + 5.971^{**}(x_6)$ $+ 0.643^{**}(x_7)$	0.9530**	4.310	0.0332
x_2, Days to Maturity	$\hat{y} = -59.43^{**} + 0.125(x_2) + 1.430^{**}(x_4)$ $+ 6.499^{**}(x_6) + 0.615^{**}(x_7)$	0.9545**	4.223	0.0015
x_1, Days to Heading	$\hat{y} = -67.04^{**} - 0.156(x_1) + 0.307^{*}(x_2)$ $+ 1.426^{**}(x_4) + 5.990^{**}(x_6) + 0.632^{**}(x_7)$	0.9559**	4.147	0.0014
x_3, Maturity Duration	$\hat{y} = -68.75^{**} - 1.903(x_1) + 2.064(x_2)$ $- 1.734(x_3) + 1.415^{**}(x_4) + 5.995^{**}(x_6)$ $+ 0.641^{**}(x_7)$	0.9569**	4.106	0.0010
x_5, Unproductive Tiller	$\hat{y} = -69.07^{**} - 1.953(x_1) + 2.113(x_2)$ $- 1.768(x_3) + 1.421^{**}(x_4) - 0.113(x_5)$ $+ 5.954^{**}(x_6) + 0.640^{**}(x_7)$	0.9570**	4.154	0.001
The best equation:	$\hat{y} = -47.12^{**} + 1.458^{**}(x_4) + 5.971^{**}(x_6)$ $+ 0.643^{**}(x_7)$	0.9545**	4.223	

*, **Significant at P = 0.05 and 0.01, respectively.

1/ $R^2_L - R^2_{L-1}$, the proportion of variation in y accounted for by the last variable added.

Table 27. Equations relating yield (y) per plant and seven agronomic traits (x_1-x_7) for parents and F_1, BC_1, BC_2, F_2, and F_3 generations grown on the Hyslop Agronomy Farm in 1977.

Variable Order[1/]	Regression Equation	R^2_L	S^2	$R^2_L - R^2_{L-1}$ [2/]
x_7, Fertility	$\hat{y} = -10.62^{**} + 0.850^{**}(x_7)$	0.5559**	41.578	0.5559
x_4, Tiller	$\hat{y} = -37.13^{**} + 2.207^{**}(x_4) + 0.795\,(x_7)$	0.9330**	6.317	0.3771
x_6, 100 Kernel Weight	$\hat{y} = -61.20^{**} + 2.480^{**}(x_4) + 6.040^{**}(x_6) + 0.635^{**}(x_7)$	0.9732**	2.545	0.0402
x_1, Days to Heading	$\hat{y} = -61.87^{**} + 0.054^{**}(x_1) + 2.405^{**}(x_4) + 6.180^{**}(x_6) + 0.623^{**}(x_7)$	0.9750**	2.401	0.0018
x_2, Days to Maturity	$\hat{y} = -55.88^{**} + 0.095^{*}(x_1) - 0.088\,(x_2) + 2.410^{**}(x_4) + 6.070^{**}(x_6) + 0.631^{**}(x_7)$	0.9752**	2.397	0.0002
x_5, Unproductive Tiller	$\hat{y} = -56.31^{**} + 0.082\,(x_1) - 0.07\,(x_2) + 2.392^{**}(x_4) - 0.139\,(x_5) + 6.008^{**}(x_6) + 0.633\,(x_7)$	0.9753**	2.402	0.0001
The best equation:	$\hat{y} = -61.87^{**} + 0.054^{**}(x_1) + 2.405^{**}(x_4) + 6.180^{**}(x_6) + 0.623^{**}(x_7)$	0.9750**	2.401	

*, **Significant at P= 0.05 and 0.01, respectively.

1/ Variable x_3, Maturity duration, was dropped, since it was very highly correlated with variable x_1, days to heading (r_{13}=0.93).

2/ $R^2_L - R^2_{L-1}$, the proportion of variation in y accounted for by the last variable added.

having a low direct effect on grain yield.

From the results obtained from the regression analyses for both high and low rainfall conditions involving four winter x spring wheat crosses, the following conclusions can be drawn: (1) linear relationships exist between yield and each of the seven measured agronomic traits. Exceptions occurred in maturity duration, unproductive tiller number and kernel weight when compared across locations and years. Curvilinear relationships were observed only between yield and in turn maturity date, tiller number and unproductive tiller number depending on the experimental site and year. (2) Earliness-related traits appeared to be less important than yield-related traits in terms of contributing to coefficient of determination. (3) Grain yield may be described best as a linear function of all the components measured which included tiller number, fertility and kernel weight.

An overall summary, based on the results presented in this study would indicate that winter x spring wheat crosses have a great potential to increase genetic variability available to the breeders. The greater variability was observed when the F_1's were backcrossed to the winter parents. Differences in heading date between BC_1's and BC_2's suggested that earliness could be fixed by backcrossing to an early maturing parent. The positive association of grain yield and days to heading was somewhat unexpected under dryland conditions;

however, it seems possible to select for a degree of earliness without sacrificing grain yield. The variation in yield was almost totally accounted for by its components, namely: tiller number, fertility, and kernel weight as indicated by the coefficient of variation (R^2) which ranged between 0.95 to 0.98. This suggests that breeders can make effective progress in utilizing the three components as a selection criteria in developing superior cultivars. This result was confirmed by the positive association between grain yield and these components. However the existence of negative correlation or of compensating effects between tiller number and kernel weight would greatly influence progress toward obtaining maximum yield by overemphasizing of one of these two components. Therefore, in selection the breeder should strike a balance between tiller number and kernel weight. Especially under dryland conditions, selection concentrated solely for tiller number would decrease grain yield because of the curvilinear relationship between grain yield and tiller number. The consistent positive association of kernel weight with fertility indicated that it would not be hard to breed large grain into a fertile spike.

Under space-planted conditions the components of yield (tiller number, fertility and kernel weight) should be considered all together when selecting individual plant from segregating generations. Under both high and low rainfall conditions a high yielding individual plant may be described as that which has a medium number of tillers with fertile spikes and medium to large grain. It is also suggested that selection for extreme earliness must be avoided. The statistical relationship between grain yield and days to maturity was curvilinear at the Hyslop site, implying that as days to maturity increase, grain yield increases. This increase continues up to 89.5 days and then begins to decline. The date of maturity where maximum yield was obtained is only one day earlier than the days to maturity for the cultivar Hyslop (90.2 days). Thus, it is concluded that suitable earliness in these populations can be a few days earlier than the cultivar Hyslop without sacrificing grain yield.

SUMMARY AND CONCLUSIONS

Four genetically different winter wheat cultivars (Hyslop, Yamhill, Bezostaia 1, and Sprague) and one spring wheat cultivar (Inia 66) were used to study the inheritance and association of earliness and grain yield in four winter x spring wheat crosses. The parental cultivars were chosen on the basis of their relative maturity and contrasting agronomic characteristics. The four winter wheat cultivars were each crossed reciprocally with the spring cultivar to produce the F_1 generation. The F_2 generation was obtained by selfing while some F_1 plants were backcrossed to both their respective winter and spring parents forming BC_1's and BC_2's, respectively. Three selected F_3 families, F_3 (E) and F_3 (Y), were developed by selecting the earliest 1% and the highest yielding 1% of F_2 individuals in each cross. During the first year of the experiment reciprocal populations were kept separate, however, since no consistent differences were observed they were bulked during the second year.

Two experiments consisting of the parental cultivars, F_1, BC_1, and BC_2, and F_2 generations were conducted at Hyslop Agronomy Farm, Corvallis (1000 mm of rainfall) and Sherman Experimental Station, Moro (250 mm of rainfall) in 1976. The F_3 selected families were included to the experimental material during the second year at Hyslop Agronomy Farm. A parallel study with the same populations was also conducted the second year by vernalizing and planting the material in the spring at the Horticulture Farm, Corvallis.

Data were collected on an individual plant basis from space-planted nurseries and included: days to heading, days to maturity, maturity duration, unproductive tiller number, grain yield and its components; i.e., tiller number, kernel weight, and fertility.

The major objective of this study was to gain an understanding of earliness as it might influence maximum grain yield.

Analyses of variance were conducted on all characters at each experimental site. The frequency distributions for days to heading of parent, F_1, F_2, and BC's were examined to determine segregation pattern. The formula suggested by Wright was utilized to estimate the minimum number of segregating of loci involved in heading date. Estimates of F_1-midparent deviations, degree of dominance, and heritability in the narrow sense were determined for each cross. Simple correlations were calculated among all agronomic traits, and further partitioned into the direct and indirect influences on grain yield. Polynomial and multiple regression analyses were performed at each location to further examine the nature of the possible relationship for the traits measured. The following conclusions were drawn:

1. The parents, generations and crosses differed widely for eight measured characters particularly in terms of earliness.

Variability found within generations and crosses was sufficient to prompt further investigation of the inheritance of earliness, grain yield and yield-related traits.

2. Maternal inheritance was not involved in the genetic control of earliness, grain yield or the components of yield in four winter x spring wheat crosses.

3. A reversal of earliness between two winter cultivars, Hyslop and Sprague, and their crosses occurred between fall and spring plantings. A more detailed research will be required to investigate the response of these winter x spring wheat crosses to day-length and vernalization.

4. One to five partially dominant major genes, depending on the particular cross, appeared to be responsible for producing variation in heading date. The remaining unexplained variations were postulated to be due to modifying factors.

5. Estimates of gene action involved in the inheritance of earliness was primarily additive indicating that selection for earliness would be effective as early as the F_2 generation under both wet and dryland conditions.

6. Low narrow-sense heritability estimates were obtained for yield <u>per se</u>. Selection for this trait might not be effective; although, some actual advance was made in F_3 selected families over the F_2 or best parent in most of the crosses studied.

7. Higher heritability estimates for the components of yield indicated that there was more genetic variability associated with the yield components than yield *per se*.

8. Occurrence of additive genetic variation by location interactions implies that selection should be practiced simultaneously under as many different environments as possible if wide adaptability of potential lines is desired.

9. Heritability estimates for each of yield components were not consistent and ranged from 0 to greater than 1. Because of a pronounced additive effect by year interactions involving yield components, there would be no reason to delay selection for these traits. Selection, therefore, should be initiated in the F_2 generation. A large number of lines in the F_3 and later generations will be necessary to insure effectiveness of selection.

10. Positive correlations were obtained between yield and days to heading when compared over all generations. However, in the F_2 generations, it seems possible to combine the desired earliness with high yields as indicated by the low association between these two traits.

11. The path-coefficient analyses suggested that tiller number had the highest direct effect on grain yield. However, since there was a negative association between number of tillers and kernel weight, selection practices should be balanced between these two

components.

12. Linear relationships existed between yield and seven measured traits respectively across locations and years with only a few exceptions. Curvilinear relationships were observed only between yield and maturity date, tiller number, and unproductive tiller number, respectively.

13. Earliness-related traits appeared to be less important than yield-related traits with regard to contributing to the coefficient of determination.

14. Grain yield may be described best as a linear function of its components, tiller number, fertility and kernel weight.

15. Winter x spring wheat crosses appeared to provide the desired genetic variation to develop earlier maturing cultivars.

16. It is possible to select for earlier maturity dates without sacrificing grain yield using the experimental populations in this study. However, the extreme earliness observed for the spring parent, Inia 66, must be avoided due to late spring frost.

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Appendix Table 1. Pedigree and description of cultivars

HYSLOP : Nord Desprez - Sel. 101^2; A soft white, common, semi-dwarf, awned, mid-dense spike, high yielding winter wheat cultivar released by Oregon State University. Resistant to stripe rust (*Puccinia striiformis*) and common bunt (*Tilletia caries* and *T. foetida*), moderately resistant to powdery mildew (*Erysiphe graminis* f. sp. *tritici*), leaf rust (*Puccinia recondita*), and septoria (*Septoria tritici*). Medium earliness, large head size, medium kernel weight, good baking and milling quality.

YAMHILL : Heines VII - Redmond (Alba); A low tillering, medium height, high yielding, soft white, awned winter wheat cultivar released by Oregon State University. Good milling and baking qualities. Resistant to stripe rust and powdery mildew. Late, large fertile spikes and medium to large kernels.

BEZOSTAIA 1: Developed in the Kuban region of the USSR. An awnless, hard red, mid-dense and mid-long spike, low tillering, large kernel, and winter wheat cultivar. Susceptible to stem rust (*Puccinia graminis* f. sp. *tritici*), septoria, and moderately susceptible to stripe rust and powdery mildew. Good baking and milling qualities. An early maturing cultivar.

SPRAGUE : PI. 181268 - Gaines; A semi-dwarf but weak straw cultivar released by Washington State University for dryland areas where snow mold is a problem and rainfall is about 250 mm. Medium earliness, small head size, good tillering, low fertility, awned, small kernel, soft white winter wheat cultivar. Resistant to snow mold (*Fusarium nivale* and *Typhula idahoensis*), stripe rust and common bunt but susceptible to dwarf bunt (*Tilletia controversa*) and cercosporella foot rot (*Cercosporella herpotrichoides*).

INIA 66 : A semi-dwarf, awned, hard red spring wheat cultivars. Developed in Mexico. Long, medium size kernels. High test weight, excellent milling and baking qualities. High yielding in spring wheat areas, light insensitive and very early cultivar. Resistant to stem rust but susceptible to leaf rust.

Appendix Table 2. Summary of climatic data for Corvallis and Moro locations during the study.

Location and year	Months	Precipitation (mm)	Temperature (°C) Max.	Min.	Mean
Corvallis 1975-76	October	109.2	15.8	6.5	11.2
	November	139.9	11.1	1.9	6.5
	December	164.3	9.1	2.2	5.7
	January	167.4	8.6	1.5	5.1
	February	170.4	9.6	0.5	5.1
	March	113.0	11.3	1.5	6.4
	April	50.3	14.5	3.2	8.9
	May	29.0	18.6	5.1	11.8
	June	1.2	21.0	7.0	14.0
	July	8.4	26.1	10.2	18.2
	Total	953.1	--	--	--
Moro 1975-76	October	29.7	15.1	3.9	9.5
	November	34.0	8.3	-1.1	3.7
	December	32.0	5.9	-1.2	2.4
	January	31.8	6.4	-2.2	2.1
	February	23.6	6.2	-2.6	1.8
	March	24.1	8.8	-1.8	3.5
	April	26.9	12.7	1.1	6.9
	May	3.6	19.3	4.7	12.0
	June	0.2	19.0	10.7	14.9
	July	20.1	26.3	15.8	21.0
	Total	226.0	--	--	--
Corvallis 1976-77	October	31.8	19.1	5.1	12.1
	November	36.1	13.1	3.4	8.3
	December	37.3	6.4	-0.4	3.1
	January	24.4	7.1	-2.3	2.4
	February	75.4	12.5	1.4	7.0
	March	129.3	11.4	1.4	6.4
	April	25.9	17.1	3.1	10.2
	May	87.1	16.5	5.3	10.9
	June	28.7	23.6	8.7	16.2
	July	3.1	26.0	9.5	17.8
	Total	479.1	--	--	--

Appendix Table 3. Correlation coefficients between mean heading dates of fall and spring planted experiments grown on the Hyslop Agronomy and Horticulture Farms in 1977.

Spring planted experiment on the Horticulture Farm	Fall planted experiment on the Hyslop Agronomy Farm: Parents	F_1's	Parents and F_1's	F_2's	Parents, F_1's, BC_1's BC_2's, F_2's, and F_3's
Parents	0.973**[1/]				
F_1's		0.634*			
Parents and F_1's			0.959**		
F_2's				0.339	
Parents, F_1's, BC_1's, BC_2's, F_2's, and F_3's					0.935**

*, **Significant at the 5% and 1% levels, respectively.

[1/] Degrees of freedom:

For parents = 13,

For F_1's = 10,

For parents and F_1's = 25,

For F_2's = 10,

For parents, F_1's, BC_1's, BC_2's, F_2's, and F_3's = 127.

Appendix Table 4. Correlation coefficients of eight measured characters for the four F_2 populations grown on the Hyslop Agronomy Farm in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.078	-0.180	-0.390	0.482*	-0.238	0.356	0.284
Days to Heading		0.868**	-0.631**	0.310	0.092	-0.425	-0.133
Days to Maturity			-0.170	-0.058	0.383	-0.299	0.072
Maturity Duration				-0.761**	0.346	0.455*	0.465*
Tiller					-0.076	-0.535*	-0.652**
Unproductive Tiller						-0.119	-0.064
100 Kernel Weight							0.694**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 19.

Appendix Table 5. Correlation coefficients of eight measured characters for the parent and F_1 populations grown on the Hyslop Agronomy Farm in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.259	0.229	-0.214	0.705**	-0.251	0.418**	0.714**
Days to Heading		0.907**	-0.763**	0.376*	-0.470**	-0.307	0.109
Days to Maturity			-0.421**	0.318*	-0.156	-0.299	0.129
Maturity Duration				-0.324*	0.778**	-0.191	-0.041
Tiller					-0.113	-0.204	0.078
Unproductive Tiller						-0.016	-0.257
100 Kernel Weight							0.646**

*Significant at the 5% level.

**Significant at the 1% level.

1/ D.F. = 37.

Appendix Table 6. Correlation coefficients of eight measured characters for the five parent populations grown on the Hyslop Agronomy Farm in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.462	0.424	-0.466	0.800**	-0.441	0.497	0.820**
Days to Heading		0.974**	-0.881**	0.351	-0.679**	-0.131	0.608*
Days to Maturity			-0.751**	0.310	-0.533*	-0.150	0.583*
Maturity Duration				-0.373	0.861**	0.048	-0.553*
Tiller					-0.160	0.012	0.401
Unproductive Tiller						-0.215	-0.621*
100 Kernel Weight							0.600*

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 13.

Appendix Table 7. Correlation coefficients of eight measured characters for the four F_1 populations grown on the Hyslop Agronomy Farm in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.218	0.017	-0.222	0.648**	-0.279	0.350	0.603**
Days to Heading		0.756**	0.109	0.256	0.163	-0.303	0.081
Days to Maturity			0.732**	0.135	0.566**	-0.257	-0.082
Maturity Duration				-0.065	0.701**	-0.097	-0.231
Tiller					0.084	-0.315	-0.163
Unproductive Tiller						-0.165	-0.456*
100 Kernel Weight							0.623**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 22.

Appendix Table 8. Correlation coefficients of eight measured characters for the four F_2 populations grown on the Sherman Experimental Station in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	-0.085	0.182	0.616**	0.640**	0.623**	0.353	0.238
Days to Heading		0.919**	-0.482*	0.083	0.004	-0.358	-0.189
Days to Maturity			-0.107	0.227	0.245	-0.208	-0.098
Maturity Duration				0.209	0.422	0.521*	0.380
Tiller					0.803**	-0.449*	-0.553**
Unproductive Tiller						-0.210	-0.437*
100 Kernel Weight							0.842**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 19.

Appendix Table 9. Correlation coefficients of eight measured characters for the parent and F_1 populations grown on the Sherman Experimental Station in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.455**	0.518**	-0.216	0.779**	0.298	-0.089	0.578**
Days to Heading		0.882**	-0.795**	0.501**	-0.152	-0.502**	0.290
Days to Maturity			-0.415**	0.502**	0.063	-0.405*	0.306
Maturity Duration				-0.324*	0.374*	0.450**	-0.163
Tiller					0.506**	-0.567**	0.040
Unproductive Tiller						-0.229	-0.198
100 Kernel Weight							0.328*

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 37.

Appendix Table 10. Correlation coefficients of eight measured characters for the five parent populations grown on the Sherman Experimental Station in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.708**	0.811**	-0.449	0.714**	0.106	-0.200	0.691**
Days to Heading		0.961**	-0.909**	0.665**	-0.103	-0.562*	0.495
Days to Maturity			-0.758**	0.664**	-0.090	-0.454	0.580*
Maturity Duration				-0.566*	0.108	0.638*	-0.294
Tiller					0.545*	-0.767**	0.053
Unproductive Tiller						-0.480	-0.444
100 Kernel Weight							0.362

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 13.

Appendix Table 11. Correlation coefficients of eight measured characters for the four F_1 populations grown on the Sherman Experimental Station in 1976.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.115	0.172	0.058	0.867**	0.476*	0.137	0.461*
Days to Heading		0.796**	-0.504*	0.159	-0.114	-0.243	-0.061
Days to Maturity			0.121	0.228	0.272	-0.259	-0.051
Maturity Duration				0.059	0.568**	0.039	0.042
Tiller					0.557**	-0.097	-0.002
Unproductive Tiller						0.002	0.013
100 Kernel Weight							0.372

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 22.

Appendix Table 12. Correlation coefficients of eight measured characters for the four F_2 populations grown on the Hyslop Agronomy Farm in 1977.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	-0.205	0.101	0.380	0.484	-0.635*	0.592*	0.855**
Days to Heading		0.710**	-0.773**	-0.830**	0.034	0.357	0.198
Days to Maturity			-0.101	-0.372	0.217	0.151	0.414
Maturity Duration				0.838**	0.147	-0.368	0.094
Tiller					-0.149	-0.235	0.090
Unproductive Tiller						-0.806**	-0.406
100 Kernel Weight							0.582*

*Significant at the 5% level.

**Significant at the 1% level.

1/ D.F. = 10.

Appendix Table 13. Correlation coefficients of eight measured characters for the parent and F_1 populations grown on the Hyslop Agronomy Farm in 1977.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.194	0.209	-0.165	0.680**	0.163	0.377	0.745**
Days to Heading		0.969**	-0.965**	0.493**	-0.496**	-0.227	-0.224
Days to Maturity			-0.870**	0.562**	-0.368	0.327	-0.244
Maturity Duration				-0.386*	0.599**	0.105	0.187
Tiller					0.338	-0.352	0.072
Unproductive Tiller						-0.027	0.246
100 Kernel Weight							0.679**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 25.

Appendix Table 14. Correlation coefficients of eight measured characters for the five parent populations grown on the Hyslop Agronomy Farm in 1977.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductive Tiller	100 Kernel Weight	Fertility
Yield	0.407	0.449	-0.341	0.787**	-0.462	0.326	0.828**
Days to Heading		0.965**	-0.969**	0.506	-0.694**	-0.046	0.145
Days to Maturity			-0.869**	0.585*	-0.546*	-0.151	0.182
Maturity Duration				-0.399	0.789**	-0.055	-0.102
Tiller					-0.403	-0.275	0.351
Unproductive Tiller						-0.279	-0.184
100 Kernel Weight							0.603*

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 13.

Appendix Table 15. Correlation coefficients of eight measured characters for the four F_1 populations grown on the Hyslop Agronomy Farm in 1977.

Character[1/]	Days to Heading	Days to Maturity	Maturity Duration	Tiller	Unproductuve Tiller	100 Kernel Weight	Fertility
Yield	0.148	0.317	0.039	0.509	0.558	0.416	0.757**
Days to Heading		0.862*	-0.890**	0.033	0.040	0.103	0.089
Days to Maturity			-0.537	0.375	0.223	-0.077	0.075
Maturity Duration				0.283	0.134	-0.242	-0.080
Tiller					-0.102	-0.499	-0.152
Unproductive Tiller						0.497	0.789**
100 Kernel Weight							0.787**

*Significant at the 5% level.

**Significant at the 1% level.

[1/] D.F. = 10.

Appendix Table 16. Path-coefficient analyses of direct and indirect effects of four traits on grain yield per plant involving parent and F_1 populations grown on the Hyslop Agronomy Farm in 1976.

Relationships of Yield and:	Association with Yield (r)	Direct Effect (b')	Indirect Effects Via ($b'_{yj} \times r_{ij}$)			
			Days to Heading	Tiller	100 Kernel Weight	Fertility
Days to Heading	0.259	0.012	--	0.267	-0.075	0.055
Tiller	0.705	0.711	0.005	--	-0.050	0.039
100 Kernel Weight	0.418	0.244	-0.004	-0.145	--	0.323
Fertility	0.714	0.500	0.001	0.055	0.158	--

$R^2 = [\sum_{i=1}^{4} (r_{yi} \times b'_{yi})], = 0.963$

Appendix Table 17. Path-coefficient analyses of direct and indirect effects of four traits on grain yield per plant involving parent and F_1 populations grown on the Sherman Experimental Station in 1976.

Relationships of Yield and:	Association with Yield (r)	Direct Effect (b')	Indirect Effects Via ($b'_{yj} \times r_{ij}$)			
			Days to Heading	Tiller	100 Kernel Weight	Fertility
Days to Heading	0.455	0.016	--	0.462	-0.150	0.127
Tiller	0.779	0.922	0.008	--	-0.169	0.018
100 Kernel Weight	-0.089	0.298	-0.008	-0.523	--	0.144
Fertility	0.578	0.438	0.005	0.037	0.098	--

$R^2 = [\sum_{i=1}^{4} (r_{yi} \times b'_{yi})], = 0.952$

Appendix Table 18. Path-coefficient analyses of direct and indirect effects of four traits on grain yield per plant involving parent and F_1 populations grown on the Hyslop Agronomy Farm in 1977.

Relationships of Yield and:	Association with Yield (r)	Direct Effect (b')	Indirect Effects Via ($b'_{yj} \times r_{ij}$)			
			Days to Heading	Tiller	100 Kernel Weight	Fertility
Days to Heading	0.194	-0.004	--	0.377	-0.075	-0.104
Tiller	0.680	0.764	-0.002	--	-0.116	0.034
100 Kernel Weight	0.377	0.329	0.001	-0.269	--	0.316
Fertility	0.745	0.466	0.001	0.055	0.223	--

R^2, $[\sum_{i=1}^{4} (r_{yi} \times b'_{yi})]$, = 0.990