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Title: Duration and Rate of the Grain Filling Period and Subsequent Grain Yield in Crosses between Facultative and Winter Wheat Cultivars (*Triticum aestivum* L. em Thell)

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Concerns about the genetic control and environmental influence of various stages of development including the grain filling period, and the relationship between early maturity and grain yield prompted this study.

The experimental material consisted of two facultative and two winter wheat cultivars. A diallel cross, excluding reciprocals, was also developed to provide an F1 generation. Information was collected for 14 traits and subjected to statistical analyses.

Genetic differences among varieties were found for time of heading, flowering and physiological maturity, duration and rate of the grain filling period, grain yield and yield components. The facultative types, AI Feng 2 and Selection CB 83-52, showed earlier heading, flowering and physiological maturity, longer lag period (period between heading and flowering), and longer duration and lower rate of grain filling, resulting in lower grain yield. The winter cultivars, Stephens and Yamhill Dwarf, in contrast had later heading, flowering and maturity, shorter lag period, and shorter duration and

higher rate of grain filling, giving higher grain yield. For the developmental stages after heading, larger differences were observed in the lag period while differences in duration of grain filling period were relatively small among the cultivars.

Depending on the specific F1 population, there was a tendency toward dominance for early heading, a range from no to complete dominance for early flowering and no dominance for physiological maturity. Long duration and fast rate of grain filling were generally dominant.

Grain yield was positively associated with the number of days to heading, flowering and physiological maturity. Also positive associations of grain yield were obtained with tiller number, kernel weight, grain weight per spike, biological yield and rate of grain filling. Negative associations of grain yield were noted with lag period and duration of grain filling period. No clear associations between physiological maturity and the yield components were found. Grain filling duration showed no association with yield components while grain filling rate exhibited positive association with tiller number and kernel weight. There was negative association between duration and rate of grain filling period.

According to heading responses from different planting dates, Stephens and Yamhill Dwarf had high sensitivity while Selection CB 83-52 and AI Feng 2 showed low sensitivity to vernalization. Genotype X environment interaction was observed with each cultivar responding differently for several traits depending on the planting dates.

Duration and Rate of the Grain Filling Period and Subsequent Grain Yield in Crosses between Facultative and Winter Wheat Cultivars (*Triticum aestivum* L. em Thell)

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IN DEDICATION TO

MY FAMILY

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INTRODUCTION

The development of early maturing wheat cultivars is receiving increasing attention from breeders. Early maturity may aid in avoiding such factors as high temperature, drought or excessive moisture, diseases, insects, and other abiotic and biotic stresses, associated with reduced grain yield and quality. Combinations of early maturity and acceptable grain yield would also allow wheat to be more adaptable to multiple cropping systems thus intensifying cropping both in time and space.

The life cycle of the wheat plant is controlled by genetic, physiological and environmental factors. Time of heading, anthesis and physiological maturity are important latter stages of wheat development and influence the duration and rate of the grain filling period. These stages are also modified by such factors as vernalization, photoperiod and temperature.

Multiple cropping systems like wheat-rice-rice, wheat-corn, wheat-cotton, etc. have been widely developed in China due to the increasing food demands. Adapting to such a situation, one of the most significant characters of Chinese wheat varieties is their earliness. This resulted from long term natural or artificial selection. However, the genetic and environmental control of the growing cycle and especially the maturation period of these varieties have not been fully investigated. Furthermore, there often seems to be a negative association between early maturity and grain yield. If cultivars with early maturity and acceptable grain yield are to be developed, more information is needed regarding the nature, inheritance and environmental influence with various stages of development. The inter-relationships between growth stages and yield components as well as grain yield must also be investigated in greater detail.

In order to provide such information the following objectives were addressed in this study:

1) to determine if there are genetic differences among wheat cultivars for time of heading, anthesis, physiological maturity and their influence on the duration and rate of the grain filling period;

2) to determine if the possible effects of the traits on grain yield exist in crosses of Chinese early-maturing cultivars and high-yielding cultivars developed by Oregon State University;

3) to examine the inheritance of selected traits as they relate to wheat breeding;

4) to examine developmental response and subsequent grain yield of cultivars as influenced by different dates of planting.

LITERATURE REVIEW

Earliness

The life cycle of the wheat plant can be defined by various stages of growth and development. These include seed germination, seedling emergence, tillering, stem elongation, heading, anthesis, grain filling and maturity. Time and duration of each stage influences the ultimate time of maturity (Large, 1954; Li, 1976).

Cultivar differences for early growth and development have been described in wheat. A report from Kiangsu Institute of Agricultural Sciences (1976) indicated that there are several types of earliness. Some early spring cultivars grow rapidly to stem elongation and heading, then slow down from heading to maturity. On the contrary, some early winter varieties may grow slowly from seedling emergence to heading, but develop faster from heading to maturity. Choi (1982) found that great variation occurred in the stem elongation stage for five winter and five spring cultivars when planted at different dates.

The developmental differences between wheat and barley have been noted. For barley, it was found that the stem elongation was often later, while the pollen development was earlier and faster when compared to wheat. In general, from stem elongation onward, the development of barley accelerates, reaching maturity earlier than wheat. Also, barley plants can head and flower at relatively low temperatures (Li, 1976; Xue, 1979).

Earliness in cereal crops is scored in several ways. Days to floral initiation, internode elongation, flag leaf unfolding, heading, anthesis, and physiological maturity have all been used to monitor earliness. However, the heading date is most frequently used as an indicator of earliness in wheat as it can be easily identified and is often closely associated with maturity date (Li, 1976).

Many investigations have been conducted to study the inheritance of the heading date in wheat. Early generation analyses generally suggested that early heading was dominant (Kiangsu Institute of Agricultural Sciences, 1976; Avey and Ohm, 1982; Yu,1982). The Kiangsu Institute of Agricultural Sciences (1976) reported that early heading plants were usually more numerous than late ones in F2 generations of seven crosses between early and late heading cultivars. Yu (1982) observed transgressive segregation for both earlier and later heading in F2 generations in 10 out of 15 crosses.

Using a diallel cross analysis of heading date, Crumpacker and Allard (1962) indicated that a few major genes with dominance effects were the most important feature of the genetic system governing heading date in spring wheat. They also noted the presence of minor genes which displayed little or no dominance. No evidence for major epistatic effects was found. The narrow sense heritability estimates were 55, 67 and 74 per cent respectively in the three years in which their study was conducted. They also indicated that the genotypic-environmental interactions were small for heading date. Allard and Harding (1963) reported that most of the variation in heading time is governed by one gene pair in their early generation analysis of derivatives from a wheat cross, Ramona X Baart 46. In a study of three wheat crosses, Avey and Ohm (1982) suggested one or more major genes controlling days to heading with possible modification by an underlying minor gene system. They found that fixable components, additive or additive X additive effects, were predominant in the genetic variance, although dominance or epistatic effects may be of some consequence in specific crosses. It has been suggested that gains from selection should be possible in early generations, especially for the major gene effects (Crumpacker and Allard, 1962; Amaya et al, 1972; Avey and Ohm, 1982). Scientists indicated that the hybrid vigor may also play a role in the expression of earliness in early generations (Kiangsu Institute of Agricultural Sciences, 1976).

Influences of Vernalization, Photoperiod and Temperature on Earliness

The growth and development of the wheat plant can be strongly influenced by several environmental factors. These include light, temperature, water, nutrition, etc.. Among these vernalization, photoperiod and temperature are considered to be the most important in determining earliness.

A. Vernalization Requirement

Response to vernalization is an attribute affecting growth habit in wheat. Winter wheat plants require a period of cold treatment during their development before they shift from a vegetative to a reproductive phase. If lacking, they either fail to reach heading or their heading is much reduced. The Russian geneticist Lysenko found that artificial cold treatment of seeds of winter wheat which are beginning to germinate would permit them to head like spring wheat when planted in the spring (Choi, 1982).

A wide range of vernalization response among wheat cultivars was reported by Halse and Weir (1970). They studied sixteen Australian wheat cultivars in growth chambers and found a range of responses to seed vernalization varying from little or no promotion of floral initiation in some varieties to about 3 weeks in some others. Levy and Peterson (1972) found that following cold treatment, the heading time of winter wheat is greatly promoted and that many spring wheats also show a small but definite acceleration.

In genetic studies for vernalization response, Pugsley (1963) indicated the presence of a single-gene difference governing this behavior in two near-isogenic lines of spring wheat. In crosses between spring and winter wheat, the spring habit is generally dominant over winter habit and, depending on the parents involved in the cross, one, two, or three independently inherited genes were found to control these characters (Yasuda, 1968; Pugsley, 1971; Klaimi and Qualset, 1974). Klaimi and Qualset (1974) also reported that besides the presence of major genes, minor genes and multiple alleles were involved in governing vernalization response.

It has been found that the vernalization effect can be reversed in its early stages by heat treatment. Chujo (1970) vernalized plants of winter wheat cultivar Norin 27 immediately after sowing for 30 or 40 days at 1, 4, 8, 11 and 15^{o}C respectively, using continuous illumination. After the vernalization treatment, he exposed the plants to relatively high temperature treatments of 12, 18 or 24^{o}C for 10 days. The plants were then transplanted into a greenhouse and exposed to a 15^{o}C and 20-hour photoperiod. He found that the vernalization effect achieved at 1 or 4^{o}C were reversed markedly by the subsequent exposure to high temperature such as 18 or 24^{o}C, but the effect obtained at 8 or 11^{o}C were reversed only slightly by the same treatments.

B. Photoperiod Response

Historically wheat has been classified as a long-day or short night species based on its photoperiodic response. A wheat plant will continue to grow vegetatively until its photoperiod requirement is met, even under relatively warm temperatures. Photoperiod response influences initiation and differentiation of floral primordia. In an experiment conducted in a growth chamber, Halse and Weir (1970) found that all 16 wheat cultivars tested achieved floral initiation earlier in long days (14 hr photoperiod vs 10 hr). Pinthus and Nerson (1984) observed that a long photoperiod applied after the onset of spike apex elongation, but not earlier, induced the differentiation of spikelets in the axils of already existing primordia. Under a short photoperiod, leaves developed instead of spikelets.

It is known that wheat cultivars do differ in their response to daylength. Characterization of varietal differences generally is made on vernalized material by obtaining response curves representing the number of days to ear emergence in relation to daylength. Cultivars showing a steep slope between the short and long day regimes are described as photoperiod-sensitive. Those with little or no change are insensitive or day neutral (Klaimi and Qualset, 1973; Upadhya *et al*, 1977).

Borlaug *et al* (1964) suggested that relatively few major genes are involved in conditioning the sensitivity of spring wheats to changes in photoperiod. Undoubtly, the insensitivity to daylength of the wheat cultivars developed at CIMMYT (International Maize and Wheat Improvement Center) is one of the factors contributing to their wide adaptability. The daylength insensitivity has minimized the genotype X environment interaction due to daylength response when a cultivar is grown in a wide array of latitudes. Syme (1968) studied the photoperiod response of 16 Mexican, European and Australian wheat cultivars in the growth chamber. He reported that the European cultivars showed a high sensitivity to daylength, materials developed in Mexico had a low sensitivity with Australian cultivars being intermediate in sensitivity. Most spring wheats developed and grown in the northern latitudes of the United States have a long-day photoperiod requirement (Busch and Chamberlain, 1981). Levy and Peterson (1972) reported that all 13 spring cultivars tested headed earlier with increasing photoperiods in a series of treatments from 9 to 17 hours. Early-maturing cultivars responded least to lengthened photoperiods, and late-maturing cultivars responded more. They suggested that photoperiod alone rather than vernalization is the primary factor controlling maturity in spring wheats.

Minor gene modifiers and multiple alleles have also been postulated to account for observed genetic variation in wheat. Klaimi and Qualset (1973) described the photoperiod response in selected wheat crosses to be based on two loci with potentially three alleles available per locus with other minor genes affecting the expression of this response in a quantitative manner. Their F1 data indicated that daylength insensitivity is not always dominant and that the dominance relationship with respect to photoperiod response depends on the alleles present in the parents. They also indicated significant additive and nonadditive (dominance) genetic variances, with a high average degree of dominance for photoperiod insensitivity using a diallel cross analysis of the number of days to heading. Epistasis was also detected by the generation mean analysis. Keim et al (1973) found insensitivity in wheat to be controlled by two major genes with dominant epistasis, and minor modifiers being present in crosses of photoperiod sensitive by insensitive cultivars.

Many studies have indicated the presence of interactions between photoperiod and vernalization effect. Halse and Weir (1970) reported that under short day (10 hr vs 14 hr photoperiod) the promotion of floral initiation by seed vernalization in Australian wheat cultivars was reduced. Levy and Peterson (1972) found that all spring and winter wheat cultivars tested headed earlier if vernalized with increasing photoperiods in a series of treatments from 9 to 17 hours. A highly significant interaction was obtained between vernalization and photoperiod response in a cultivar showing small responses to these individual treatments. Interactions between these environmental factors may explain some of the observed reversals in order of heading of some cultivars when grown in different geographic regions. Within limits, it appears that extending the vernalization time can replace a photoperiod deficiency, or, conversely, extending the photoperiod can replace a vernalization deficiency (Levy and Peterson, 1972; Klaimi and Qualset, 1974). However, the existence of wheat cultivars exhibiting various combinations of response to photoperiod and vernalization indicates that these two attributes are not associated in inheritance and provides for the possibility that a desirable pattern of earliness may be obtained by manipulating genes for daylength or vernalization or both.

C. Temperature effect

Temperature is also known to be an important factor affecting the growth and development in wheat. Halse and Weir (1970) found that higher temperatures (18/13^{o}C vs 12/7^{o}C day/night) accelerated development to floral initiation and anthesis in all sixteen Australian wheat cultivars tested, with only minor differences in magnitude of response. It is known that the ideal temperatures for different stages of the wheat plant vary from 22 to 25^{o}C for germination, 16 to 20^{o}C for tillering and 20 to 22^{o}C for active growth (Kolhe et al, 1977). It has been reported that wheat cultivars reach heading more rapidly at higher temperatures. Following the satisfaction of the vernalization requirement, photoperiod and increasing temperature are the main determining factors in heading (Kiangsu Institute of Agricultural Sciences, 1976; Pirasteh and Welsh, 1980).

Growing degree days have been used to study the growth and development of wheat plants. Growing degree day also known as heat unit or thermal unit is the average of the highest and lowest air temperature that occured in a day. By subtracting the base temperature (usually 0 to 4.5^{o}C for wheat) from the mean temperature, growing degree days for a 24 hour period are obtained. Rickman and Klepper (1983) found that 50 percent emergence can be expected between 85 and 100 growing degree days (with a 3^{o}C base) after planting. One leaf will develop on the main stem and on every tiller present for every 55 growing degree days after emergence. In studying the effect of temperature on the heading date, Pirasteh and Welsh (1980) devised a similar method of evaluation called degree-hours by subtracting 4.4°C from the daytime temperature and multiplying by the total number of hours of light at each temperature. They found that cultivars varied widely in the number of degree-hours required to arrive at heading. However, the similarities in averages and ranges of degree-hours to heading between the winter and spring cultivars suggested that once the cold requirements for vernalization are satisfied in obligate winter types, the subsequent plant development is driven by the same sets of energy and photoperiod requirements as for spring cultivars. From planting to heading, more degree-hours were used by all 10 cultivars tested at the warmer temperature (21.0/12.7°C vs 15.5/7.2°C day/night) indicating that only part of the increased temperature was translated into accelerated heading.

Other factors affecting wheat earliness have also been reported. Syme (1968) found that Siete Cerros 66 and Sonora 64 had identical vernalization and photoperiodic responses. However, the former headed from 5 to 25 days later than the latter in the field, depending on time of planting. He indicated that this was due to an inherited earliness factor independent of daylength and vernalization response. Keim et al (1973) also indicated that an earliness character that is different from the vernalization and photoperiod responses appears to exist in wheat. Factors governing this appear to be minor in their effect when compared with the genes governing the photoperiod response. Klaimi and Qualset (1974) reported that spring and winter cultivars became comparable in heading time when grown under continuous light after 8 weeks of cold treatment. However, even under this treatment, significant differences among cultivars in heading time were still found, suggesting the presence of other factors influencing this character.

Duration and Rate of Grain Filling

Duration of grain filling period in cereal crops has been interpreted differently by scientists. It may include the total grain growth period from heading to maturity (Spiertz et al, 1971) or from anthesis to maturity (Wiegand and Cuellar, 1981; Sayed and Gadallah, 1983), and as from anthesis to physiological maturity (Lee, 1977; Choi, 1982). Physiological maturity is defined as the date beyond which there is no significant increase in kernel dry weight.

Grain filling rate is the result of the translocation of photosynthate from source to sink. Pinthus and Sar-Shalom (1978) reported that dry matter accumulation in the wheat grains from 5 mg per grain onwards was linear with the rates of 0.901 to 1.703 mg per grain per day, depending on varieties and planting dates.

Research results indicated that genetic differences between wheat cultivars exist for both duration and rate of grain filling. Choi (1982) found that early maturing cultivars had earlier spike initiation, shorter duration of spike growth period, and longer duration and lower rate of grain filling. While late maturing cultivars had later spike initiation, longer duration of spike growth period, and shorter duration and higher rate of grain filling. Gebeyehou et al (1982) reported that cultivars of durum wheat differed significantly in rate of grain filling, duration of grain filling period and grain weight.

Limited data are available regarding the inheritance of the duration or rate of grain filling in wheat. Choi (1983) found that the narrow sense heritability estimates were high for duration of grain filling period but lower for rate of grain filling. He further indicated the presence of both additive and nonadditive gene action in a four parent diallel of winter and spring wheat cultivars.

Grain filling in wheat is also known to be influenced by environmental factors, among which temperature has been considered the most important (Kolhe et al, 1977; Xue, 1979; Liu, 1979). Wardlaw (1970) reported that higher temperatures (27/22^{o}C vs 15/10^{o}C day/night) resulted in a greater rate of grain development, with a corresponding increase in the rate of cell division in the endosperm tissue, and reduced grain yield per ear at maturity. Meredith and Jenkins (1976) found that raising the temperature during grain development from 21 to 30^{o}C did not affect growth rate, but caused early cessation of development leading to low final kernel weight. Decreasing the temperature from 21 to 15^{o}C gave a lower growth rate, but did not affect maximum kernel weight. In a study of four sowing dates and five cultivars, Pinthus and Sar-Shalom (1978) noted that late heading (because of late sowing) resulted in a reduction in the duration of grain filling and, in all cultivars except one, an increase in the rate of grain filling. This was concomitant with an increase in the temperature prevailing during the post-heading period. Wiegand and Cuellar (1981) indicated a 3.1 day shortening of grain filling per degree C increase in mean daily air temperature during grain filling period. Kernel weight in their study decreased 2.8 mg/kernel/C for each degree C increase in temperature. They concluded that temperature is accelerating plant senescence and commonly shortening the duration of grain filling in commercial winter and spring wheats. They further indicated that genetic factors (cultivar) dominate the rate of grain filling, and that environment (temperature) dominates the duration of grain filling in wheat.

Where wheat is grown under rainfed conditions, high temperature during grain filling is frequently associated with depleted soil water reserves (drought). Wiegand and Cuellar (1981) reported that in the plots where wheat plants were severely water stressed during grain filling, kernels produced were 4 to 6 mg lighter than for the irrigated treatments. In an experiment conducted in a semi-arid area, Sayed and Gadallah (1983) found that a continuous increase in dry matter occurred until the wheat plants matured, suggesting that the plants were forced to mature by rising temperatures and water stress.

Wardlaw (1970) reported that low light intensity (17.5% of daylight) reduced dry weight accumulation in both the stem and ear, and resulted in a reduction in the final number of endosperm cells formed in the kernel of wheat. They also found that seed number was maximal when temperatures were low, and light intensity was high from the time of anthesis, and ranged from 28 grains per ear at 27/22^{o}C under 17.5% sunlight to 49 grains per ear at 15/10^{o}C under full sunlight.

Relationship between Earliness and Grain Yield

The relationship between earliness and grain yield in wheat is a debated subject. Wheat earliness often appears to be negatively associated with the grain yield. However, many Mexican wheat varieties with early maturity and high productivity have gained recognization throughout the world. Also, many new, early-maturing cultivars are more productive than, or comparable to, the older, late-maturing cultivars in yield (Li, 1976; Avey et al, 1982; Choi, 1982).

Many studies have demonstrated that the spikelet number of wheat is closely and positively associated with the number of days to floral initiation, and longer period of spike differentiation increases the number of spikelets and florets (Halse and Weir, 1970; Li, 1976; Kolhe et al, 1977; Pinthus and Nerson, 1984). Li (1976) and Choi (1982) indicated, however, that early-maturing cultivars had earlier spike initiation and shorter duration of the spike growth period than late-maturing cultivars, and this would be unfavourable for early-maturing cultivars to have a large number of seed set.

Li (1976) reported that there was no significant difference between early and late maturing wheat cultivars in grain number per spike and grain weight. Early-maturing varieties had stronger spring growth habit or insensitivity to photoperiod and faster growth in the early stage, resulting in shorter tillering period, less tillers and less fertile tillers per plant than late-maturing varieties. He suggested that this may be compensated by higher planting density leading to larger and more uniform main and primary spikes which are favourable to high yield.

Concerns have been expressed in that it might not be possible to accelerate some or all stages of development without adversely affecting grain yield. Busch and Chamberlain (1981) reported that the daylength sensitive, late-heading wheat varieties were superior to the insensitive and early-heading varieties in mean yield in three of the four environments, but they did not differ following late-seeding. Avey et al (1982) indicated that physiological limits are expected for early heading date without sacrifice of yield, and a point will be reached at which the potential loss due to frost at anthesis will outweigh the potential advantages of early heading.

In studies on the relationships between grain yield and grain filling period in wheat, Bingham (1969), Spiertz (1971) and Evans (1975) suggested that the duration of grain filling period was a more powerful determinant of yield than the rate of grain filling. In contrast, Nass and Reiser (1975), Choi (1982), and Sayed and Gadallah (1983) reported that grain yield in wheat was more closely related to the rate of grain filling than to the duration of grain filling.

It was found that the rate of dry matter accumulation was markedly higher in heavy-grained wheat than in light-grained cultivars (Pinthus and Sar-Shalom, 1978; Millet and Pinthus, 1983). Gebeyehou et al (1982) found that rate and duration of grain filling were positively associated with final grain weight in durum wheat. They also found that there appeared to be little genetic association between rate of grain filling and duration of grain filling, suggesting that it should be possible to simultaneously improve rate of grain filling and grain weight without lengthening duration of grain filling. Choi (1982) suggested that a higher rate of grain filling in wheat could be selected via a shorter grain filling period and heavy grain weight per spike.

Min (1981) reported that grain filling duration showed a consistent positive-relationship with kernel weight in early and late populations of wheat. Grain filling duration also influenced grain yield mainly by the indirect effects of kernel number and kernel weight.

Li (1976) indicated that the assimilates for grain filling mainly come from the green tissues of the top three leaves, peduncles, glumes and awns in wheat. In a normal situation, grain weight is largely related to the area and duration of these green tissues, grain capacity, and rate and duration of grain filling, but not to the maturity date. He further indicated that early-maturing cultivars may actually lessen or avoid the influence of adverse environment on grain filling and yield in late growth stages. Warrington et al (1977) reported a high positive correlation between flag leaf area duration and total grain yield. Hanft and Wych (1982) found that the cessation of grain filling corresponds closely with the disappearance of chlorophyll or green tissue from heads, peduncles and flag leaves.

MATERIALS AND METHODS

Two winter cultivars developed by Oregon State University, "Yamhill Dwarf" and "Stephens", and two Chinese facultative types "AI Feng 2" and "Selection CB 83-52" were used as parents in this study. They differ in growth habit, heading and flowering dates, grain filling, maturity time, components of yield and grain yield. The descriptions and pedigrees for the cultivars are presented in Appendix Table 1.

A diallel cross, excluding reciprocals, was made to produce the F1 generation. Individual seeds representing the parents and F1s were planted on October 8, 1983 in the greenhouse in 2 1/4 X 2 1/4 inch peat pots, containing a silt loam soil. Seedlings were preconditioned prior to transplanting by placing them in cold frames for a week. They were then transplanted at the Hyslop Agronomy Farm, which is located 11 km northeast of Corvallis, Oregon.

A randomized complete block design with four replications was employed. Each treatment contained a single row of twenty plants with 30 cm between plants and 30 cm between rows. Barley plants were planted around the blocks to provide protection and a more uniform environment. The soil type is a woodburn silt loam. The fertilizer application was 30 lb/acre of N as 16-20-0 of the formulation $N-P_2O_5-K_2O$ during seedbed preparation. Another 25 lb/acre of N as ammonium chloride was applied in February, 1984. An application of "Tilt" was used to control septoria (*Septoria tritici*), stripe rust (*Puccinia striiformis*) and leaf rust (*Puccinia recondita*). The experimental area was covered with a screen from June through harvest to prevent bird damage. A summary of climatic data obtained during this experiment is provided in Appendix Table 2.

In a second experiment, the four parents were sown every two weeks in the field at the East Farm, Corvallis, Oregon, starting on February 17 and concluding on May 2, 1984. Each variety was planted in six rows with 10 plants per row. Rows were spaced 60 cm apart, and plants were 30 cm apart within the rows. The soil type is a sandy loam. One hundred pounds per acre of N as urea was applied in April, 1984. "Tilt" was sprayed to control foliar diseases.

Observations and measurements of characters were taken on an individual plant basis. Dates of heading, flowering and physiological maturity were recorded in two-day intervals. For the first experiment, the following traits were measured:

1. Heading date was recorded when half of the first spike on the plant emerged from the boot.

2. Flowering date was recorded when the first spike on the plant began to shed pollen.

3. Physiological maturity date was recorded when the first spike and peduncle lost its green color.

4. The time from heading to flowering was calculated as lag period.

5. Duration of grain filling period was calculated as days from flowering to physiological maturity.

6. Plant height was measured in cm at harvest from the ground surface to the tip of the tallest spike of the plant, excluding awns if present.

7. The tillers bearing fertile spikes were counted to determine

the number of tillers per plant.

8. Biological yield was obtained by cutting the base of the plant just above ground surface at harvest.

9. Grain yield was the total weight in grams of cleaned seeds from each plant.

10. Harvest index, expressed in percent, was calculated as the ratio of grain yield per plant to biological yield.

11. One hundred kernel weight was weighed in grams of 100 kernels randomly selected from each plant.

12. Average number of kernels per spike was calculated from the following formula:

$$\frac{100\ (\text{grain yield per plant}/100\text{-kernel weight})}{\text{Number of spikes per plant}}$$

13. Kernel weight per spike was calculated from the following formula:

$$\frac{\text{Grain yield per plant}}{\text{Number of spikes per plant}}$$

14. Rate of grain filling was calculated in mg from the following formula:

$$\frac{\text{Grain yield per plant}}{\text{Duration of grain filling period}}$$

For the second experiment, only dates of heading, flowering and physiological maturity, grain yield per plant, tiller number, kernels per spike, 100-kernel weight, biological yield and plant height were recorded.

The per plant values were averaged due to unequal sample sizes and the analysis was conducted on the basis of plot means. For the first experiment, all of the characters measured were subjected to analysis of variance and t-test to determine if differences existed among varieties. Simple correlations among the characters measured and coefficients of determination were computed.

EXPERIMENTAL RESULTS

Results of this investigation are presented based on two experiments. The first study involved two winter and two facultative wheat parents and resulting F1's populations from a diallel cross grown at the Hyslop Experiment Station. Experiment II consisted of the four parents planted at six dates at the East Experiment Farm.

Experiment I

A. Analysis of Variance

The observed mean square values for time of heading, flowering and physiological maturity, lag period, duration and rate of grain filling, grain yield and yield components, biological yield, harvest index and plant height for parents and F1s are presented in Table 1. Significant differences in mean values for parents and F1s were found for all 14 characters measured indicating genetic differences for these traits were present in these populations.

Mean values, standard deviations and coefficients of variation for 14 characters for parent and F1 populations are provided in Table 2. Coefficients of variations were low for heading date (0.63), flowering date (0.46), physiological maturity date (0.62), duration of grain filling period (1.92) and plant height (2.10). Values were high for grain yield (13.72), rate of grain filling (12.57), number of tillers per plant (11.61) and biological yield (11.41). Those for 100-kernel weight (3.94), harvest index (4.38), lag period (4.95), number of kernels per spike (5.74) and grain weight per spike (7.01) were intermediate.

Table 1. Observed mean square values of 14 characters measured for two winter and two facultative wheat parents and resulting F1 populations from a diallel cross grown on the Hyslop Farm near Corvallis, Oregon, 1983-84.

Source of variation	DF	Heading date	Flowering date	PMD[1]	Lag period	DGFP[2]
Blocks	3	3.78	1.37	3.29	1.00	4.47
Genotypes	9	373.71**	187.73**	103.21**	33.70**	24.45**
Parents vs F1s	1	98.06**	36.29**	1.90	15.73**	32.86**
Within parents	3	632.27**	309.81**	188.94**	58.24**	27.44**
Within F1s	5	273.62**	144.78**	72.03**	22.57**	20.97**
Error	27	0.70	0.44	1.43	0.24	0.90
Total	39					

Source of variation	DF	Grain yield	Tillers/ plant	Kernels/ spike	Kernel weight	GWS[3]
Blocks	3	49.31	5.42	44.94	0.12	0.07
Genotypes	9	856.01**	47.31**	562.83**	1.23**	1.35**
Parents vs F1s	1	2279.70**	27.42*	558.88**	0.60**	3.01**
Within parents	3	1106.28**	114.36**	843.72**	2.59**	1.98**
Within F1s	5	421.11**	11.06*	395.10**	0.55**	3.23**
Error	27	54.42	3.87	12.13	0.04	0.05
Total	39					

Source of variation	DF	RGF[4]	Biological yield	Harvest index	Plant height
Blocks	3	10326.27	310.15	0.32	30.39
Genotypes	9	424401.05**	4375.30**	58.59**	215.77**
Parents vs F1s	1	678236.54**	8062.47**	73.13**	687.09**
Within parents	3	615799.51**	7605.94**	106.91**	328.62**
Within F1s	5	258794.87**	1699.48**	26.70**	53.80**
Error	27	18928.53	242.53	2.93	4.62
Total	39				

* : Significant at the 0.05 probability level;
** : Significant at the 0.01 probability level.

1 PMD = Physiological maturity date.
2 DGFP= Duration of grain filling period.
3 GWS = Grain weight per spike.
4 RGF = Rate of grain filling.

Table 2. Observed mean values, standard deviations and coefficients of variation of 14 characters for four winter and facultative wheat parents and six F1s grown on the Hyslop Farm near Corvallis, Oregon, 1983-84.

Characters	Mean	S	CV,%
Heading date	133.53	0.84	0.63
Flowering date	143.40	0.66	0.46
PMD[1]	192.77	1.19	0.62
Lag period	9.88	0.49	4.95
DGFP[2]	49.37	0.95	1.92
Grain yield, g/plant	53.75	7.38	13.72
Tillers/plant	16.94	1.97	11.61
Kernels/spike	60.69	3.48	5.74
100-kernel weight, g	5.29	0.21	3.94
Grain weight/spike, g	3.18	0.22	7.01
RGF[3], mg/plant/day	1094.38	137.58	12.57
Biological yield, g	136.46	15.57	11.41
Harvest index, %	39.14	1.71	4.38
Plant height, cm	102.40	2.15	2.10

1 PMD = Physiological maturity date.

2 DGFP= Duration of grain filling period.

3 RGF = Rate of grain filling.

Note: S means a value of standard deviation, $S=\sqrt{MSE}$.

B. Differences among Parents in Development to Maturity

Days to heading, flowering, physiological maturity, duration and rate of grain filling for the four parents are presented in Table 3. Differences in mean values among the four parents were observed for days to heading. The two facultative parents, AI Feng 2 and Selection CB 83-52, were earlier in heading time requiring 120 and 130 days respectively, while the two winter parents, Stephens and Yamhill Dwarf, required 143 and 148 days, respectively. A similar situation was observed for days to flowering with Selection CB 83-52 being the earliest and Yamhill Dwarf the latest. Differences among the four parents were also found in duration of lag period, however, the earlier heading parents had a longer lag period. Selection CB 83-52 needed 14 days from heading to flowering, while Yamhill Dwarf required only 5 days. The facultative parents were also earlier in reaching physiological maturity, with Selection CB 83-52 being the earliest. Stephens was one day later than Yamhill Dwarf in attaining physiological maturity, although the difference was not significant. The facultative types had longer duration of grain filling period, whereas the difference between these two, AI Feng 2 and Selection CB 83-52, was not significant. The winter types, however, had higher rate of grain filling, with Yamhill Dwarf (1399.8 mg/plant/day) being the fastest and the facultative AI Feng 2 (483.0 mg/plant/day) being the slowest.

The range for the four genotypes was 27.8 days for heading date, 18.9 days for flowering date, and 14.8 days for physiological maturity. The range values decreased in accordance with spike and kernel development. The range was 8.9 days for lag period but only

Table 3. Mean time of heading, flowering and physiological maturity (days from January 1), lag period, rate and duration of grain filling for four parents across four replications. Hyslop Farm, Corvallis, Oregon, 1983-84.

Variety	Days to Heading	Days to Flowering	Days to Physiological maturity
Yamhill Dwarf	148.1a+	153.1a	197.6a
Stephens	143.1b	150.5b	199.0a
AI Feng 2	130.3c	140.4c	190.5b
Selection CB 83-52	120.3d	134.2d	184.2c
Mean	135.4	144.6	192.8
Range	27.8	18.9	14.8

Variety	Duration of Lag period (day)	Duration of grain filling (day)	Rate of grain filling (mg/plant/day)
Selection CB 83-52	13.9a	50.0a	784.5c
AI Feng 2	10.2b	50.1a	483.0d
Stephens	7.4c	48.5b	1072.4b
Yamhill Dwarf	5.0d	44.5c	1399.8a
Mean	9.1	48.3	934.9
Range	8.9	5.6	916.8

+ : Varieties denoted by the same letter in the same column are not significantly different at 0.05 level using LSD method.

5.6 days for duration of grain filling period.

C. Inheritance in F1 Generation for the Characters Related to Earliness

Mean values of heading date for six F1's populations are compared with their parents in Table 4a. Among the F1s, the combination of two facultative types AI Feng 2 X Selection CB 83-52 (120.6 days) was earlier in heading, while the F1 between the two winter types Yamhill Dwarf X Stephens (145.2 days) was later than other F1s. Crosses between facultative and winter types were intermediate in heading time. All F1 populations were earlier in heading than their late parents, and the F1s were all earlier in heading than the means of their parents except in the Yamhill Dwarf X Stephens F1's population. However, all combinations were later in heading than their early parents except AI Feng 2 X Selection CB 83-52. Therefore, there was a general tendency toward dominance for early heading with AI Feng 2 X Selection CB 83-52 exhibiting complete dominance for earliness and other crosses showing partial dominance for earliness except Yamhill Dwarf X Stephens whose F1 value was similar to the midparent value.

Similar results were obtained for flowering date (Table 4b). The same ranking as in heading time was observed among the F1 populations. All F1 populations were earlier in flowering time than their late parents, and were earlier than the means of their parents although the differences for AI Feng 2 X Yamhill Dwarf and Yamhill Dwarf X Stephens were not significant. The F1 combinations were generally later than their early parents, but AI Feng 2 X Selection CB 83-52 and Yamhill Dwarf X Stephens did not differ significantly from

Table 4a. Mean values of heading date from January 1 for six F1's populations as compared with their parents in a diallel cross grown on Hyslop Farm near Corvallis, Oregon, 1983-84 (Value of early or late parent is placed corresponding to the parent in the cross column).

Cross	F1	early parent	F1-early parent	late parent	F1-late parent	Mean+ Of parents	F1-mean of parents
Yamhill Dwarf X Stephens	145.2a++	143.1	2.1**	148.1	-2.9**	145.6	-0.4
AI Feng 2 X Yamhill Dwarf	136.5b	130.3	6.2**	148.1	-11.6**	139.2	-2.7**
AI Feng 2 X Stephens	132.1c	130.3	1.8**	143.1	-11.0**	136.7	-4.6**
CB 83-52 X Yamhill Dwarf	131.2c	120.3	10.9**	148.1	-16.9**	134.2	-3.0**
CB 83-52 X Stephens	127.9d	120.3	7.6**	143.1	-15.2**	131.7	-3.8**
AI Feng 2 X CB 83-52	120.6e	120.3	0.3	130.3	-9.7**	125.3	-4.7**

+ : Mean of parents = $(\bar{X}_{11} + \bar{X}_{22})/2$, where $\bar{X}_{11}$ and $\bar{X}_{22}$ are the early and late parental means, respectively, in a particular cross. CB 83-52 = Selection CB 83-52.

++: F1s denoted by the same letter are not significantly different at 0.05 level using LSD method.
* : Significant at 0.05 level, **: Significant at 0.01 level.

Table 4b. Mean values of flowering date from January 1 for six F1's populations as compared with their parents in a diallel cross grown on Hyslop farm near Corvallis, Oregon, 1983-84 (Value of early or late parent is placed corresponding to the parent in the cross column).

Cross	F1	Early parent	F1-early parent	late parent	F1-late parent	Mean[+] of parents	F1-mean of parents
Yamhill Dwarf X Stephens	151.3a++	150.5	0.8	153.1	-1.8**	151.8	-0.5
AI Feng 2 X Yamhill Dwarf	146.5b	140.4	6.1**	153.1	-6.6**	146.8	-0.3
AI Feng 2 X Stephens	143.3c	140.4	2.9**	150.5	-7.2**	145.5	-2.2**
CB 83-52 X Yamhill Dwarf	141.7d	134.2	7.5**	153.1	-11.4**	143.7	-2.0**
CB 83-52 X Stephens	139.4e	134.2	5.2**	150.5	-11.1**	142.4	-3.0**
AI Feng 2 X CB 83-52	133.7f	134.2	-0.5	140.4	-6.7**	137.3	-3.6**

+ : Mean of parents = $(\bar{X}_{11} + \bar{X}_{22})/2$, where $\bar{X}_{11}$ and $\bar{X}_{22}$ are the early and late parental means, respectively, in a particular cross. CB 83-52 = Selection CB 83-52.

++: F1s denoted by the same letter are not significantly different at 0.05 level using LSD method.
* : Significant at 0.05 level, **: Significant at 0.01 level.

their early parents. Therefore, the F1 populations varied from no dominance to partial or complete dominance for early flowering. No dominance for lateness or overdominance was observed.

Mean values of physiological maturity for six F1 populations are provided in Table 4c. AI Feng 2 X Selection CB 83-52 (187.1 days) was earlier in maturity and Yamhill Dwarf X Stephens (198.7 days) was the latest. Except Yamhill Dwarf X Stephens, the F1 populations were earlier in maturity than their late parents, but were later than their early parents. However, no significant difference between F1 and the mean of parents was found in any individual cross. The F1s generally showed no dominance for physiological maturity time.

The durations of grain filling period for the six F1 populations are compared with their parents in Table 4d. Among the crosses, AI Feng 2 X Selection CB 83-52 had the longest duration of grain filling period (53.4 days) while Yamhill Dwarf X Stephens exhibited the shortest (47.4 days). The durations for all F1s were longer than their short-duration parents, and were longer than the means of their parents although the difference for Yamhill Dwarf X Stephens was not significant. AI Feng 2 X Selection CB 83-52 and AI Feng 2 X Stephens even showed longer durations of grain filling than their long-duration parents. However, AI Feng 2 X Yamhill Dwarf had a shorter duration than its long-duration parent, while the remaining three crosses did not differ significantly from their long duration parents. Therefore, the F1 populations generally exhibited partial dominance, complete dominance or overdominance for long duration of grain filling period.

Mean values of grain-filling rate for the F1s are presented in Table 4e. Yamhill Dwarf X Stephens showed the fastest rate (1589.9

Table 4c. Mean values of the date of physiological maturity from January 1 for six F1's populations as compared with their parents of a diallel cross grown on Hyslop Farm near Corvallis, Oregon, 1983-84 (value of early or late parent is placed corresponding to the parent in the cross column).

Cross	F1	Early parent	F1-early parent	Late parent	F1-late parent	mean+ of parents	F1-mean of parents
Yamhill Dwarf X Stephens	198.7a++	197.6	1.1	199.0	-0.3	198.3	0.4
AI Feng 2 X Yamhill Dwarf	195.1b	190.5	4.6**	197.6	-2.5**	194.1	1.0
AI Feng 2 X Stephens	195.1b	190.5	4.6**	199.0	-3.9**	194.8	0.3
CB 83-52 X Stephens	190.3c	184.2	6.1**	199.0	-8.7**	191.6	-1.3
CB 83-52 X Yamhill Dwarf	190.2c	184.2	6.0**	197.6	-7.4**	190.9	-0.7
AI Feng 2 X CB 83-52	187.1d	184.2	2.9**	190.5	-3.4**	187.4	-0.3

+ : Mean of parents = $(\bar{X}_{11} + \bar{X}_{22})/2$, where $\bar{X}_{11}$ and $\bar{X}_{22}$ are the early and late parental means, respectively, in a particular cross. CB 83-52 = Selection CB 83-52.

++: F1s denoted by the same letter are not significantly different at 0.05 level using LSD method.

* : Significant at 0.05 level, **: Significant at 0.01 level.

Table 4d. Mean values of duration of grain filling period for six F1's populations as compared with their parents in a diallel cross grown on Hyslop Farm near Corvallis, Oregon, 1983-84 (value of short or long duration parent is placed corresponding to the parent in the Cross column).

Cross	F1	Short parent	F1-short parent	Long parent	F1-long parent	Mean[+] of parents	F1-mean of parents
AI Feng 2 X CB 83-52	53.4a++	49.9	3.5**	50.1	3.3**	50.0	3.4**
AI Feng 2 X Stephens	51.8b	48.6	3.2**	50.1	1.7*	49.4	2.4**
CB 83-52 X Stephens	51.0b	48.6	2.4**	49.9	1.1	49.3	1.7**
AI Feng 2 X Yamhill Dwarf	48.6c	44.5	4.1**	50.1	-1.5*	47.3	1.3*
CB 83-52 X Yamhill Dwarf	48.6c	44.5	4.1**	49.9	-1.3	47.2	1.4*
Yamhill Dwarf X Stephens	47.4c	44.5	2.9**	48.6	-1.2	46.6	0.8

+ : Mean of parents = $(\bar{X}_{11} + \bar{X}_{22})/2$, where $\bar{X}_{11}$ and $\bar{X}_{22}$ are the long and short parental means, respectively, in a particular cross. CB 83-52 = Selection CB 83-52.

++: F1s denoted by the same letter are not significantly different at 0.05 level using LSD method.

* : Significant at 0.05 level, **: Significant at 0.01 level.

Table 4e. Mean values of grain filling rate for six F1's populations as compared with their parents in a diallel cross grown on Hyslop Farm near Corvallis, Oregon, 1983-84 (value of slow or fast rate parent is placed corresponding to the parent in the Cross column).

Cross	F1	Slow parent	F1-slow parent	fast parent	F1-fast parent	Mean[+] of parents	F1-mean of parents
Yamhill Dwarf X Stephens	1589.9a++	1072.4	517.5**	1399.8	190.1	1236.1	353.8**
AI Feng 2 X Yamhill Dwarf	1335.8b	483.0	852.8**	1399.8	-64.0	941.4	394.4**
CB 83-52 X Yamhill Dwarf	1230.1bc	784.5	445.6**	1399.8	-169.7	1092.2	138.0
CB 83-52 X Stephens	1138.3bc	784.5	353.8**	1072.4	65.9	928.5	209.9*
AI Feng 2 X Stephens	1074.1c	483.0	591.1**	1072.4	1.7	777.7	296.4**
AI Feng 2 X CB 83-52	836.0d	483.0	353.0**	784.5	51.5	633.8	202.2*

+ : Mean of parents = $(\bar{X}_{11} + \bar{X}_{22})/2$, where $\bar{X}_{11}$ and $\bar{X}_{22}$ are the slow and fast parental means, respectively, in a particular cross. CB 83-52 = Selection CB 83-52.

++: F1s denoted by the same letter are not significantly different at 0.05 level using LSD method.

* : Significant at 0.05 level, **: Significant at 0.01 level.

mg/plant/day), and AI Feng 2 X Selection CB 83-52 had the slowest rate(836 mg/plant/day) among the crosses. All F1 populations were faster in grain filling than their slower parents. The F1s did not differ from their faster-rate parents, but did differ from the means of their parents, except Selection CB 83-52 X Yamhill Dwarf. The mean value for Selection CB 83-52 X Yamhill Dwarf was not significantly different either from the mean of its parents or from its faster parent. Therefore, the crosses suggested a general tendency toward complete dominance for fast grain-filling rate.

D. Performance of Parents and Respective F1 Populations in Grain Yield and Components of Yield

The mean values for grain yield, yield components and other related characters are presented in Table 5 for parents and F1 populations. Among the parents, the two winter cultivars Yamhill Dwarf and Stephens were intermediate in number of tillers and number of kernels per spike, but high in 100-kernel weight resulting in high grain yield. Selection CB 83-52 was high in number of tillers, but low in number of kernels per spike and intermediate in 100-kernel weight giving intermediate grain yield. AI Feng 2 had a large number of kernels per spike, but few tillers and low kernel weight, and therefore low grain yield. Grain weight per spike was high for Yamhill Dwarf and Stephens (3.35 g), intermediate for AI Feng 2 (2.80 g) and low for Selection CB 83-52 (1.86). Harvest index was high for Stephens (41.3) and AI Feng 2 (40.6), while being intermediate for Yamhill Dwarf (38.0) and low for Selection CB 83-52 (30.0).

Among the F1s, the combination of two winter types Yamhill Dwarf X Stephens had the highest grain yield, while the cross between two

Table 5. Mean values of eight agronomic characters for two winter and two facultative wheat parents and resulting Fl's populations from a diallel cross grown on the Hyslop Farm near Corvallis, Oregon, 1983-84.

Parents and Fls	Grain yield g	Tiller number	Kernels/ spike	100 Kernel weight g	GWS[1] g	Plant height cm	Biological yield g	Harvest index %
AI Feng 2	24.1f[+]	8.6e	70.5b	3.98d	2.80e	83.9f	59.2f	40.6bcd
CB 83-52	39.2e	20.9a	35.9e	5.20bc	1.86f	100.9de	127.3de	30.0g
Yamhill Dwarf	62.7bc	18.6abc	59.7c	5.62a	3.35bc	100.7e	163.8ab	38.0ef
Stephens	52.1cd	15.6d	58.4cd	5.74a	3.35bc	103.8cd	126.1de	41.3abc
AI Feng 2 X CB 83-52	44.7de	15.6d	56.1cd	5.26b	2.91de	105.1bc	122.6e	36.4f
AI Feng 2 X Yamhill Dwarf	65.3ab	16.8bcd	77.5a	5.02bc	3.89a	99.8e	150.0bc	43.5a
AI Feng 2 X Stephens	55.6bc	16.1cd	71.2b	4.93c	3.50b	104.8bc	132.0cde	42.3ab
CB 83-52 X Yamhill Dwarf	60.1bc	18.9abc	55.2cd	5.73a	3.16cd	106.6bc	153.4bc	38.8def
CB 83-52 X Stephens	58.3bc	18.7abc	54.1d	5.77a	3.11cde	110.8a	147.8bcd	39.3cde
Yamhill Dwarf X Stephens	75.6a	19.6ab	68.5b	5.60a	3.83a	107.6b	182.5a	41.2abcd

1 GWS = Grain weight per spike. + : Genotypes denoted by the same letter in the same column are not significantly different at 0.05 level using LSD method. CB 83-52 = Selection CB 83-52.

facultative types AI Feng 2 X Selection CB 83-52 gave the lowest. Most F1s were not significantly different from their high parents in grain yield nor for the components of yield, however they did exhibit a degree of heterosis. Heteroses were also observed for plant height and harvest index. F1 populations were not significantly different from their high parents for biological yield.

E. Associations among the Characters Measured

The correlation coefficients and coefficients of determination of the 14 traits for parents and F1s are shown in Table 6. Heading date was positively correlated with flowering and physiological maturity date, grain yield, grain weight per spike and rate of grain filling in both parents and F1 generation. Heading date showed a negative correlation with lag period and duration of grain filling period in both parents and F1s. The R^2 values were high for these traits, suggesting that large variations associated with these traits were accounted for by heading date in both parents and F1 generation. There were also significant correlations of heading date with kernels per spike and harvest index in both generations, but the R^2 values were relatively low. The correlation between heading date and biological yield was significant in F1s, but not significant in parents.

Flowering date is positively correlated with physiological maturity date, grain yield, grain weight per spike, rate of grain filling for both parents and F1 generation. However, the flowering date was negatively correlated with lag period and duration of grain filing period for both generations. The high R^2 value for these traits suggested that for both parents and F1s large variations in

Table 6. Associations of 14 characters for the parents and F1s of a 4 X 4 diallel cross planted at Hyslop Farm, Corvallis, Oregon, 1983-84.

Characters	Parents r	Parents r^2	F1s r	F1s r^2
Heading date vs				
Flowering date	0.997**	0.994	0.993**	0.986
PMD 1/	0.951**	0.904	0.913**	0.843
Lag period	-0.985**	0.970	-0.952**	0.906
Grain yield	0.679**	0.461	0.790**	0.624
Tillers/plant	-0.041	0.002	0.332	0.110
Kernels/spike	0.522*	0.272	0.599**	0.359
Kernel weight	0.492	0.242	0.045	0.002
GWS 2/	0.910**	0.828	0.810**	0.656
DGFP 3/	-0.741**	0.549	-0.799**	0.638
RGF 4/	0.727**	0.529	0.857**	0.734
Biological yield	0.452	0.204	0.692**	0.479
Harvest index	0.636**	0.404	0.632**	0.399
Plant height	0.289	0.084	-0.128	0.016
Flowering date vs				
PMD 1/	0.960**	0.922	0.934**	0.872
Lag period	-0.970**	0.941	-0.908**	0.824
Grain yield	0.705**	0.497	0.789**	0.623
Tillers/plant	-0.006	0.000	0.308	0.095
Kernels/spike	0.493	0.243	0.663**	0.440
Kernel weight	0.532*	0.283	-0.027	0.001
GWS 2/	0.909**	0.826	0.845**	0.714
DGFP 3/	-0.728**	0.530	-0.781**	0.610
RGF 4/	0.747**	0.558	0.850**	0.723
Biological yield	0.477	0.228	0.667**	0.445
Harvest index	0.635**	0.403	0.700**	0.490
Plant height	0.339	0.115	-0.177	0.031

Note: N = 16 and 24 for parents and F1s, respectively.

1/ PMD = Physiological maturity date.
2/ GWS = Grain weight per spike.
3/ DGFP = Duration of grain filling period.
4/ RGF = Rate of grain filling.

*: Significant at the 0.05 level, **: Significant at the 0.01 level.

Table 6. Continued.

Characters	Parents r	Parents r^2	F1s r	F1s r^2
PMD 1/ vs				
Lag period	-0.911**	0.830	-0.801**	0.642
Grain yield	0.638**	0.407	0.757**	0.573
Tillers/plant	-0.098	0.010	0.266	0.071
Kernels/spike	0.551*	0.304	0.740**	0.548
Kernel weight	0.490	0.240	-0.173	0.030
GWS 2/	0.933**	0.870	0.852**	0.726
DGFP 3/	-0.507*	0.257	-0.507*	0.257
RGF 4/	0.652**	0.425	0.768**	0.590
Biological yield	0.366	0.134	0.609**	0.371
Harvest index	0.765**	0.585	0.762**	0.581
Plant height	0.286	0.082	-0.208	0.043
Lag period vs				
Grain yield	-0.607*	0.368	-0.741**	0.549
Tillers/plant	0.120	0.014	-0.370	0.137
Kernels/spike	-0.577*	0.333	-0.400	0.160
Kernel weight	-0.390	0.152	-0.223	0.050
GWS 2/	-0.894**	0.799	-0.669**	0.448
DGFP 3/	0.756**	0.572	0.791**	0.626
RGF 4/	-0.667**	0.445	-0.818**	0.669
Biological yield	-0.384	0.147	-0.707**	0.500
Harvest index	-0.627**	0.393	-0.417*	0.174
Plant height	-0.171	0.029	-0.005	0.000
Grain yield vs				
Tillers/plant	0.661**	0.437	0.758**	0.575
Kernels/spike	-0.090	0.008	0.448*	0.201
Kernel weight	0.867**	0.752	0.120	0.014
GWS 2/	0.561*	0.315	0.654**	0.428
DGFP 3/	-0.607*	0.368	-0.580**	0.336
RGF 4/	0.992**	0.984	0.985**	0.970
Biological yield	0.941**	0.885	0.958**	0.918
Harvest index	0.152	0.023	0.568**	0.323
Plant height	0.735**	0.540	-0.065	0.004

1/ PMD = Physiological maturity date.
2/ GWS = Grain weight per spike.
3/ DGFP = Duration of grain filling period.
4/ RGF = Rate of grain filling.

*: Significant at the 0.05 level, **: Significant at the 0.01 level.

Table 6. Continued.

Characters	Parents r	Parents r^2	F1s r	F1s r^2
Tillers/plant vs				
Kernels/spike	-0.778**	0.605	-0.161	0.026
Kernel weight	0.734**	0.539	0.334	0.112
GWS 1/	-0.242	0.059	0.014	0.000
DGFP 2/	-0.221	0.049	-0.279	0.078
RGF 3/	0.623**	0.388	0.706**	0.498
Biological yield	0.859**	0.738	0.852**	0.726
Harvest index	-0.580*	0.336	0.116	0.013
Plant height	0.794**	0.630	0.276	0.076
Kernels/spike vs				
Kernel weight	-0.396	0.157	-0.632**	0.399
GWS 1/	0.727**	0.529	0.890**	0.792
DGFP 2/	-0.168	0.028	-0.308	0.095
RGF 3/	-0.045	0.002	0.458*	0.210
Biological yield	-0.384	0.147	0.231	0.053
Harvest index	0.865**	0.748	0.786**	0.618
Plant height	-0.557*	0.310	-0.656**	0.430
Kernel weight vs				
GWS 1/	0.341	0.116	-0.221	0.049
DGFP 2/	-0.436	0.190	-0.237	0.056
RGF 3/	0.836**	0.699	0.146	0.021
Biological yield	0.867**	0.752	0.271	0.073
Harvest index	-0.039	0.002	-0.369	0.136
Plant height	0.913**	0.834	0.650**	0.423
GWS 1/ vs				
DGFP 2/	-0.515*	0.265	-0.551**	0.304
RGF 3/	0.586*	0.343	0.685**	0.469
Biological yield	0.264	0.070	0.467*	0.218
Harvest index	0.849**	0.721	0.795**	0.632
Plant height	0.112	0.013	-0.439*	0.193
DGFP 2/ vs				
RGF 3/	-0.701**	0.491	-0.709**	0.503
Biological yield	-0.572*	0.327	-0.546**	0.298
Harvest index	-0.079	0.006	-0.359	0.129
Plant height	-0.342	0.117	0.064	0.004

1/ GWS = Grain weight per spike.
2/ DGFP = Duration of grain filling period.
3/ RGF = Rate of grain filling.

*: Significant at the 0.05 level, **: Significant at the 0.01 level.

Table 6. Continued.

Characters	Parents		F1s	
	r	r^2	r	r^2
RGF 1/ vs				
Biological yield	0.932**	0.869	0.943**	0.889
Harvest index	0.153	0.023	0.558**	0.311
Plant height	0.698**	0.487	-0.074	0.005
Biological yield vs				
Harvest index	-0.188	0.035	0.312	0.097
Plant height	0.805**	0.648	0.084	0.007
Harvest index vs				
Plant height	-0.244	0.060	-0.399	0.159

1/ RGF = Rate of grain filling.

*: Significant at the 0.05 level, **: Significant at the 0.01 level.

these traits were accounted for by flowering date. Significant correlation between flowering date and harvest index was also found, but with relatively low R^2 values. There was significant correlation between flowering date and kernel weight for parents, but not for F1s. On the contrary, significant correlation between flowering date and biological yield was found only in the F1 generation.

Physiological maturity date was found to have positive correlations with grain weight per spike and harvest index, and negative correlation with lag period for both parents and F1s. The R^2 values were high for these traits. Physiological maturity date also correlated significantly with grain yield, kernels per spike and rate of grain filling, with the R^2 values being higher for F1 generation than for parents. There was also significant and negative correlation between physiological maturity date and duration of grain filling period, but the R^2 values were low. Significant correlation between physiological maturity and biological yield was found only in F1 populations.

Lag period correlated positively with duration of grain filling period, and negatively with grain weight per spike and rate of grain filling. There were high R^2 values for these characters, suggesting that large variations in these traits were accounted for by lag period for both parents and F1s. Negative correlations between lag period and grain yield were significant for both generations, but the R^2 value for F1s was higher than for parents. Lag period also had significant and negative correlation with harvest index, although the R^2 values were low for both generations. Significant and negative correlation between lag period and kernels per spike was found for the parents, but not for the F1 generation.

Grain yield showed positive correlations with tillers per plant, rate of grain filling and biological yield for both parents and F1s. The R^2 values for these characters were high, suggesting that large variation in grain yield was accounted for by these traits for both generations. Grain yield also correlated positively with grain weight per spike, and negatively with duration of grain filling period, but R^2 values for these traits were relatively low. The correlations of grain yield with kernel weight and plant height were significant only in parents, while the correlations of grain yield with kernels per spike and harvest index were only found significant in the F1 generation.

Tiller number was positively correlated with biological yield with high R^2 values for both parents and F1s being observed. The positive correlations between tiller number and rate of grain filling were significant, but the R^2 values were relatively small especially for the parents. The tiller number showed positive correlations with kernel weight and plant height, and negative correlations with kernels per spike and harvest index, but these associations were significant only for parents.

Kernel number per spike was positively correlated with grain weight per spike and harvest index in both parents and F1 generation. There were high R^2 values for these traits, suggesting that large variations in these variables were accounted for by kernel number for both generations. Negative correlations between kernel number and plant height were significant in both generations, but the R^2 values were relatively low. The positive correlation between kernel number and rate of grain filling and the negative correlation between kernel number and kernel weight were significant in F1 generation only.

Positive correlations between kernel weight and plant height were found significant in both generations, although the R^2 value was relatively low for F1s. Kernel weight also had positive correlations with rate of grain filling and biological yield, but these associations were only significant in parents.

Grain weight per spike positively correlated with rate of grain filling and harvest index in both generations, although the R^2 value was relatively low for rate of grain filling in parents. Negative correlations between grain weight per spike and duration of grain filling period were found significant in both parents and F1s with relatively low R^2 values. Grain weight per spike also showed a positive correlation with biological yield and a negative association with plant height in F1 generation.

Duration of grain filling period had negative correlations with rate of grain filling in both parents and F1 generation. The relatively high R^2 value suggested that much of the variation in rate of grain filling was accounted for by duration of grain filling period in both generations. The negative correlations between duration of grain filling period and biological yield were also found to be significant, but the R^2 values were relatively small in both parents and F1s.

For rate of grain filling, a positive correlation with biological yield was found in both parents and F1s with large R^2 values. Thus, large variation in rate of grain filling was accounted for by biological yield in both generations. Rate of grain filling also had significant correlation with harvest index in the F1 generation, and with plant height in the parents. Positive correlation between biological yield and plant height was significant only in the parents.

Experiment II

Experiment results regarding heading, flowering, physiological maturity and subsequent grain yield of four parental cultivars in relation to different planting dates at East Farm are provided in this section.

The number of days to heading over a range of planting dates for four cultivars is presented in Table 7a. When the two facultative cultivars, AI Feng 2 and Selection CB 83-52, are compared across planting dates, a decrease in the number of days to heading was observed with the later planting dates. This trend was true for AI Feng 2 up until April 2 and for Selection CB 83-52 until March 19. After these dates an increase in the number of days to heading was found with a maximum number being reached on May 2 for both cultivars. The two winter cultivars, Stephens and Yamhill Dwarf, required longer periods to reach the heading stage. The latter two cultivars did not head when planted on April 17 or May 2.

A similar pattern was also observed for days to flowering (Table 7b). Fewer days to reach the flowering stage with later planting dates were noted until April 2 when Selection CB 83-52, Stephens and Yamhill Dwarf again required additional days to reach this stage. Again the maximum number of days to reach flowering was observed from May 2 planting date for the facultative cultivars. The winter types did not flower when planted on April 17 or later.

For physiological maturity (Table 7c) the trend was with later planting dates, fewer days were required to reach physiological maturity. However, Selection CB 83-52 and Stephens on April 2

Table 7a. Observed mean values and standard deviations ($\bar{X} \pm S$) of days to heading for four cultivars planted at six dates. East farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	Al Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	108.7±2.49	117.2±3.65	122.4±1.51	133.6±2.37
March 2	103.3±1.28	108.9±2.01	115.5±2.06	125.9±2.25
March 19	91.8±1.66	107.5±5.42	115.5±6.79	132.3±4.14
April 2	88.5±3.72	120.8±11.55	126.9±13.56	171.9±20.68
April 17	101.1±11.61	144.6±26.75	----	----
May 2	141.9±14.95	146.4±16.98	----	----

Table 7b. Observed mean values and standard deviations ($\bar{X} \pm S$) of days to flowering for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	Al Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	116.0±1.72	121.6±3.09	127.6±1.15	136.2±1.91
March 2	108.3±1.59	113.7±1.84	119.3±1.71	127.0±2.24
March 19	96.7±1.35	109.4±4.69	117.1±6.82	134.2±4.16
April 2	91.0±2.88	122.7±11.68	129.2±13.91	175.5±22.79
April 17	103.8±11.76	147.7±27.84	----	----
May 2	144.4±15.49	149.2±18.34	----	----

Table 7c. Observed mean values and standard deviations ($\bar{X}$+S) of days to physiological maturity for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	158.0±1.86	157.5±2.24	164.5±2.13	169.1±1.66
March 2	147.6±1.51	148.5±2.48	155.6±2.04	159.4±1.93
March 19	133.5±2.27	141.4±5.38	154.6±8.05	168.3±5.81
April 2	126.0±2.87	158.1±11.99	165.4±13.29	----
April 17	142.9±14.44	----	----	----
May 2	----	----	----	----

Table 7d. Observed mean values and standard deviations ($\bar{X}$+S) of grain yield per plant (g) for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	32.45±10.79	40.00±18.74	42.34±11.74	40.57±15.02
March 2	29.21±8.20	43.32±16.80	38.19±11.08	40.12±14.19
March 19	20.55±8.77	19.77±7.92	16.34±7.11	15.35±8.15
April 2	8.94±3.89	8.42±4.47	6.97±4.12	----
April 17	4.89±2.42	----	----	----
May 2	----	----	----	----

Table 7e. Observed mean values and standard deviations ($\bar{X} \pm S$) of tillers per plant for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar: AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	17.36±4.43	24.96±8.33	22.55±5.70	25.64±7.98
March 2	16.62±4.35	27.29±8.94	25.80±6.20	31.12±10.48
March 19	14.80±5.00	18.39±5.47	15.56±5.43	15.02±6.68
April 2	7.47±2.74	9.07±3.72	8.56±4.60	----
April 17	6.42±2.96	----	----	----
May 2	----	----	----	----

Table 7f. Observed mean values and standard deviations ($\bar{X} \pm S$) of kernels per spike for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar: AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	47.17±3.76	32.90±5.58	44.27±3.92	49.74±5.34
March 2	50.07±4.49	37.49±4.85	38.17±3.15	38.28±4.07
March 19	42.30±4.47	32.79±5.05	30.08±5.81	30.05±3.76
April 2	43.98±7.59	25.45±7.91	24.26±6.92	----
April 17	29.18±7.69	----	----	----
May 2	----	----	----	----

Table 7g. Observed mean values and standard deviations ($\bar{X}$±S) of 100-kernel weight (g) for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	4.01±0.24	4.40±0.40	4.25±0.19	3.35±0.18
March 2	3.64±0.16	4.14±0.34	3.76±0.29	3.33±0.25
March 19	3.47±0.22	3.23±0.33	3.79±0.27	3.51±0.18
April 2	2.85±0.20	3.60±0.39	4.09±0.17	----
April 17	3.29±0.40	----	----	----
May 2	----	----	----	----

Table 7h. Observed mean values and standard deviations ($\bar{X}$±S) of biological yield (g) for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	70.53±22.61	95.04±41.99	111.21±30.84	106.42±38.59
March 2	66.73±18.47	105.00±38.88	107.58±28.44	114.83±39.36
March 19	50.56±20.55	66.64±21.83	59.16±25.58	65.78±29.50
April 2	22.63±9.83	33.83±13.95	32.65±14.22	----
April 17	15.90±7.04	----	----	----
May 2	----	----	----	----

Table 7i. Observed mean values and standard deviations ($\bar{X} \pm S$) of plant height for four cultivars planted at six dates. East Farm, Corvallis, Oregon, 1984.

Planting Date	Cultivar			
	AI Feng 2	Selection CB 83-52	Stephens	Yamhill Dwarf
February 17	67.2±3.36	77.2±5.66	79.6±3.93	69.5±3.28
March 2	68.5±3.84	76.7±5.42	76.2±4.44	64.9±5.44
March 19	67.1±3.41	69.4±7.49	69.5±6.08	59.1±4.52
April 2	59.1±4.15	66.8±8.18	63.0±7.84	47.3±6.89
April 17	52.9±6.99	60.7±5.27	----	----
May 2	50.3±7.22	59.2±9.14	----	----

planting date and AI Feng 2 planted on April 17 required more days to reach this stage. Yamhill Dwarf never reached physiological maturity when planted on April 2 or later.

In Table 7d, the responses of different planting dates on grain yield are presented. Yields for the four cultivars were similar when planted either on February 17 or March 2. Substantial reductions in yield for all four varieties were apparent when planted on March 19 or on later dates. This was also true for tillers per plant (Table 7e) where large reductions were experienced.

For kernels per spike (Table 7f) differences were apparent between cultivars and dates of planting. AI Feng 2 appeared to retain the number of kernels per spike even when planted on April 2. Large reductions for kernel number occurred for the other cultivars when planted at this date.

For 100-kernel weight (Table 7g) there was a trend toward less kernel weight with later dates of planting. There were several exceptions. Yamhill Dwarf had a higher 100-kernel weight when planted on March 19, while the other three cultivars reached higher kernel weights when planted on February 17.

When considering biological yield the major reduction came when the material was planted on March 19 in contrast to the earlier planting dates (Table 7h).

A reduction in plant height occurred as the planting dates were delayed. This was consistant across dates for all cultivars (Table 7i).

DISCUSSION

Results of this study confirm that genetic differences do exist between cultivars of wheat for various growth stages. Also various environmental factors influence the rate and expression of various factors associated with plant development. It would appear that it is possible for the wheat breeder to develop earlier maturing cultivars to avoid moisture stress or fit into various cropping systems. To do so would require some information in terms of the vernalization period and perhaps the photoperiod and temperature requirements. Depending on the specific location and when considering fall sown cultivars, a certain level of winter hardiness is necessary. Since early spring growth would be desirable in developing early maturing lines, a compromise may have to be reached between degree of winter hardiness needed and quick spring recovery. Another limiting factor to earliness would be the frost free date. Should a cultivar flower prior to the last frost in the spring a large percentage of sterility will result. Thus the breeder in selecting for earliness must recognize these constraints.

A further concern must be the potential negative relationship between earliness and grain yield. By reducing the length of the growing stages it is quite possible that a reduction in grain yield would result. It was a further objective of this study to evaluate earliness not only in reference to heading and anthesis date, but also in light of physiological maturity and rate and duration of the grain filling period. It also must be emphasized that the results of this study must be interpreted in terms of the cultivars used and the environment in which the experiments were conducted.

Developmental Stages and Grain Yield

The life cycle of the wheat plant is composed of many important stages which are related to components of grain yield. Both spike and spikelet number are established at heading, floret number is determined at flowering, and final kernel number and weight are established between anthesis and physiological maturity. The duration of each stage may influence not only the length of life cycle but also the subsequent grain yield via components of yield.

Genetic differences among cultivars were found in days to heading, flowering, physiological maturity, duration and rate of grain filling, grain yield and yield components. Therefore, improvements of these traits are possible via crosses among different cultivars and selection. The four parents exhibited large differences in lag period, whereas the differences in duration of grain filling period were quite small. Thus lag period was quite important in determining the length of later development stages. Since lag period contributes little to final grain yield, it may be reduced in developing shorter life cycle cultivars.

The early maturing cultivars had earlier heading and flowering dates, a longer lag and duration period and lower rate of grain filling which resulted in a lower grain yield. Late maturing cultivars were characterized by later heading and flowering, a shorter lag and duration period and higher rate of grain filling, giving higher grain yield. Grain yield was highly correlated with grain filling rate, but a negative association between grain yield and duration of grain filling period was observed although the R^2 value was relatively small. This suggests that grain filling rate was more important in contributing to grain yield than duration of grain filling period.

Negative association between early physiological maturity and grain yield was found for the cultivars used in this experiment with a intermediate R^2 value. This suggested that a difficulty may exist in attempting to combine early maturity and high-yielding in a cultivar. As far as yield components are concerned, tiller number per plant and 100-kernel weight showed no significant correlations with physiological maturity date. Kernel number per spike was significantly and positively correlated with maturity date, but the R^2 value was relatively small. In addition, early-maturing variety AI Feng 2 had significantly more kernels per spike than late-maturing cultivars. Thus, it may be possible to manipulate these yield components in breeding for earliness to give acceptable grain yield. However, should there be biological limits between the components of yield, the net results of selecting for one may reduce a second with grain yield remaining the same.

Significant and positive correlation between grain yield and biological yield was observed with high coefficient of determine (R^2), suggesting that large total variation in grain yield would be accounted for by the variations associated with biological yield or source potential. Biological yield was also significantly correlated with tiller number per plant, 100-kernel weight and grain filling rate. Source potential, therefore, contributed to grain yield through sink capacity and rate of assimilate translocation from source to sink.

Nevertheless, biological yield was not correlated with physiological maturity date. Considering the small associations between maturity date and yield components but negative association between early maturity and grain-filling rate, it can be postulated that source potential and sink capacity are not necessarily limiting for early-maturing cultivars, while their rate of photosynthate translocation from source to sink is often limited. Hence, grain filling rate may be the key factor in breeding for early-maturing cultivars with acceptable grain yield.

Genotype X Environment Interactions

The responses to environments of six planting dates in Experiment II assist in explaining much of the variation in cultivar response in Experiment I.

From March onward, the daylengths in Corvallis were more than 12 hours, or long enough to promote inflorescence initiation (Downs and Hellmers, 1975). Therefore, the time to heading was dependent mainly on sensitivity to vernalization. It was reported that vernalization can be achieved artificially by exposing growing plants to temperatures between about -6 and 14^{o}C, although those between 0 and 10^{o}C are most effective. A period of continuous low temperature is more effective in causing induction than the same period interrupted by temperatures no higher than 18^{o}C (Purvis and Gregory, 1952). In the early sowings of Experiment II, field temperatures were below 10^{o}C

(Appendix Table 2) and plants were vernalized during both the day and night. Higher temperatures accelerated plant development and resulted in reductions in heading time with planting dates. For the late plantings, the average temperatures were above 10^{o}C and plants could only achieve vernalization during the night period. Therefore, the time needed to pass through the vernalization process was lengthened with later planting dates and the large vernalization requirement of sensitive cultivars may not be fulfiled in late sowing dates as field temperatures increased. Thus the variations in days to heading among sensitive and insensitive varieties became larger with planting time, and Yamhill Dwarf and Stephens did not head from the last two plantings. Therefore, Yamhill Dwarf showed a high sensitivity to vernalization, followed by Stephens, while the two facultative cultivars exhibited low sensitivity, especially AI Feng 2.

It is noteworthy that AI Feng 2 was consistently earlier in heading than Selection CB 83-52 in spring plantings while the situation was just the opposite when sown in fall. This might be due to a higher sensitivity of AI Feng 2 to daylength than Selection CB 83-52, or due to vernalization X photoperiod interaction.

Most plants of Yamhill Dwarf headed in September when planted on April 2. The summer temperature contributed little to vernalizing the plants, with the high day-temperature even reversing the already achieved effect of vernalization. However, plants eventually reached heading after being exposed to long days in summer, indicating that long daylength might replace to some degree the effect of vernalization in some cultivars.

Coupled with changes in length of growth stage, grain yield was also influenced by the environment as it generally decreased with planting dates. The effect of environment on yield can be analysed through yield components. Tillers per plant generally decreased with late plantings, since high temperature and long days were unfavourable for tillering and less tillers being vernalized to produce fertile spikes. Tiller numbers were the highest when the cultivars were planted on March 2, except for AI Feng 2. This might be due to the N fertilization applied on April 20 which promoted tillering, but was too late to promote tillering in the early-developing AI Feng 2. Kernel number per spike also generally decreased with planting dates. For later plantings, high temperature might have accelerated the differentiation of the inflorescence resulting in less spikelets and florets, or resulted in a stress which might cause style injury and desiccation of pollen. AI Feng 2 and Selection CB 83-52 had highest kernel number when planted on March 2 date, which might be due to the N fertilizer which promoted the differentiation of growing point or reduced abortion of the seed set. Kernel weight decreased with earlier plantings as high temperature and water stress cut the grain filling duration short. Nevertheless, as tiller number and kernels per tiller decreased in later plantings, kernel weight increased because of the compensation relationship among yield components. Therefore, grain yield and yield components are greatly influenced by environment. It can also be seen that early maturity is important in reducing yield losses caused by adverse conditions in late season. Furthermore, breeders should design growth stages to fit into favorable environments for the development of yield components in breeding early varieties with acceptable grain yield.

A genotype X environment interaction was found as each variety responded differently to the planting dates. It might be desirable to plant breeding materials at several dates when screening newly introduced varieties or selecting plants or lines from segregating populations for early types, as different genotypes might have different optimum planting dates to give early maturity and high grain yield. This is especially true for those materials with different vernalization and photoperiod requirements.

Breeding for Early Maturity and High Productivity

Establishing appropriate breeding objectives is essential in developing early maturity cultivars. It appears that early-maturing varieties should have a lower vernalization requirement and be less sensitive to daylength. Such early varieties should have rapid growth associated with acceptable winterhardiness in early stages to produce more early and fertile tillers. Early inflorescence initiation followed by accelerated differentiation under relatively shorter daylength and lower temperature would generate more seed sets while not delaying spike emergence. It would be ideal if early varieties have a short lag period and grain filling period with a high grain filling rate, leading to high grain yield.

Although negative association between early maturity and grain yield was found in this experiment, it should be kept in mind that early-maturing cultivars may allow two or more crops to fit into the multiple cropping system so that the total production per unit area per year is increased. Therefore, certain yield reduction of a component crop may be necessary as long as the total production can be maximized.

Early heading was dominant in the F1 generation while short grain filling duration was recessive, and maturity time exhibited no dominance. This suggests that early maturity is harder to obtain than early heading. There should be at least one early parent in the cross for early-maturing cultivars or early hybrid wheat as the early parent can shorten the life cycle of the late parent. In addition, heading time was negatively correlated with lag period and duration of grain filling period but positively associated with rate of grain filling. Early heading would be difficult to combine with a short lag or grain-filling period and high grain-filling rate. Although rapid grain filling rate was dominant in the F1 generation, that might be related to hybrid vigor which could not be fixed in a conventional selfing breeding program.

Grain filling duration and rate were found to be negatively associated in this experiment. Since grain filling rate was more closely related to grain yield, it appears that breeders should put emphasis on increasing grain filling rate while decreasing grain filling duration to a certain extent. This would be especially true in areas where late frost is a problem, as short grain filling period is needed in developing cultivars with delayed flowering but early maturity. Breeding for shorter life cycle cultivars with high productivity may be possible by crossing among genotypes with different vernalization or photoperiod requirement and yield potential. Such would be the case when making crosses between winter and spring types. Breeders could also use physical or chemical agents to induce mutation for earliness or introduce early genes from exotic species to increase genetic variability.

Heading date and flowering date were all highly correlated with the date of physiological maturity, and therefore can all be used to monitor earliness. As far as field selection is considered, heading date is easier to identify than flowering date. However, early heading does not always mean early maturity. For example, Stephens was 5 days earlier in heading time than Yamhill Dwarf, but became one and a half day later than Yamhill Dwarf at physiological maturity in Experiment I. Even though the development of the wheat plant after heading is controlled by its genotype, environmental factors also play an important role, especially temperature. Compared to heading, flowering has a more critical temperature requirement. Large variations in lag period were observed in this experiment. Later heading types have shorter lag period than early heading cultivars and the grain filling of later flowering types may also be speeded up with higher temperatures in the late summer. Grain filling duration of genotypes can be examined by recording the dates of flowering and physiological maturity. Therefore, the dates of heading, flowering and physiological maturity may all need to be considered in selection for earliness, while a final decision can be made by taking the optimum combination of these three dates.

SUMMARY AND CONCLUSIONS

The major objectives of this study were: 1) to determine the genetic differences among wheat cultivars for time of heading, anthesis and physiological maturity as they influence the duration and rate of grain filling period; 2) to determine if the possible effects of the traits on grain yield exist in crosses of Chinese early-maturing and Oregon high-yielding varieties; 3) to examine the inheritance of the traits as related to wheat breeding; 4) to examine developmental response and subsequent grain yield of varieties as influenced by different sowing time.

A diallel cross, excluding reciprocals, among two Chinese facultative types and two Oregon winter cultivars was studied under field conditions. The four parents were studied in a second field experiment with six planting dates. Data were collected on an individual plant basis for 14 traits. Characters measured were subjected to analysis of variance and t-test to determine if differences exist among varieties. Simple correlations and coefficients of determination among the traits measured were also computed.

The results and conclusions from this study are summarized as follows:

1. Genetic differences among cultivars were found for time of heading, flowering and physiological maturity, for duration and rate of grain filling period, grain yield and yield components.
2. Low coefficients of variation were observed for date of heading, flowering and physiological maturity, and duration of grain

filling period. Values were intermediate for 100-kernel weight, harvest index, lag period, kernels per spike and kernel weight per spike. Biological yield, tiller number, rate of grain filling and grain yield per plant exhibited high CV values.

3. The facultative types, AI Feng 2 and Selection CB 83-52, showed earlier heading, flowering and physiological maturity, longer lag period, and longer duration and lower rate of grain filling, resulting in lower grain yield. The winter cultivars, Stephens and Yamhill Dwarf, had later heading, flowering and maturity, shorter lag period, and shorter duration and higher rate of grain filling, leading to higher grain yield.
4. For the developmental stages after heading, larger differences were observed in the lag period while differences in duration of grain filling period were relatively small among the cultivars.
5. Analysis of the F1 generation showed that there was a general tendency toward dominance for early heading, no dominance to complete dominance for early flowering depending on the cross, and no dominance for physiological maturity. Long duration and fast rate of grain filling were generally dominant in the F1 generation.
6. Among F1 crosses, AI Feng 2 X Selection CB 83-52 had the earliest dates of heading, flowering and maturity, and longest duration and lowest rate of grain filling, resulting in lowest grain yield. Yamhill Dwarf X Stephens showed latest dates of heading, flowering and maturity, and shortest duration and highest rate of grain filling, giving the highest grain yield. Crosses between facultative and winter types were intermediate

for these traits.

7. Grain yield was positively and significantly correlated with dates of heading, flowering and physiological maturity, tiller number, kernel weight, grain weight per spike, rate of grain filling, biological yield and plant height. Grain yield was negatively and significantly associated with lag period and duration of grain filling period.
8. No clear associations between maturity time and the yield components were found in the experimental materials. Grain filling duration showed no associations with yield components, whereas grain filling rate exhibited positive associations with tiller number and kernel weight. There was a negative association between grain filling duration and rate.
9. Heading and flowering dates were highly correlated with maturity date. Nevertheless, the magnitude of range and variation among varieties decreased from heading to flowering and maturity.
10. According to heading responses to planting dates, Stephens and Yamhill Dwarf had high sensitivity while Selection CB 83-52 and AI Feng 2 showed low sensitivity to vernalization.
11. Grain yield and yield components generally decreased with planting dates except kernel weight which increased slightly in later sowings.
12. Genotype X environment interaction was found as each variety responded differently to the planting dates. AI Feng 2 showed consistantly earlier heading than Selection CB 83-52 in spring plantings while the situation was opposite when sown in fall.

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APPENDICES

Appendix Table 1. Pedigree and description of the parents used in the diallel cross.

AI Feng 2:	(Feng Chan 3//Xian Nong 39/Selection 58(18)2). A hard white facultative wheat developed by Northwestern College of Agriculture, People's Republic of China. Early maturity, semi-dwarf, low tillering and excellent head fertility. Awned, large number of kernels per spike and low grain yield.
Selection CB 83-52:	(PKG 16/LOV 13//JKG 3). A hard white facultative wheat from Chinese Academy of Agriculture. Very early maturity, normal height and awned. High tillering levels, medium to large kernels and medium grain yield.
Stephens:	(Nord Desprez/Pullman Selection 101). An awned, standard height, soft white winter wheat released by Oregon State University. Mid-late maturity, medium to high tillering levels, moderate head fertility and a high seed weight. Wide adaptability and excellent yield potential.
Yamhill Dwarf:	Pedigree unknown. A soft white winter wheat from Oregon State University. Late maturity, medium height, high yielding and awnless. Large fertile spikes and medium to large kernels. Excellent tolerance to wet soil.

Appendix Table 2. Summary of meterological data for Corvallis, Oregon (1983-84).

Month	Average temperature, °C Max.	Min.	Mean	Precipitation mm	Evaporation mm	Radiation Langley
September	22.8	8.8	15.8	13.5	127.0	414
October	17.4	4.7	11.1	26.7	49.3	232
November	11.9	5.5	8.7	252.2	----	85
December	4.8	-0.5	2.2	306.1	----	67
January	9.3	1.7	5.5	82.8	----	101
February	11.2	2.1	6.7	175.8	----	154
March	14.4	4.6	9.5	97.0	----	259
April	14.0	3.8	8.9	86.6	67.1	353
May	17.6	5.9	11.8	93.2	94.2	438
June	20.9	8.1	14.5	110.2	123.7	547
July	27.3	10.3	18.8	5.1	214.1	687
August	27.4	9.6	18.5	Trace	190.8	547
September	23.7	8.6	16.2	18.8	117.9	362

Note: Observations were taken from Hyslop Field Laboratory.