

AN ABSTRACT OF THE THESIS OF

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Title: Duration and Rate of Grain Filling and Subsequent Grain Protein Content
in Selected Winter Wheat Populations

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The lack of information regarding the inheritance of the duration and rate of grain filling, and the possible relationship between grain fill and grain protein content in wheat prompted this study.

Early maturing Chinese cultivars, 'AI Feng 2' and 'CB 83-52', and late maturing cultivars adapted to Oregon, 'Stephens' and 'Yamhill Dwarf', were examined for vernalization and photoperiod responses. Progeny from a diallel cross of the genotypes was evaluated for grain filling parameters, grain protein content and other agronomic traits for two years.

'Yamhill Dwarf' required six weeks of vernalization, while other cultivars needed only four weeks. The two Oregon developed genotypes were more sensitive

to photoperiod than Chinese genotypes. Variation in developmental patterns among genotypes was related to differences in leaf number, spikelet number, rate of spikelet initiation, and rate of grain fill. Compared to solid planting, space-planting reduced the grain filling period.

Significant genotypic variation for grain filling rate, duration, and kernel weight was observed in both seasons. Genotype X year interaction was not significant for any of the grain filling traits. General combining ability effects for grain filling rate, duration, and kernel weight were much larger than specific combining ability effects. Additive gene action made the major contribution to the inheritance of the grain filling traits. However, dominance effects appeared also to be involved in the genetic control of grain filling duration and kernel weight. Narrow sense heritability estimates were high for all three grain filling traits. Results indicated that early generation selection for both duration and rate of grain fill should be effective in these populations.

Rate, but not duration of grain fill was closely associated with kernel weight. There was an inverse relationship between duration and rate of grain filling. Kernel protein percentage was positively associated with duration, but negatively related to rate of the grain filling. Results suggest that starch and protein accumulations in the kernel are two highly independent processes and may not necessarily compete for assimilates or energy. It may be necessary under the environments of this study to increase the duration of the grain fill to obtain high protein content with acceptable grain yield.

**Duration and Rate of Grain Filling and Subsequent Grain Protein Content
in Selected Winter Wheat Populations**

by

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Typed by Beiquan Mou

IN DEDICATION TO

my wife,

Mei Guo

my son,

Eric Mou

and my parents,

Wenling Song and Yunguan Mou

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Duration and Rate of Grain Filling and Subsequent Grain Protein Content in Selected Winter Wheat Populations

INTRODUCTION

The development of early maturing wheat cultivars is receiving more attention from plant breeders. Early maturing cultivars may aid in avoiding such adverse factors to plant growth as high temperature, drought, excessive moisture, diseases, insects, and other abiotic and biotic stresses. 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 later stages of plant development as they influence the duration and rate of the grain filling period. These stages can be modified by responses to vernalization, photoperiod, and temperature.

Multiple cropping systems like wheat-rice-rice, wheat-corn, wheat-cotton, etc. have been widely employed in a number of countries to increase food production. As a consequence, a significant characteristic of Chinese wheat cultivars is their early maturity. This has resulted from long term natural and artificial selection. However, the genetic and environmental conditions which control the growing cycle and the maturation period of these cultivars have not been fully investigated. In addition, there is little information regarding the inheritance of the duration and rate

of grain filling period. The possible relationship between grain filling and grain protein content is also unknown.

In this study, early maturing Chinese cultivars were crossed to late maturing cultivars adapted to the Pacific Northwest and the resulting progenies were investigated to address the following objectives:

- 1) to examine the developmental responses of selected cultivars to different vernalization and photoperiod treatments;
- 2) to determine if there are genetic differences among wheat cultivars for developmental patterns including the rate and duration of grain filling period;
- 3) to identify the nature of inheritance for the duration and rate of grain filling period;
- 4) to study the relationship between grain filling and grain protein content as well as other agronomic traits.

LITERATURE REVIEW

Maturity

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).

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 early maturity. Some early, spring type cultivars grow rapidly to stem elongation and heading stages, then slow down from heading to maturity. In contrast, some early winter cultivars may grow slowly from seedling emergence to heading, but accelerate their growth from heading to maturity. Choi (1982) observed large differences in 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).

Early maturity 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, in wheat the heading date is most frequently used as an indicator of earliness as it can be easily identified and is often closely associated with maturity date (Li, 1976), although heading date is not always an accurate measure of maturity (Van Sanford, 1985; May and Van Sanford, 1992).

Many investigations have been conducted to study the inheritance of 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 in F_2 generations of seven crosses between early and late heading cultivars. Yu (1982) observed transgressive segregation for both earlier and later heading in F_2 generation in 10 out of 15 crosses.

Using a diallel cross analysis to study 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 and no major epistatic effects were found. The narrow sense heritability estimates were 55, 67 and 74 percent respectively in the three years in which their study was conducted. They 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 'Bart 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). 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 Maturity

The growth and development of the wheat plant is strongly influenced by environmental factors, i.e., temperature, water, nutrition, etc.. Such factors can influence vernalization, photoperiod and temperature requirements which in turn determines maturity.

A. Vernalization Requirement

Response to vernalization is an attribute affecting growth habit in wheat.

Winter wheat plants require a cold period before they shift from a vegetative to a reproductive growth phase. If a sufficient cold period is lacking, they either fail to reach the heading stage or their heading is much delayed.

A wide range of vernalization responses among wheat cultivars were reported by Halse and Weir (1970). They studied 16 Australian wheat cultivars grown in growth chambers at 3-4 °C for 6 weeks. Responses to seed vernalization varied from little or no promotion of floral initiation in some cultivars to about 3 weeks in others. Levy and Peterson (1972) observed that following a cold treatment, the heading time of winter wheat is greatly promoted and many spring wheats also show a small but definite acceleration in time of heading.

In genetic studies of vernalization requirement, Pugsley (1963) indicated the presence of a single-gene difference governing this response in two near-isogenic lines of spring wheat. In crosses between spring and winter wheat, the spring habit is generally dominant and, depending on the parents involved, one, two, or three independently inherited genes were found to control this character (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 by heat treatment in the early stages of growth following vernalization. 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°C respectively, using continuous illumination. After the

vernalization treatment, he exposed the plants to relatively high temperature treatments of 12, 18 or 24°C for 10 days. The plants were then transplanted into a greenhouse and exposed to a 15°C and 20-hour photoperiod. He found that the vernalization effect achieved at 1 or 4°C were reversed markedly by the subsequent exposure to high temperature such as 18 or 24°C, but the effect obtained at 8 or 11°C were reversed only slightly by the same treatments.

B. Photoperiod Response

Historically wheat has been classified as a quantitative long-day or short-night species based on its photoperiodic response. The heading of a wheat plant may be prohibited or greatly delayed if its photoperiod requirement is not met. 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 Australian wheat cultivars tested achieved floral initiation earlier under 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.

Wheat cultivars do differ in their response to daylength. Characterization of cultivar differences for photoperiod sensitivity generally is done 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).

Syme (1968) studied the photoperiod response of 16 Mexican, European and Australian wheat cultivars in the growth chamber. He reported that in terms of sensitivity to daylength the European, Mexico and Australian cultivars had high, low and intermediate responses, respectively. 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. Less response to lengthened photoperiods was observed with early-maturing cultivars. They suggested that photoperiod rather than vernalization requirement is the primary factor controlling maturity in spring wheats.

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 the International Maize and Wheat Improvement Center (CIMMYT) 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 over a wide array of latitudes (Keim et al., 1973).

Minor gene modifiers and multiple alleles have also been postulated to account for observed genetic variation in photoperiod response in wheat. Klaimi and Qualset

(1973) described the 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 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 daylength 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.

C. Temperature Effect

Halse and Weir (1970) found that higher temperatures (18/13°C vs 12/7°C day/night) accelerated development to floral initiation and anthesis in all 16 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°C for germination, 16 to 20°C for tillering and 20 to 22°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 (Pirasteh and Welsh, 1980).

Growing degree days have been used to study the growth and development of

the wheat plant. Known also as heat unit or a thermal unit it is determined by taking the average of the highest and lowest air temperature that occurred in a day and subtracting the base temperature (usually 0 to 4.5°C for wheat) from the mean temperature, which gives growing degree days for a 24 hour period. Rickman and Klepper (1983) found that 50 percent emergence can be expected between 85 and 100 growing degree days (with a 3°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. Using growing degree days, Wong and Baker (1986) found that the difference between three early and two late genotypes of spring wheat in time to maturity could be attributed to the difference in duration of the preanthesis period.

Other factors affecting earliness in wheat 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, 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 a cold treatment of 8 weeks. However, even under this treatment, significant differences among cultivars in heading time were still found, suggesting the presence of other factors influencing this character. Masle *et al*. (1989) proposed three genetically independent components of the rate of development: vernalization requirements, relative sensitivity to photoperiod and temperature, and intrinsic earliness.

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.

Hanft and Wych (1982) found that complete loss of green color from the glumes occurred close to physiological maturity in eight Hard Red Spring Wheat cultivars. Smith and Donnelly (1991) reported that complete loss of green color from the rachis, glumes, and the crease of kernels occurred within 1 day of physiological maturity in all the five hard red and one soft white winter wheat cultivars studied. Chen et al. (1990) found that *in vivo* spectral shifts of wheat flag leaf and physiological maturity of grain showed correlations under growth chamber conditions, but not in field experiments. Under field conditions, chlorophyll content was a better marker for physiological maturity. By studying six barley cultivars, Copeland and Crookston (1985) found the loss of green color from glumes or peduncle to be a good indicator of physiological maturity. In maize, black layer development on the kernel has been used as an reliable indicator of physiological maturity (Daynard and Duncan, 1969; Hunter et al., 1991).

Grain filling rate is the result of the translocation of photosynthate from source to sink. Eighty to 90 percent of the carbohydrate for grain growth are from photosynthesis after anthesis, whereas 10-20 % of the carbon are from available reserves (Spiertz and Vos, 1985). Pinthus and Sar-Shalom (1978) reported that dry matter accumulation in the wheat kernels from 5 mg/grain onwards was linear with the rates of 0.901 to 1.703 mg/grain/day, depending on cultivars and planting dates.

Research results indicated that genetic differences between wheat cultivars exist for both duration and rate of grain filling. Choi (1982) observed that early maturing cultivars had earlier spike initiation, shorter duration of the spike growth period, and a longer duration and a lower rate of grain filling. Late maturing cultivars had a later spike initiation, longer duration of spike growth, and a shorter duration and a 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 fill and grain weight.

Limited data are available regarding the inheritance of the duration or rate of grain filling in wheat. Chen (1988) found that additive and non-additive gene actions were both significant in the inheritance of the grain filling rate and effective duration with low narrow sense heritability estimates noted for both traits. In a diallel analysis of seven inbred lines of corn, Cross (1975) reported that the general combining ability effects for duration and rate of grain fill were larger than specific combining ability effects. In soybean, Pfeiffer and Egli (1988) found nonsignificant heritability estimates for effective filling period which is calculated by dividing the final kernel weight by the rate of accumulation of dry matter by the seed during the linear phase of kernel growth.

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; Bruckner and Frohberg, 1987). Wardlaw (1970) reported that higher temperatures (27/22°C vs 15/10°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°C did not affect growth rate, but caused early cessation of development leading to lower final kernel weight. Decreasing the temperature from 21 to 15°C gave a lower growth rate, but did not affect maximum kernel weight. In a study of four planting dates and five cultivars, Pinthus and Sar-Shalom (1978) noted that late heading (because of late planting) resulted in a reduction in the duration of grain filling and, in all cultivars except one, an increase in the grain filling rate. This was concomitant with an increase in the temperature prevailing during the post-heading period. Wiegand and Cuellar (1981) observed an average of 3.1 day shortening of grain filling per degree increase in mean daily air temperature during grain filling period for 20 spring and winter wheat cultivars. Kernel weight decreased 2.8 mg/kernel for each degree increase in temperature. They concluded that temperature accelerates plant senescence and commonly shortens the duration of grain filling in commercial winter and spring wheats, also that genetic factors (cultivar) dominate the rate of grain filling, while 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 plots where wheat plants were severely water stressed during grain filling, the resulting kernels 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 linear increase in dry matter occurred in 11 bread wheat cultivars until the wheat plants matured, suggesting that the plants were forced to mature by raising temperatures and water stress.

Wardlaw (1970) reported that low light intensity (17.5 % of daylight) reduced dry weight accumulation in both the stem and spike, and resulted in a reduction in the final number of endosperm cells formed in the kernel of wheat. They also found that kernel number was maximal when temperatures were low, and light intensity was high from the time of anthesis to maturity, and ranged from 28 grains per spike at 27/22°C under 17.5 % sunlight to 49 grains per ear at 15/10°C under full sunlight. Grabau et al. (1990) also reported that shading during grain filling period reduced kernel growth rate and kernel weight, resulting in yield reduction.

Grain Protein Concentration as Influenced by Carbohydrate and Nitrogen Deposition

The world's food protein comes from cereals (50%), grain legumes (20%), and animal products (30%). In developing countries, animal products contribute only 10 percent while cereals provide 70 percent of the protein (Axtell, 1981). As wheat is a staple food for more than one-third of the world's population, its grain protein is very important to human nutrition.

In a survey of 12,613 wheat strains from the USDA collection, a range in protein from 6.9 to 22.0 % was obtained (Poehlman, 1987). Both the environment

and genetic factors have a large influence on protein content. Precipitation and temperature conditions prevailing at the time when the kernels are filled, as well as irrigation and nutrient supply, especially nitrogen, equally affect protein content (Lelley, 1976). Differences in the protein content were found between plants within the same population, among heads of the same plant, and even between grains in a spike (Stuber *et al.*, 1962).

Nitrogenous compounds for wheat grain protein are mainly supplied by the vegetative aerial parts (65-80%), the remainder originate from uptake and relocation by the roots after anthesis (Waldren and Flowerday, 1979; Spiertz and Vos, 1985). Bauer *et al.* (1987b) showed that about 71 % of the spike N content at hard dough stage had occurred via translocation from leaves and stems. McNeal *et al.* (1968) reported that chaff N concentration declined 10 g/kg from anthesis to maturity, assuming it was translocated to the grain. In studying a winter wheat cultivar 'Centurk', Waldren and Flowerday (1979) found that the grain contained 71 % of the total plant N at maturity.

Bauer *et al.* (1987c) found that N uptake by kernels closely paralleled the kernel dry matter assimilation, and peak N content occurred about 2 days after maximum assimilation of kernel dry matter. Decline in kernel N concentration after anthesis, followed by near-constant concentrations thereafter has been reported for winter and spring wheat (Spiertz and Ellen, 1978; Bauer *et al.*, 1987c). However, Karlen and Whiney (1980) observed no change in kernel N concentration during grain filling of Hard Red Winter Wheat, while in spring wheat, McNeal *et al.* (1968) observed

increases in concentration after the dough stage of about 1.0 and 3.0 g/kg under dryland and irrigation management, respectively.

Frey (1977) indicated that in several cereal species including wheat, grain yield and grain protein percentages are negatively correlated. The process of dry matter (carbohydrate) and protein accumulation may compete for assimilates and energy. According to Penning de Vries *et al* (1974), 1 g of glucose produced by photosynthesis can be used by the crop to produce 0.83 g of carbohydrate or 0.40 g of protein (assuming nitrate to be the N source). This implies that increases in protein content would use more photosynthate decreasing carbohydrate content and thus ultimately leading to decreases in dry matter yield. Also, the amount of N may be "diluted" by the carbohydrate translocated into kernels. Khokhlov (1979) divided the grain content into, 1) the carbohydrate constituent (which is associated with harvest index) and 2) the nitrogen component (related to nitrogen translocation and its use in the synthesis of protein). The inverse relationship between yield and protein is largely due to the effect of the carbohydrate constituent. He also found little genetic variability in the nitrogen component. However, Brunori and Micke (1979), in a study of 23 wheat genotypes, concluded that dry matter and N accumulation do not necessarily compete for resources. This is supported by the fact that it is possible to breed for higher grain protein concentration while at the same time maintaining acceptable grain yields. Genes from 'Atlas 66' have been utilized to elevate protein concentration in 'Lancota' cultivar by 1 to 2 percent without a reduction in grain yield. Lancota absorbed more soil nitrogen, exhibited higher

nitrate reductase activity (NRA), maintained NRA longer during the growing season, and translocated a higher percentage of absorbed N to its grain than did 'Lancer', a check cultivar (Johnson *et al.*, 1979). Johnson *et al.* (1975) found that the size of the caryopsis does not affect protein content.

Studies have shown that in addition to selection for grain protein concentration and grain yield per se, selection for grain protein related traits and/or selection for grain yield related traits may prove effective in enhancing grain yield while maintaining or enhancing grain protein concentration. Grain protein yield (Loffler and Busch, 1982; Cox *et al.*, 1985), total plant nitrogen at maturity (Loffler *et al.*, 1985), nitrogen harvest index (Loffler and Busch, 1982; Loffler *et al.*, 1985; Cox *et al.*, 1986), total dry matter (Loffler and Busch, 1982; Loffler *et al.*, 1985) and harvest index (Fischer and Kertesz, 1976) have all been suggested as possible selection criteria. Selection for only high grain protein percentage may be associated with a reduced capacity to synthesize and store carbohydrates, rather than with high protein storage. Rao *et al.* (1977) indicated that the selection of genotypes with both high grain protein percentage and grain yield was difficult when based on individual physiological traits. These authors recommend concurrent studies of two or more traits.

Cox (1981) indicated that high protein percentage is generally related to lateness, tallness, and especially low harvest index, i.e., it is related to greater vegetative growth. This is usually explained by noting that a small plant cannot provide as much nitrogen to transport to the grain and still maintain the leaves for

starch production. Stuber et al. (1962), Randhawe and Gill (1978) and El-sayed and Stolen (1979) reported a positive correlation between grain protein content and days to flowering. However, Loffler and Busch (1982) reported that grain protein percentage or grain protein yield showed no correlation with days to heading or days to maturity in 72 F₇ lines from three crosses of Hard Red Spring Wheat. Even strong negative associations between grain protein concentration and maturity time ($r = -0.60$ to -0.67) were observed among 96 F₅ lines derived from a spring wheat cross, although no significant correlations existed between grain protein yield and maturity (Cox *et al.*, 1985).

Relationship between Earliness and Grain Yield

The relationship between earliness and grain yield in wheat is a debated subject. Earliness often appears to be negatively associated with the grain yield. However, many Mexican wheat cultivars with early maturity and high productivity have gained recognition 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. This would be unfavorable 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 cultivars had a stronger spring growth habit or insensitivity to photoperiod and faster growth in early stage, resulting in shorter tillering period, less tillers and less fertile tillers per plant than late-maturing cultivars. He suggested that this may be compensated by higher planting density leading to larger and more uniform main and primary spikes which are favorable 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 cultivars were superior to the insensitive and early-heading cultivars in mean yield in three of 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, as 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 et al (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), Sayed and Gadallah (1983) and Mou (1985) reported that grain yield in wheat was more closely related to the rate of grain filling than to the duration of grain filling. Metzger et al. (1984) failed to detect a yield advantage due to differences in grain-filling duration in barley lines with similar maturity, suggesting that any advantage derived from alteration of the grain-filling period may have been outweighed by the coincident change in length of the vegetative period.

It was found that the rate of dry matter accumulation was markedly higher in large-kernel cultivars than in small-kernel cultivars (Pinthus and Sar-Shalom, 1978; Simmons et al, 1982; 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.

Using random sets of F6 and F7 lines from three durum wheat crosses, Knott and Gebeyehou (1987) found that the lengths of the vegetative and filling periods were negatively correlated. Correlations between yield and the length of the two growth periods were inconsistent and generally small. Bruckner and Frohberg (1987) suggested that simultaneous selection for high grain filling rate and high

kernel weight is possible without lengthening grain filling duration, and that selection for high grain filling rate through selection for high kernel weight is possible in spring wheat.

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 tissue of the top three leaves, peduncles, glumes and awns in wheat. In 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. A high positive correlation between flag leaf area duration and total grain yield was reported by Warrington *et al* (1977). 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.

CHAPTER I

Vernalization Requirement, Photoperiod Response, and Developmental Patterns in Four Winter Wheat Genotypes

ABSTRACT

Development of early maturing cultivars requires a better understanding of the genetic differences and environmental influences in growth stages during the life cycle of winter wheat (*Triticum aestivum* L.). This study was undertaken to examine the vernalization requirement, photoperiod response, and developmental patterns of two Oregon cultivars and two early-maturing Chinese genotypes. Genotypes were subjected to 8-17 hours of daylength in growth chamber, 0-8 weeks of vernalization at 1-3°C before grown in greenhouse, and solid and space-planted conditions in the field for two years. Plants were sampled and dissected at 2-3 day intervals to determine the stages of spike differentiation. 'Yamhill Dwarf' required six weeks to satisfy the vernalization requirement, while other cultivars needed only four weeks. The two Oregon genotypes were more sensitive to photoperiod than Chinese genotypes. In the field, the Chinese cultivars were earlier in stem elongation, heading, anthesis, and maturity. The main difference in the reproductive phase was in the spikelet initiation period. Variation in developmental patterns among

genotypes were related to differences in leaf number, spikelet number, rate of spikelet initiation, and rate of grain fill. Compared to solid planting, space-planting reduced the grain filling period. The preanthesis period appears to provide greater potential for enhancing early maturity.

INTRODUCTION

Early maturing cultivars may aid in avoiding such adverse factors to plant growth as high temperature, drought, excessive moisture, diseases, insects, and other abiotic and biotic stresses. Combination 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. Therefore, wheat breeders are focusing more attention on the development of early-maturing cultivars.

Heading date is most frequently used in genetic studies of earliness in wheat as it can be easily identified and is often closely associated with maturity time (Crumpacker and Allard, 1962; Amaya et al., 1972; Avey and Ohm, 1982; May and Van Sanford, 1992). Genotypic differences in grain filling period have also been detected in wheat (Gebeyehou et al., 1982; Van Sanford, 1985; Bruckner and Frohberg, 1987; Darroch and Baker, 1990).

These studies examined time to maturity near or at the end of the plant's life cycle. Ross (1955) pointed out that a knowledge of earlier development is important to the understanding of the nature of time to maturity. Wong and Baker (1986) found that the difference between the two Canadian spring wheat cultivars and the three alien genotypes in time to maturity could be attributed to the difference in duration of the preanthesis period. Early developmental stages are greatly influenced by vernalization and photoperiod which can promote the differentiation and growth of the spike (Gott, 1961; Halse and Weir, 1970; Rahman and Wilson, 1977).

Many early-maturing genotypes from China have been brought into the OSU wheat breeding program. These cultivars have evolved as a result of long term selection to adapt to the multiple-cropping systems. This study was designed to compare the vernalization requirements, photoperiod responses, and developmental patterns of two Oregon winter wheat cultivars with two Chinese genotypes. Also, possible associations of developmental periods and spacing treatments were examined.

MATERIALS AND METHODS

Two winter wheat cultivars developed by Oregon State University, 'Stephens' and 'Yamhill Dwarf', and two Chinese winter cultivars, 'AI Feng 2' and 'CB 83-52', were used in this investigation. These genotypes differ in many traits including heading, flowering and maturity time, and the components of grain yield.

Vernalization Experiment

Seeds of the four cultivars, presoaked for 24 hours at room temperature, were placed in plastic pans containing vermiculite and put in a dark growth chamber at 1-3°C at two week intervals for 8 weeks from October 23 to December 18, 1986. At the end of this period, one set that received no vernalization was presoaked for 48 hours before all seeds from all treatments were transferred into a chamber operating at 15°C and 16 hour light for one week to "fix" the vernalization effect. The seeds were then transplanted to 15-cm-diam. plastic pots containing soil-peat-sand-pumice (1:1:1:2) and grown in the greenhouse under 16 hour light to avoid possible interactions between daylength sensitivity and cold requirement. The photosynthetic photon flux intensity was $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ at plant level.

A complete randomized block design with seven replications was used with each replication containing one plant for observation for each treatment. Extra plants in each replication were randomly sampled and dissected under a microscope

at 2-3 day intervals to examine the spike differentiation for each treatment, starting from the three-leaf stage. The scale used by Friend et al. (1963) was employed. The preheading period was subdivided into vegetative and reproductive periods. The vegetative period was from the end of vernalization to the appearance of double ridges. The reproductive period was from the appearance of double ridges to heading and was further subdivided into spikelet initiation period (from the appearance of double ridge to terminal spikelet formation) and spike growth period (from terminal spikelet formation to heading). Days from the end of vernalization to tillering, flag leaf emergence, and heading were recorded on the main shoot of each plant using the code developed by Zadoks et al. (1974). Data collected were subjected to analysis of variance, and LSD values were calculated using the error mean square and t -value at $\alpha = 0.05$.

Photoperiod Experiment

The germinating seeds of the four cultivars were vernalized for 9 weeks in a dark growth chamber operating at 1-3°C starting from January 1, 1987. Under this condition, the vernalization requirements would be fulfilled and the possible effect of interactions between daylength and cold requirement on plant development would be avoided. Following the vernalization period, the plants were transplanted to 15-cm-diam. plastic pots containing soil-peat-sand-pumice and grown in growth chambers with 8, 11, 14, and 17 hour photoperiods and 16°C. The photosynthetic photon flux

intensity in different growth chambers varied from 290 to 390 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant level. A split-plot design with two replications was used with photoperiod as main treatment. In each replication, each treatment contained eight plants for observation. Additional plants were sampled at three day intervals to examine spike differentiation. Observations made were similar to the vernalization experiment, and LSD ($\alpha = 0.05$) values were computed following the analysis of variance.

Field Experiments

In 1986-87 growing season, seeds of the four cultivars were planted on October 15 at the Crop Science Field Laboratory, Corvallis, Oregon. The soil type at the experiment site is a fine silty mixed mesic Aquultic Argixeroll. A randomized complete block design with four replications was employed. Plots consisted of four rows for each genotype per replication. Rows were 4.5 m in length with 30 cm between rows and 15 cm between plants within the row allowing for a total of 30 plants/row. Before planting, the plots received 56 kg/ha of N as ammonium nitrate. An additional 90 kg/ha of N broadcast was split equally in late February and late April. Fungicide "Tilt", at the rate of 0.22 l/ha, was applied once a month from March to June to control leaf diseases. The plots were bordered by barley plants to avoid possible differential environment influences.

In each plot, 10 plants were randomly selected to record the heading and anthesis dates and spikelet number on the main tiller of each plant. At anthesis, 140

flowering main spikes were tagged for each plot. The terminal plants from each end were avoided to minimize border effects. Five tagged spikes were collected from each plot at 2-3 day intervals from 3 days after anthesis to past harvest maturity. Samples were oven-dried at 70°C for 24 hours, subsequently 20 kernels from each spike were separated from the two basal florets of the middle spikelets. Kernels were redried at 70°C for 20 hours and weighed immediately.

A polynomial model was fitted to the dry weight data from each plot using SAS statistical package (SAS Institute Inc., 1987). The stepwise variable selection method was used to select the best equation for each plot. Data fit the models well; r^2 values generally ranged from 0.97 to 0.99, and exceeded 0.94 in all cases. The date of physiological maturity was determined by taking the derivative of the equation, setting $dy/dx = 0$, and solving for time as an independent variable. The estimate of grain filling duration was the time from anthesis to physiological maturity. Mean grain filling rate for each plot was estimated as predicted maximum grain dry weight divided by grain filling duration.

In 1987-88 season, the four genotypes were sown on October 23 at Crop Science Field Laboratory, Corvallis. A split-plot design was used with the cultivars as main treatments and three plant spacings as sub-treatments. The spacing treatments were 45 cm, 15 cm between plants within row, and a solid planting at 168 kg/ha. Rows were 4.5 m long and 30 cm between rows. The experiment was replicated four times. Fertilizer applications and disease control were similar to 1986-87 season.

Ten plants in each sub-plot were randomly selected to record the appearance of each leaf, heading and flowering dates, and spikelet number. In each sub-plot, one plant was randomly selected every 3 days to observe spike differentiation and time of stem elongation under microscope. The beginning of active stem elongation was defined as the time when the average distance between the summit of the apex and the base of the lower embryonic internode reached 1 cm (Kirby, 1986; Masle et al., 1989). The sub-plots were also sampled for grain-filling measurements in the same manner as in the previous season.

Number of leaves was divided by days to flag-leaf emergence to obtain the average rate of leaf appearance. Linear regression of number of spikelet primordia on days from sowing was used to estimate the rate of spikelet initiation. In this study, the period between heading and anthesis is referred to as the lag period. Maturity date was determined as days to anthesis plus grain filling period. Results were evaluated by analysis of variance, and the means of the treatments were compared using LSD values at $\alpha = 0.05$ level.

RESULTS AND DISCUSSION

Vernalization Requirements

Heading responses of the four cultivars to vernalization treatments are shown in Fig. 1. The two Chinese genotypes, AI Feng 2 and CB 83-52, consistently headed earlier than the two Oregon cultivars. The difference between the two Chinese genotypes was small with longer vernalization treatments, but gradually became larger as vernalization periods got shorter. All genotypes exhibited greatly increased heading time with the reduction of the vernalization period from 4 to 2 weeks; however, Yamhill Dwarf showed a greater response to the change of vernalization period from 6 to 4 weeks than did the other varieties. Thus, Yamhill Dwarf was more sensitive to vernalization as it required 6 weeks of cold treatment to avoid a large delay in heading time, and the others needed only 4 weeks. Vernalization requirement accounted in part for its late heading and would be important factor in developing earlier maturing wheat cultivars.

Vernalization treatments greatly reduced days to flag leaf emergence and the vegetative growth period, but days to tillering and the reproductive phase of the cultivars was little affected (Table 1). The spikelet initiation period was shortened, but the spike growth period was increased with longer vernalization period, leaving reproductive period unchanged. Results suggest that vernalization treatment not only affects the time to reach double ridge (vegetative growth), but also has influences on

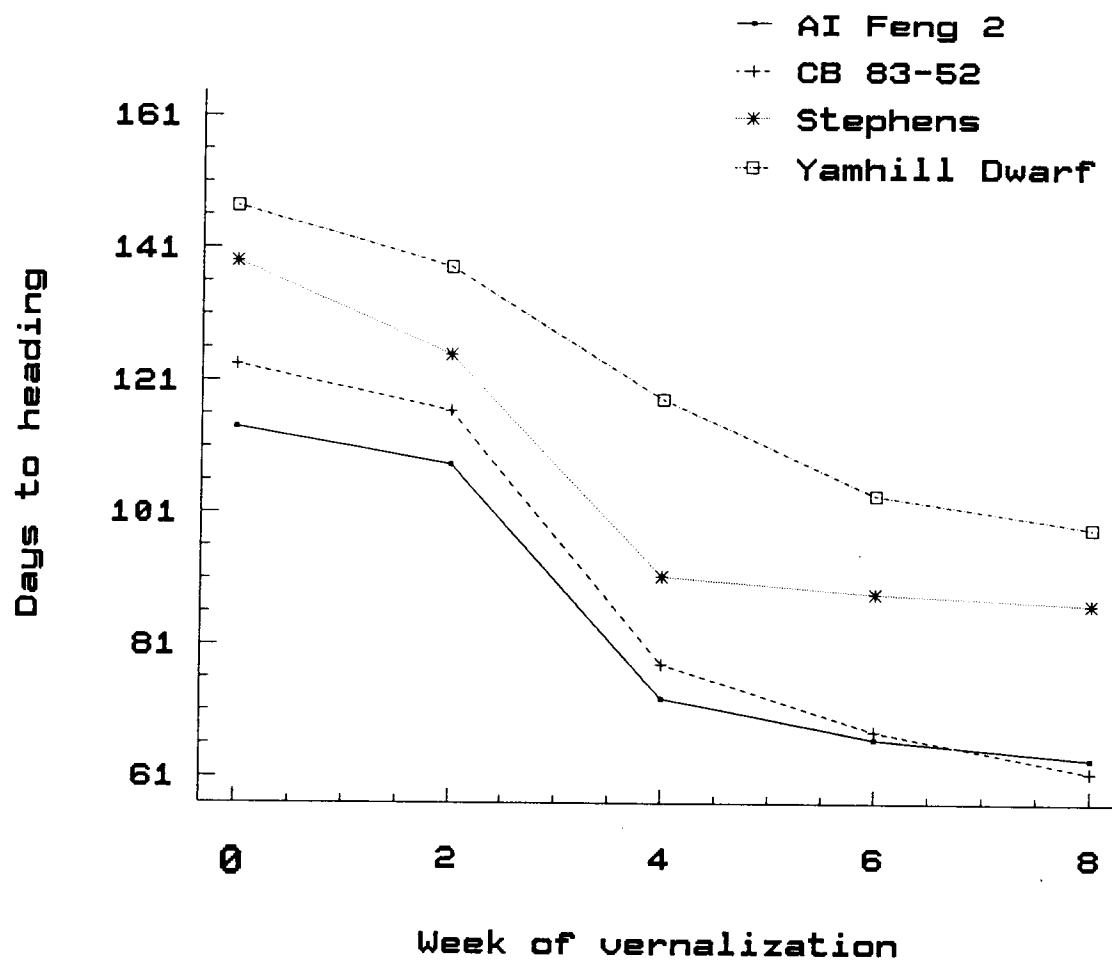


Figure I.1. Heading responses of four genotypes to different vernalization treatments in greenhouse.

Table I.1. Means for different developmental periods of four varieties in response to vernalization treatment in greenhouse.

Genotype	Vernalization	Tillering	Flag leaf emergence	Vegetative period	Reproductive period	Spikelet initiation period	spike growth period
	week	day					
AI Feng 2	0	33.0	105.1	70.0	43.9	25.0	18.9
	2	31.4	99.0	52.0	56.3	29.0	27.3
	4	37.3	60.4	29.0	43.7	11.0	32.7
	6	40.4	53.1	23.7	42.7	11.3	31.4
	8	37.3	49.4	20.0	43.7	15.7	28.0
CB 83-52	0	31.4	113.7	70.0	53.4	31.0	22.4
	2	30.6	106.4	61.0	55.4	36.0	19.4
	4	33.3	66.1	27.7	50.2	20.0	30.2
	6	34.4	53.1	23.7	44.0	12.0	32.0
	8	32.6	45.1	17.0	44.6	18.7	25.9
Stephens	0	33.3	129.9	82.0	57.0	37.7	19.3
	2	31.6	114.3	65.0	59.9	42.7	17.2
	4	31.3	76.4	38.7	52.6	20.0	32.6
	6	35.9	73.1	29.7	58.9	19.3	39.6
	8	33.3	71.7	25.3	61.8	23.0	38.8
Yamhill	0	31.7	137.0	81.7	65.6	41.0	24.6
Dwarf	2	30.6	127.9	72.0	66.1	46.7	19.4
	4	28.6	105.0	52.7	65.4	37.0	28.4
	6	33.0	88.3	40.7	62.9	25.3	37.6
	8	34.0	82.1	35.3	63.3	25.7	37.6
LSD _{0.05}		5.0	4.8	2.1	2.1	5.2	4.9

later stages such as spikelet initiation and spike growth period. Halse and Weir (1970) also found that reproductive period was generally not influenced by vernalization in sixteen Australian wheat cultivars.

Flag leaf emergence, vegetative growth, and the spikelet initiation period were prolonged by the decrease of the vernalization period from 4 to 2 weeks, but Yamhill Dwarf also showed large differences for these traits as the vernalization period changed from 6 to 4 weeks (Table 1). The sensitivity to vernalization of a cultivar can be reflected in many different stages of growth and development.

Chinese genotypes had shorter growth periods in days to flag leaf emergence, vegetative period, and reproductive development including both spikelet initiation period and spike growth period. Even under long daylength and 8 weeks of vernalization, the four cultivars still showed differences in these developmental periods. Apart from the photoperiod and vernalization requirements, a genetic factor apparently governed the time to reach each of these stages. All cultivars eventually reached heading with no vernalization, although it was greatly delayed. Obviously, long daylength can partially compensate for the effect of vernalization, at least in these genotypes.

Photoperiod Response

The heading responses of the four cultivars to different photoperiods are shown in Fig. 2. The two Chinese varieties were insensitive to photoperiod changes,

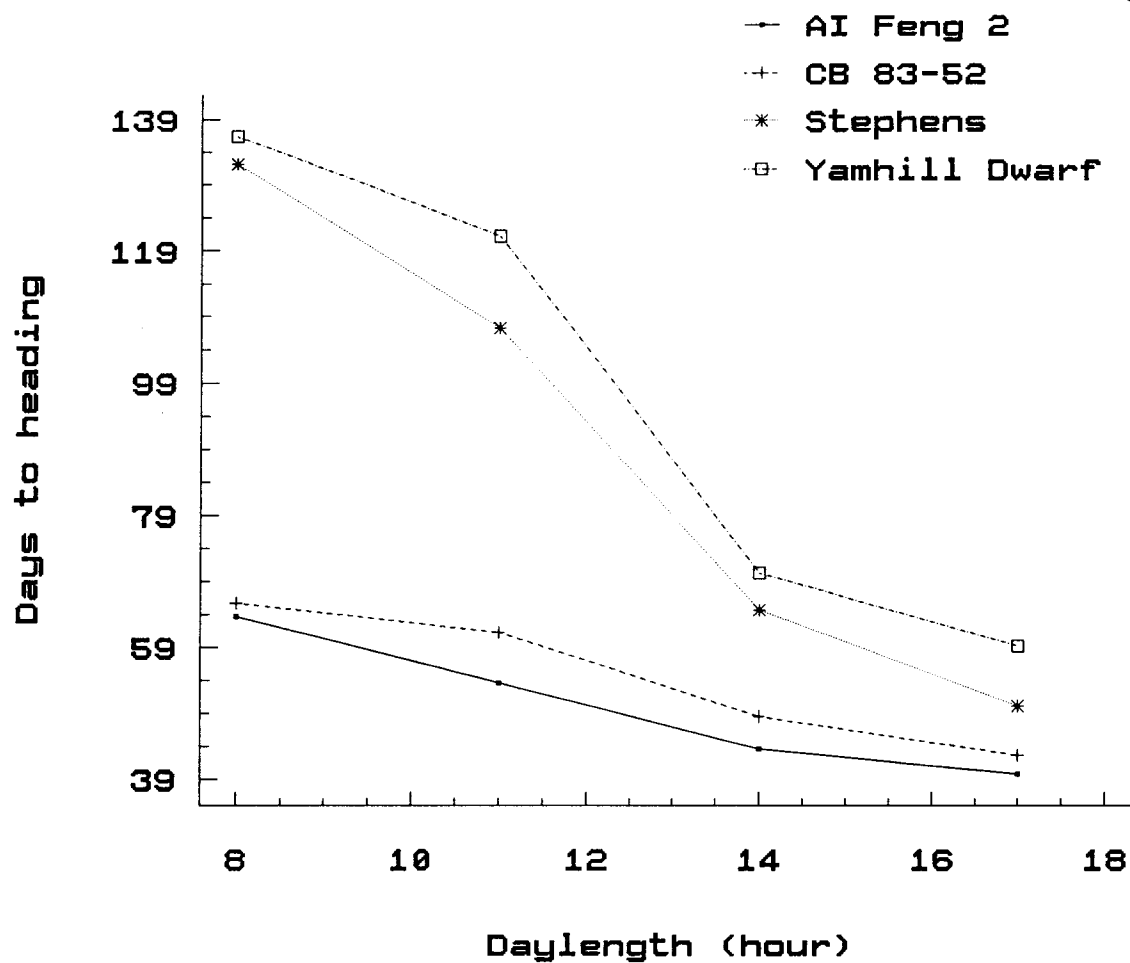


Figure I.2. Heading responses of four genotypes under different photoperiods in growth chamber.

in contrast to the Oregon lines which required a 14 hour daylength for normal heading time. Apart from photoperiod effect, some promotion of heading by longer photoperiod is expected due to an increased period of photosynthesis. Levy and Peterson (1972) also found less response to lengthened photoperiods with early maturing spring wheat cultivars. The insensitivity to daylength of many of the wheat cultivars developed at International Maize and Wheat Improvement Center (CIMMYT) is one of the factors contributing to their wide adaptability, as earliness of maturity is not affected by the length of day (Borlaug et al., 1964).

Unlike the vernalization treatment, longer photoperiods did reduce time to tillering and reproductive period (Table 2). Flag leaf emergence, vegetative and both spikelet initiation and spike growth periods were also promoted by increased daylength. For Stephens and Yamhill Dwarf, the reduction of daylength from 14 to 11 hours mainly increased the reproductive stage, especially the spike growth period. Based on the tests of five cultivars, Eguchi (1937-39) found that wheat was indifferent to photoperiod for spikelet initiation, but longer photoperiods hastened spike development. In contrast, Gott (1961) indicated that the days to spikelet initiation was strongly affected by short days but there was little effect of daylength on post-initiation development in Australian wheat. However, Halse and Weir (1970), and Rahman and Wilson (1977) reported that cultivars both achieved spikelet initiation earlier and accelerated development from initiation to anthesis in longer days. These results suggest that there is considerable genetic variation among wheat cultivars in response to different photoperiods.

Table I.2. Means for different developmental periods of four genotypes under various photoperiods in growth chambers.

Genotype	Photo-period	Tillering	Flag leaf emergence	Vegetative period	Reproductive period	Spikelet initiation period	Spike growth period
	hour	day					
AI Feng 2	8	33.5	48.8	16.2	47.6	16.4	31.2
	11	31.2	40.4	14.2	39.4	15.3	24.1
	14	24.0	33.6	11.4	32.2	9.5	22.7
	17	22.4	29.6	11.5	28.3	8.7	19.7
CB 83-52	8	30.2	49.0	16.0	49.7	12.9	36.9
	11	28.1	45.5	16.4	44.8	15.0	29.8
	14	24.3	35.7	12.0	36.5	11.0	25.5
	17	18.0	30.1	11.3	31.3	10.6	20.7
Stephens	8	39.0	107.4	34.0	98.2	36.4	61.8
	11	27.7	84.1	28.5	78.7	28.2	50.5
	14	24.4	53.1	17.5	47.2	16.5	30.7
	17	20.1	35.8	12.2	37.9	11.2	26.7
Yamhill	8	40.4	106.0	32.0	104.5	41.5	63.0
Dwarf	11	32.0	96.6	32.5	88.7	34.2	54.5
	14	24.9	55.8	20.9	49.3	18.2	31.2
	17	20.8	43.2	13.5	45.7	16.5	29.2
LSD _{0.05}		7.4	7.4	3.8	7.7	7.1	7.1
($a_i b_j - a_k b_l$)*							
LSD _{0.05}		11.9	8.3	4.4	7.7	6.3	6.7
($a_i b_j - a_k b_l$ or $a_i b_j - a_k b_l$)**							

* For two means of different varieties at same photoperiod level.

** For two means of different photoperiods at same or different variety level.

Field Performance

The two Chinese genotypes were consistently earlier in heading, anthesis, and maturity time than the two Oregon cultivars when grown under field conditions (Table 3 and 4). Also, they required less time to reach stem elongation (Table 4). These results are consistent with data from both the vernalization and photoperiod experiments.

The early maturity of AI Feng 2 can be attributed to its short vegetative period. In contrast, CB 83-52 was early maturing mainly due to its short reproductive period (Table 4). The differences in the reproductive phase were mainly in the spikelet initiation period, as there was essentially no significant differences in spike growth period among the four genotypes. Although Stephens and Yamhill Dwarf matured at almost same time, their developmental patterns were quite different. Yamhill Dwarf had shorter vegetative and grain filling period, but longer reproductive phase than Stephens. Wong and Baker (1986) also found that different combinations of the duration of the developmental periods might or might not lead to differences in time to maturity in spring wheat.

The range of the variation among genotypes was 18 days for stem elongation time, 16 days for vegetative period, 20 days for reproductive period, and 19 days for spikelet initiation period, as compared to 11 days for grain filling duration (Table 4). Therefore, there seems more genetic variability in the preanthesis period among

Table I.3. Means of eight traits for four genotypes evaluated in the field at Corvallis, Oregon in 1986-87.

Genotype	Spikelet number	Heading	Anthesis	Lag period	Maturity	Grain fill duration	Grain fill rate	Kernel weight
		-----day-----					mg/seed/day	mg
AI Feng 2	27.1	198.7	206.3	7.6	254.3	48.0	1.158	55.6
CB 83-52	20.7	198.2	205.9	7.7	254.5	48.5	1.276	61.9
Stephens	24.5	210.4	213.4	3.0	258.3	44.8	1.563	70.0
Yamhill Dwarf	29.2	216.2	217.6	1.4	258.5	41.0	1.511	61.9
LSD _{0.05}	1.1	0.8	0.5	0.6	1.8	1.6	0.055	2.6

Table I.4. Means of sixteen traits for four genotypes and three spacings evaluated in the field at Corvallis, Oregon in 1987-88.

Genotype	Trait*														
	SE	VP	RP	SIP	SGP	H	A	M	GFD	GFR	KW	LN	RLA	SN	RSI
	----- day -----									mg/ seed/ day	mg		no./ 10 day		no./ day
AI Feng 2	134.5	110.5	87.7	38.8	48.9	198.2	205.0	257.7	52.8	1.08	56.9	11.0	0.62	23.3	0.60
CB 83-52	144.8	119.5	78.5	31.2	47.3	198.0	207.1	254.5	47.3	1.20	56.4	11.6	0.65	18.9	0.55
Stephens	152.8	126.5	84.5	38.8	45.8	211.0	218.9	266.0	47.1	1.42	66.8	12.5	0.62	20.2	0.48
Yamhill Dwarf	150.0	117.8	98.1	49.7	48.5	215.9	223.1	265.0	41.8	1.40	58.4	13.4	0.66	25.0	0.44
LSD _{0.05}	3.8	3.7	2.6	2.6	3.3	1.9	1.5	1.7	0.8	0.03	1.7	0.2	0.01	0.7	0.07
45 cm	150.4	119.5	87.2	41.1	46.0	206.7	214.2	260.1	45.9	1.35	61.2	12.4	0.66	24.3	0.50
15 cm	147.1	118.8	87.7	40.8	46.9	206.5	213.7	260.5	46.9	1.25	58.1	12.4	0.65	23.3	0.54
Solid	139.1	117.4	86.7	36.8	49.9	204.2	212.8	261.8	49.0	1.23	59.6	11.6	0.61	17.9	0.51
LSD _{0.05}	2.3	1.8	1.7	2.2	1.6	0.7	0.7	1.7	1.3	0.05	0.9	0.1	0.01	0.5	0.05

* SE, time from planting to stem elongation; VP, vegetative period; RP, reproductive period; SIP, spikelet initiation period; SGP, spike growth period; H, time from planting to heading; A, time from planting to anthesis; M, time from planting to maturity; GFD, grain fill duration; GFR, grain fill rate; KW, kernel weight; LN, leaf number; RLA, rate of leaf appearance; SN, spikelet number; RSI, rate of spikelet initiation.

the four cultivars tested. The earlier development phase has more stages to manipulate and provides greater potential for breeding early maturing cultivars.

There was some variation in rate of leaf appearance among genotypes, but larger differences in leaf number were observed (Table 4). The early maturing cultivars, AI Feng 2 and CB 83-52, had fewer leaves. Bauer et al. (1984) reported that both number of leaves and rate of development are equally important in their effects on time to anthesis in spring wheat.

The two early maturing cultivars, AI Feng 2 and CB 83-52, were also faster in rate of spikelet initiation. Yamhill Dwarf had longest spikelet initiation period, due to its large spikelet number and slow rate of initiation. AI Feng 2 and Stephens were similar as to the length of time spent in this period, but had different spikelet number and initiation rate. This agrees with the results of Wong and Baker (1986) who found that duration of the spikelet initiation period was associated with both number of spikelets and rate of initiation in spring wheat. Cisar and Shands (1978) reported similar results in cultivars of oats. However, Rawson (1970), and Rashid and Halloran (1984) showed that the number of spikelets, rather than the spikelet initiation rate, was more closely associated with the duration of the spikelet initiation period in wheat.

The two early-flowering Chinese genotypes also had longer grain filling period (Table 3 and 4). This suggests that early development in preanthesis stages may be hard to combine with short postanthesis period. Yamhill Dwarf required shorter grain filling period, mainly attributed to its faster rate of grain fill, rather than lower

kernel weight. Van Sanford (1985), and Bruckner and Frohberg (1987) found that the duration of grain fill was negatively associated to grain filling rate, but not correlated to kernel weight. In contrast, Gebeyehou et al. (1982) reported that grain filling duration was associated with kernel weight but not rate of grain fill in durum wheat.

It is useful to know the effect of spacing on the growth and development patterns of wheat plants. In breeding programs where the objectives are early maturity and acceptable yield, early generations are often space-planted and subject to heavy selection pressure, whereas advanced generations are seeded at commercial densities. Compared to solid-planting, plants which were space-planted had an increased time to reach stem elongation and in spikelet initiation period, but had a reduced spike growth period, leaving reproductive period unchanged (Table 4). Vegetative period, heading, anthesis, and maturity were only slightly influenced by sowing density. However, numbers of spikelet and leaf were increased under space-planted conditions as the result of lengthened spikelet initiation stage and faster leaf appearance rate, respectively. Beuerlein and Lafever (1989) reported that seeding rate had no effect on heading date in wheat.

Grain fill duration was shortened in spaced plants, but grain filling rate did not accelerate until spacing increased to 45 cm, leading to lower kernel weight for 15-cm spaced plants than the solid planted. Frederick and Marshall (1985) did find that increasing the seeding rate increased kernel weight of winter wheat in six of eight locations.

The growth and development of the wheat plant is under genetic control and strongly influenced by environmental factors such as vernalization and photoperiod. The life cycle can be divided into several developmental stages and the duration of each stage affects the ultimate time of maturity. The preanthesis period seems to provide greater potential for improvement in early maturity and acceptable yield.

REFERENCES

- Amaya, A. A., R. U. Busch, and K. L. Lebsack. 1972. Estimates of genetic effects of heading date, plant height and grain yield in durum wheat. *Crop Sci.* 12: 478-481.
- Avey, D. P. and H. W. Ohm. 1982. Advanced generation analysis of days to heading in three winter wheat crosses. *Crop Sci.* 22: 912-915.
- Bauer, B., A.B. Frank, and A.L. Black. 1984. Estimation of spring wheat leaf growth rates and anthesis from air temperature. *Agron. J.* 76: 829-835.
- Beuerlein, J.E. and H.N. Lafever. 1989. Row spacing and seeding rate effects on soft red winter wheat yield, its components and agronomic characteristics. *Appl. Agric. Res.* Vol. 4, No. 2, pp. 106-110.
- Borlaug, N.E., J.C. Ortega, I. Narvaez, A. Garcia, and R. Rodriguez. 1964. Hybrid wheat in perspective. Hybrid Wheat Seminar Report, Crop Quality Council, Minneapolis: pp. 1-19.
- Bruckner, P.L. and R.C. Froberg. 1987. Rate and duration of grain fill in spring wheat. *Crop Sci.* 27: 451-455.
- Cisar, G. and H.L. Shands. 1978. Floral initiation and development in cultivars of oats. *Crop Sci.* 18: 461-464.
- Crumpacker, D. W. and R. W. Allard. 1962. A diallel cross analysis of heading date in wheat. *Hilgardia* 32: 275-318.
- Darroch, B.A. and R.J. Baker. 1990. Grain filling in three spring wheat genotypes: statistical analysis. *Crop Sci.* 30: 525-529.
- Eguchi, T.. 1937-39. Effects of relative length of day and night before and after differentiation on formation and development of flower bud. *Jap. J. Bot.* 9: 100-101.
- Frederick, J.R. and H.G. Marshall. 1985. Grain yield and yield components of soft red winter wheat as affected by management practices. *Agron. J.* 77: 495-499.
- Friend, D. J., J. E. Fisher and V. A. Helson. 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. *Can. J. Bot.* 41: 1660-1673.

- Gebeyehou, G., D. R. Knott and R. J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. *Crop Sci.* 22: 337-340.
- Gott, M.B.. 1961. Flowering of Australian wheats and its relation to frost injury. *Aust. J. Agric. Res.* 12: 547.
- Halse, N. J. and R. N. Weir. 1970. Effects of vernalization, photoperiod and temperature on phenological development and spikelet number of Australian wheat. *Aust. J. Agric. Res.* 21: 383-393.
- Kirby, E.J.M.. 1986. Significant stages of ear development in winter wheat. p. 7-24. *In* W. Day and R.K. Atkin (ed.) *Wheat growth and modelling*. Plenum Press, New York.
- Levy, J. and M. L. Peterson. 1972. Responses of spring wheat to vernalization and photoperiod. *Crop Sci.* 12: 487-490.
- Masle, J., G. Doussinault, and B. Sun. 1989. Response of wheat genotypes to temperature and photoperiod in natural conditions. *Crop Sci.* 29: 712-721.
- May, L. and D.A. Van Sanford. 1992. Selection for early heading and correlated response in maturity of soft red winter wheat. *Crop Sci.* 32: 47-51.
- Rahman, M.S. and J.H. Wilson. 1977. Determination of spikelet number in wheat. I. effect of varying photoperiod on ear development. *Aust. J. Agric. Res.* 28: 565-574.
- Rashid, A.H. and G.M. Halloran. 1984. Influence of photoperiod on culm elongation and apical development in semi-dwarf and standard-height wheats. *Ann. Bot.* 54: 375-382.
- Rawson, H.M.. 1970. Spiklet number, its control, and relation to yield per ear in wheat. *Aust. J. Biol. Sci.* 23: 1-15.
- Ross, W.M.. 1955. Associations of morphological characters and earliness in oats. *Agron. J.* 47: 453-457.
- SAS Institute Inc.. 1987. *SAS/STAT guide for personal computers*, version 6 edition. Cary, NC: SAS Institute Inc..
- Van Sanford, D.A.. 1985. Variation in kernel growth characters among soft red winter wheats. *Crop Sci.* 25: 626-630.

- Wong, L. S. L. and R. J. Baker. 1986. Developmental patterns in five spring wheat genotypes varying in time to maturity. *Crop Science* 26: 1167-1175.
- Zadok, J.C., T.T. Chang and C. F. Konzak. 1974. A decimal code for the growth stages of cereals. *Weed Research* 14: 415-421.

CHAPTER II

Inheritance of Grain Filling Duration and Rate in Three Winter Wheat Crosses

ABSTRACT

Following anthesis, the grain yield of wheat (*Triticum aestivum* L.) becomes proportional to kernel weight which is a function of the rate and duration of grain fill. The lack of information regarding the genetic control of grain filling rate and duration warranted this study. Parents, F1, F2 and backcross generations of three winter wheat crosses, 'Stephens' X 'AI Feng 2', 'Stephens' X 'CB 83-52' and 'Yamhill Dwarf' X 'CB 83-52', were grown in a space-planted experiment. Plots were sampled at 2-3 day intervals to obtain grain filling parameters. There was significant genetic variation among generations for grain fill duration, rate and kernel weight. Generation mean analyses revealed both additive and partial dominance gene actions in the control of kernel weight. Additive effects were the main source of genetic variation for grain filling rate and duration, while the effects of epistasis were of minor importance. Results indicated that early generation selection for both duration and rate of grain fill should be effective in these populations while selection for kernel weight would be more effective in later generations.

INTRODUCTION

Grain filling is a important stage in wheat development determining the ultimate grain yield. Following anthesis, grain yield becomes proportional to kernel weight which is a function of the rate and duration of grain fill. In multiple cropping systems, early maturity of the individual crop species is critical. Where the length of the growing season dictates when the flowering period can occur due to low temperature or plants are forced to mature by raising temperature or drought, it may be necessary to modify other stages of the life cycle including the grain filling period.

Grain filling period is the duration from anthesis to physiological maturity (beyond which there is no significant increase in kernel dry matter). Hanft and Wych (1982) found that complete loss of green color from the glumes occurred close to physiological maturity in eight hard red spring wheat cultivars. Smith and Donnelly (1991) reported that complete loss of green color from the rachis, glumes, and the crease of kernels occurred within 1 day of physiological maturity in all the five hard red and one soft white winter wheat cultivars studied.

Research results indicated that genetic differences among wheat cultivars exist for kernel weight and both rate and duration of grain filling (Gebeyehou et al., 1982; Van Sanford, 1985; Bruckner and Frohberg, 1987; Darroch and Baker, 1990). Grain filling in wheat is also known to be influenced by environmental factors, such

as temperature and light (Wardlaw, 1970; Sofield et al., 1977; Wiegand and Cuellar, 1981; Grabau et al., 1990).

Bhatt (1972) reported that the gene action involved in the inheritance of kernel weight was predominantly of the additive type in two spring wheat crosses. Ketata et al. (1976) found similar result in a winter cross. Sun et al. (1972) found evidence of nonallelic interactions but indicated that additive and dominance effects made the major and most consistent contributions to the expression of kernel weight in six spring wheat crosses. However, there is a lack of information regarding the inheritance of grain filling rate and duration in wheat. In a diallel analysis of seven inbred lines of corn, Cross (1975) reported that the general combining ability effects for duration and rate of grain fill were larger than specific combining ability effects. In soybean, Metz et al. (1985) estimated the realized heritabilities of seed-filling period ranging from 0.40 to 1.02 except for indeterminate types, but Pfeiffer and Egli (1988) found nonsignificant heritability estimates for effective filling period which was calculated by dividing the final kernel weight by the dry matter accumulation rate of the seed during the linear phase of kernel growth.

For wheat breeders to exploit different types of gene action involved in inheritance of the grain filling traits, information regarding the relative magnitude of genetic components is essential. The present study was designed to use generation mean analysis to identify the nature of the inheritance for the duration and rate of grain filling in selected winter wheat populations.

MATERIALS AND METHODS

Two winter wheat cultivars developed by Oregon State University, 'Stephens' and 'Yamhill Dwarf', and two Chinese winter cultivars, 'AI Feng 2' and 'CB 83-52', were the parental material used. These cultivars differed in heading, flowering and maturity time, plant height, components of yield and grain yield.

Three crosses, Stephens X AI Feng 2, Stephens X CB 83-52, and Yamhill Dwarf X CB 83-52, were made in the field in 1985. The F_1 was backcrossed in 1986 to each of the parents (P_1 and P_2) to produce the first backcross generations B_1 ($F_1 \times P_1$) and B_2 ($F_1 \times P_2$). Seeds produced by selfing F_1 plants were composited to provide the F_2 generation. Parents, F_1 , F_2 and backcross populations were planted at the Crop Science Field Laboratory, Corvallis, Oregon on October 24, 1987. The soil type at the experiment site is a fine silty mixed mesic Aquultic Argixeroll. A randomized complete block design with four replications was employed. Plots consisted of four rows for each parent, F_1 and backcross, and eight rows for each F_2 population per replication. Rows were 4.5 m in length with 30 cm between rows and 15 cm between plants within the row allowing a total of 30 plants/row. Before planting, the plots received 45 kg/ha of N as ammonium nitrate. An additional 45 kg/ha of N was broadcasted in late February and again in late April, 1988. Fungicide "Tilt" at the rate of 0.22 l/ha was applied once a month from March to June, 1988 to control leaf diseases. The experiment site was bordered by barley plants.

At anthesis, 140 flowering primary spikes were randomly selected and tagged in each plot. The terminal plants from each end were avoided to minimize border effects. Five tagged spikes were collected from each plot at 2-3 day intervals from 3 days after anthesis to past harvest maturity. Samples were oven-dried at 70°C for 24 hours, subsequently 20 kernels from each spike were separated from the two basal florets of the middle spikelets. Kernels were redried at 70°C for 20 hours and weighed immediately.

A polynomial model was fitted to the dry weight data from each plot using SAS statistical package (SAS Institute Inc., 1987). Stepwise variable selection method was used to select the best equation for each plot. The date of physiological maturity was determined by taking the derivative of the equation, setting $dy/dx = 0$, and solving for independent variable time. The estimate of grain filling duration was derived as the time from anthesis to physiological maturity. The rate of grain filling for each plot was obtained as the coefficient of linear regression by fitting the dry weight data in the linear phase of dry matter accumulation. The regression procedure of the SAS program first included all dry weight data points for a plot, then the non-linear data points were eliminated at the start or end of the grain filling curve. If exclusion of such a data point would improve the r^2 value of the linear regression model, the data point might not be within the limits of linear phase and was discarded.

Five main tillers of each of the 140 F_2 plants were tagged at anthesis and later the time of green color disappearance from the glume of each tagged tiller was

recorded. The grain filling duration for each F_2 plant was obtained by averaging the time periods from anthesis to complete loss of green color from glume of the five main tillers. After harvest, 20 kernels from each of the five spikes were separated from the two basal florets of the middle spikelets. The 100 seeds from each F_2 plant were oven-dried and weighed. The kernel weight was divided by the grain filling duration to give the grain filling rate for each F_2 plant.

A joint scaling test was performed using data from P_1 , P_2 , F_1 , F_2 , B_1 , and B_2 to provide estimates for the mean, additive, and dominance effects (Mather and Jinks, 1982). These estimates are obtained by the procedure of weighted least squares using the inverses of the variances of generation means as weights. This test also evaluates the goodness of fit of the 3-parameter model (mean, additive, and dominance effects) to the observed data by assuming that the weighted sum of squared deviations, i.e., $(\text{observed values} - \text{expected values})^2$, follows a χ^2 distribution with 3 df. Lack of fit implies the existence of epistatic effects.

The scaling tests of Mather (Mather, 1949; Hayman and Mather, 1955) with $A = 2\bar{B}_1 - \bar{F}_1 - \bar{P}_1$, $B = 2\bar{B}_2 - 6\bar{F}_1 - \bar{P}_2$, $C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$, and $D = 2\bar{F}_2 - \bar{B}_1 - \bar{B}_2$ were also conducted for the grain filling traits. Generation means for each character were analyzed using the method of Hayman(1958) to fit a six parameter model. These parameters are the F_2 population mean or mean effect, m ; the pooled additive effects, a ; the pooled dominance effects, d ; the pooled additive X additive epistatic effects, aa ; the pooled additive X dominance epistatic effects, ad ; and the pooled dominance X dominance epistatic effects, dd . In the following estimation equations,

P_1 will be designated to the parent with the higher value, P_2 the parent with the lower value, and B_1 and B_2 the corresponding backcrosses:

$$m = \bar{F}_2$$

$$a = \bar{B}_1 - \bar{B}_2$$

$$d = -1/2\bar{P}_1 - 1/2\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$aa = -4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$ad = -1/2\bar{P}_1 + 1/2\bar{P}_2 + \bar{B}_1 - \bar{B}_2$$

$$dd = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 - 4\bar{B}_2$$

Significance of the various gene effects for this model was tested against standard errors derived from the variances of the corresponding population means.

RESULTS AND DISCUSSION

The six generations differed significantly for kernel weight, duration and rate of grain fill, except in one cross (Table 1). The failure to detect significant difference among generations of Stephens X AI Feng 2 for grain fill duration could be due to the nearly equal parental means for this trait (Table 2). It can also be observed that when difference between parents was large, progeny generation mean values were between their parental means. If two parents did not differ much, their progeny means were often above the higher parental value. The F_1 deviated significantly from the midparent values for grain filling rate and 100-kernel weight in Yamhill Dwarf X CB 83-52, suggesting the presence of nonadditive gene action involved in the control of these traits. These results confirmed that genetic variability does exist for grain filling traits in wheat.

From Table 2, it can also be noted that heavier kernel weight is usually characterized with the higher grain filling rate. This suggests that grain filling rate may be more important in contributing to the kernel weight in the environment of this study and selection for grain filling rate may be realized by selecting kernel weight.

The results of the A, B, C, D and joint scaling tests provided information regarding the presence or absence of nonallelic interactions (Table 3). Significance of a test indicates that the epistasis is present based on that particular scale used. However, the results of different tests may not agree with each other, as each test

Table II.1. Mean squares from the analyses of variance of parental, F_1 , F_2 and backcross data for grain fill parameters in three crosses grown at the Hyslop Crop Science Field Lab, Corvallis, Oregon during 1987-88 season.

Cross	Source	df	Grain fill duration	Grain fill rate	100- kernel weight
Stephens X CB 83-52	Replication	3	3.48*	0.003	0.03
	Generation	5	3.10*	0.088**	1.12**
	Error	15	0.95	0.005	0.03
Stephens X AI Feng 2	Replication	3	1.13	0.006	0.03
	Generation	5	0.73	0.081**	0.73**
	Error	15	0.91	0.008	0.03
Yamhill Dwarf x CB 83-52	Replication	3	3.89	0.004	0.02
	Generation	5	31.79**	0.053**	0.17**
	Error	15	2.27	0.006	0.03

*, **: Significantly greater than the error mean square at $P = 0.05$ and $P = 0.01$, respectively.

Table II.2. Estimates of generation means and F_1 -midparent deviations for three grain fill characters in three crosses evaluated at Corvallis, Oregon during 1987-88 season.

Cross or Generation	Grain fill duration, day	Grain fill rate mg/kernel/day	100-Kernel weight, g
Stephens (P1) X CB 83-52 (P2)			
P1	47.5	2.09	6.96
P2	49.3	1.67	5.58
F1	49.3	1.90	6.47
F2	48.3	1.92	6.15
B1	47.1	1.97	6.67
B2	48.5	1.77	5.82
LSD _{0.05}	1.5	0.10	0.24
F_1 -midparent	0.9	0.02	0.20
Stephens (P1) X AI Feng 2 (P2)			
P1	47.6	2.07	6.93
P2	48.6	1.69	5.52
F1	48.0	1.83	6.26
F2	48.3	1.87	6.02
B1	47.4	1.98	6.24
B2	48.5	1.78	5.77
LSD _{0.05}	1.4	0.14	0.27
F_1 -midparent	-0.1	-0.05	0.04
Yamhill Dwarf (P1) X CB 83-52 (P2)			
P1	41.3	1.72	5.91
P2	49.1	1.69	5.61
F1	45.4	1.92	6.16
F2	45.5	1.93	6.04
B1	43.9	1.91	6.12
B2	47.7	1.77	5.72
LSD _{0.05}	2.27	0.11	0.28
F_1 -midparent	0.2	0.22**	0.40**

** Significantly different from zero at $P = 0.01$ level.

Table II.3. Significance of the A, B, C, D, and joint scaling tests for grain fill characters in three crosses evaluated at the Hyslop Crop Science Field Lab, Corvallis, Oregon during 1987-88 season.

Cross or Trait	Test				
	A	B	C	D	Joint
Stephens X CB 83-52					
Grain fill duration	ns	ns	ns	ns	ns
Grain fill rate	ns	ns	ns	ns	ns
Kernel weight	ns	ns	ns	ns	ns
Stephens X AI Feng 2					
Grain fill duration	ns	ns	ns	ns	**
Grain fill rate	ns	ns	ns	ns	ns
Kernel weight	*	ns	*	ns	*
Yamhill Dwarf X CB 83-52					
Grain fill duration	ns	ns	ns	ns	ns
Grain fill rate	**	ns	ns	ns	**
Kernel weight	ns	ns	ns	ns	ns

*, **, Significant at $P = 0.05$ and 0.01 , respectively. ns, Nonsignificant at $P = 0.05$.

examines different type of epistatic effects. The joint scaling test is believed to be more powerful than other tests in detecting epistasis since information is drawn from all six generations. As a matter of fact, the joint scaling test revealed epistatic effects whenever it was declared significant by individual scaling tests. In addition, the joint scaling test detected epistasis for grain filling duration which was not shown by any of the individual tests.

The joint scaling test indicated that epistasis is not involved in the inheritance of grain fill duration and therefore a three-parameter model would be satisfactory in explaining the genetic variation for this trait, except in the cross Stephens X AI Feng 2 (Table 4). Based on the three-parameter model, additive effects appeared more important in the genetic control of grain fill duration. Since the three-parameter model was not sufficient to explain the genetic differences for grain fill duration in Stephens X AI Feng 2 cross due to epistasis, the six-parameter model was invoked to determine the type and magnitude of gene action involved in this particular cross (Table 4). However, none of the gene effects estimated was significant, probably due to the lack of genetic variation for the trait in this cross (Table 1).

Based on the joint scaling test, the three-parameter model proved to be adequate for grain fill rate indicating absence of epistasis, with the exception of Yamhill Dwarf X CB 83-52 (Table 4). The three-parameter model indicated a predominance of additive gene action contributing to the control of this character. Because of epistatic effect, six-parameter model was adopted for grain fill rate in Yamhill Dwarf X CB 83-52. Both additive and additive X dominance effects were

Table II.4. Gene effects estimated using three- and six-parameter models in three crosses.

Cross and model	Gene effect	Grain fill duration	Grain fill rate	Kernel weight
Stephens X CB 83-52				
Three parameter	m	47.9**	1.88**	6.25**
	a	1.3*	0.21**	0.70**
	d	1.0	0.02	0.18**
	χ^2	2.78	1.17	6.41
	P	0.25-0.50	0.75-0.90	0.05-0.10
Six parameter	m	48.3**	1.92**	6.15**
	a	1.4	0.20**	0.85**
	d	-1.0	-0.18	0.58
	aa	-1.8	-0.21	0.37
	ad	0.5	-0.01	0.16
	dd	5.8	0.28	0.14
Stephens X AI Feng 2				
Three parameter	m	48.16**	1.89**	5.93**
	a	0.72	0.20**	0.48**
	d	-0.13	-0.06	0.29**
	χ^2	14.88	0.38	8.55
	P	<0.01	0.90-0.95	0.025-0.05
Six-parameter	m	48.3**	1.86**	6.02**
	a	1.1	0.20*	0.47**
	d	-1.4	0.01	-0.03
	aa	-1.4	0.06	-0.07
	ad	0.5	0.01	-0.24
	dd	1.6	-0.13	1.02*

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

Table II.4. (continued). Gene effects estimated using three- and six-parameter models in three crosses.

Cross and model	Gene effect	Grain fill duration	Grain fill rate	Kernel weight
Yamhill Dwarf X CB 83-52				
Three parameter	m	45.3**	1.70**	5.74**
	a	3.9**	0.04*	0.17**
	d	0.8	0.24**	0.44**
	χ^2	0.25	14.68	5.29
	P	0.95-0.975	<0.01	0.10-0.25
Six parameter	m	45.5**	1.93**	6.04**
	a	3.8**	0.14*	0.40**
	d	1.45	-0.13	-0.08
	aa	1.3	-0.36	-0.50
	ad	-0.2	0.11*	0.23
	dd	-3.18	0.22	0.63

*, **, significant at $P=0.05$ and 0.01 , respectively.

significant with this model. It is worth noting that for both grain fill duration and rate, epistasis was detected by scaling tests only in crosses where small differences in parental mean values were observed (Table 2).

Although there was some evidence of nonallelic interaction, additive effect seemed to play a major role in the expression of the grain filling rate and duration. This was also supported by data from the F_2 generation (Fig. 1 and Fig. 2). Variation for these grain filling parameters were continuous, and F_1 and F_2 means fell between parental means. Transgressive segregation was observed for both traits.

The three-parameter model was sufficient in explaining the genetic variability for kernel weight found in Stephens X CB 83-52 and Yamhill Dwarf X CB 83-52 (Table 4). Both additive and positive dominance effects made significant contributions to the expression of kernel weight. This agrees with results reported by Sun et al. (1972) which indicated that additive and dominance effects were the major and most consistent contributors to the expression of kernel weight. The joint scaling test detected epistasis for kernel weight in Stephens X AI Feng 2 (Table 3). The six-parameter model showed significant additive and dominance X dominance effects for this trait. Chapman and McNeal (1971) found no significant epistatic effects in a spring wheat cross, while Ketata et al. (1976) failed to detect epistasis in a winter cross for kernel weight. Sun et al. (1972) found evidence of nonallelic interactions but pointed out that their effects were minor as compared to additive and dominance effect in the inheritance of kernel weight in six spring wheat crosses.

This experiment did not provide information regarding genotype-environment

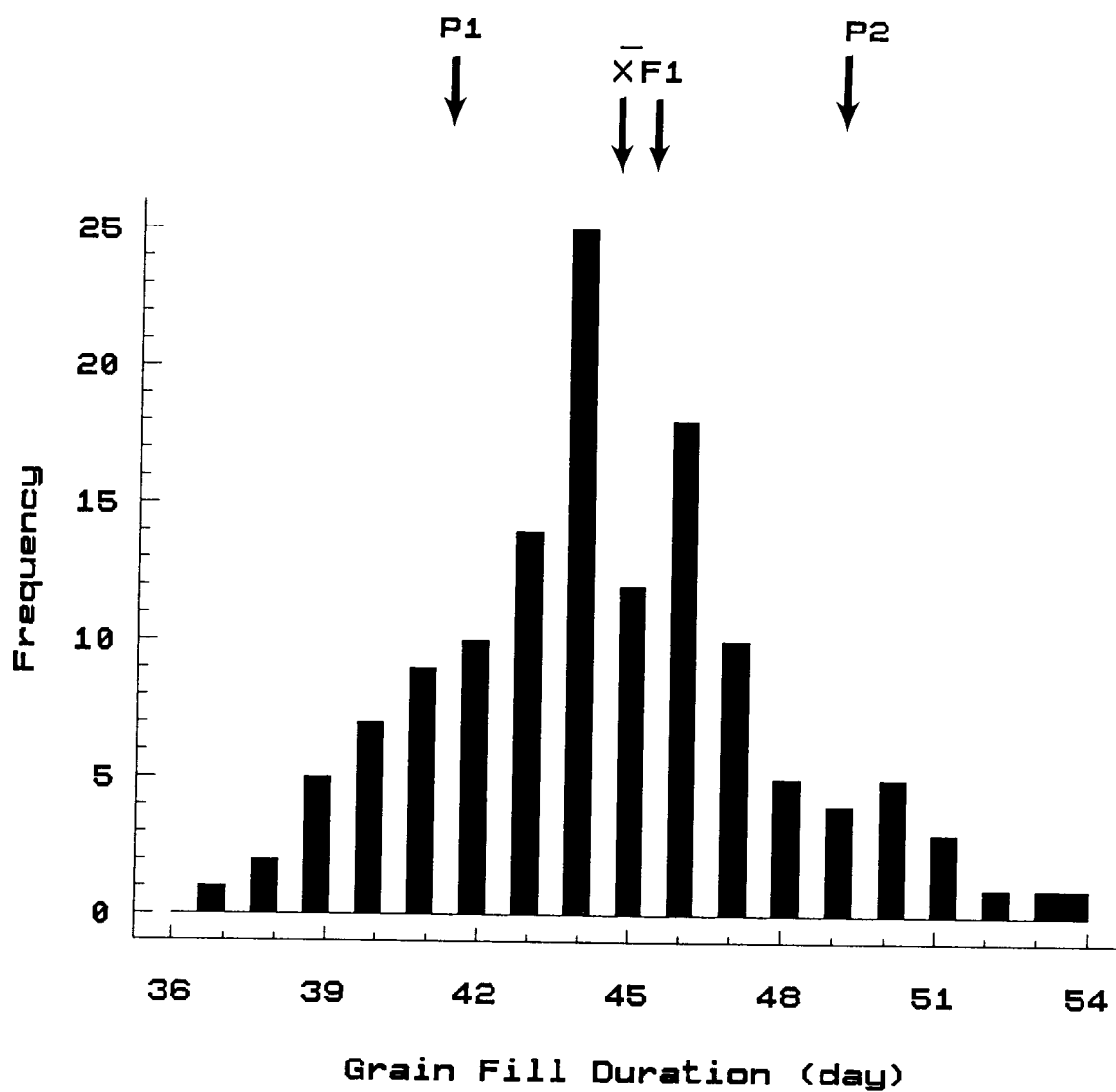


Fig. II.1. Distribution of grain filling duration for F₂ plants (n = 135) of the cross Yamhill Dwarf(P1) X CB 83-52(P2) as compared with parental and F₁ means.

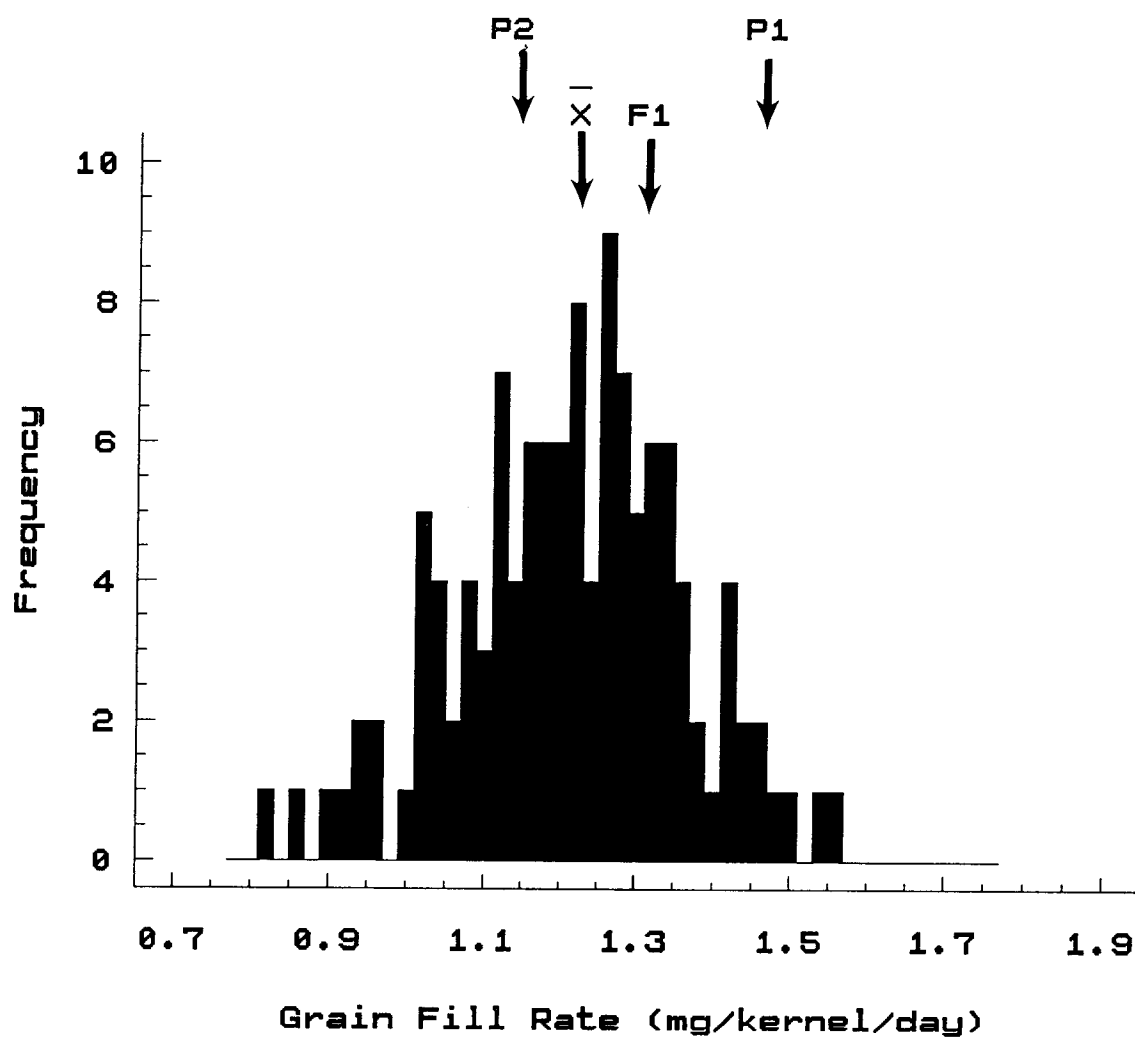


Fig. II.2. Distribution of grain filling rate for F₂ plants (n = 120) of the cross

Stephens (P1) X AI Feng 2 (P2) as compared with parental and F₁ means.

interaction which may be involved in the expression of the grain filling traits.

However, our preliminary study (unpublished data) showed no significant genotype X year interaction for either rate or duration of grain fill, or kernel weight. The present investigation did indicate that additive effects made the major contributions to the inheritance of the grain filling rate and duration. As long as sufficient genetic variation exists, early generation selection for grain filling duration and rate should be effective in these crosses while selection for kernel weight may be more efficient if conducted in F_4 or later generations.

REFERENCES

- Bhatt, G.M.. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. *Crop Sci.* 12: 95-98.
- Bruckner, P.L. and R.C. Frohberg. 1987. Rate and duration of grain fill in spring wheat. *Crop Sci.* 27: 451-455.
- Chapman, S.R. and F.H. McNeal. 1971. Gene action for yield components and plant height in a spring wheat cross. *Crop Sci.* 11: 384-386.
- Cross, H.Z.. 1975. Diallel analysis of duration and rate of grain filling of seven inbred lines of corn. *Crop Sci.* 15: 532-535.
- Darroch, B.A. and R.J. Baker. 1990. Grain filling in three spring wheat genotypes: statistical analysis. *Crop Sci.* 30: 525-529.
- Gebeyehou, G., D.R. Knott, and R.J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. *Crop Sci.* 22: 337-340.
- Grabau, L.J., D.A. Van Sanford, and Q.W. Meng. 1990. Reproductive characters of winter wheat cultivars subjected to postanthesis shading. *Crop Sci.* 30: 771-774.
- Hanft, J.M. and R.D. Wych. 1982. Visual indicators of physiological maturity of hard red spring wheat. *Crop Sci.* 22: 584-587.
- Hayman, B.I.. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12: 371-390.
- Hayman, B.I. and K. Mather. 1955. The description of genetic interaction in continuous variation. *Biometrics* 11: 69-82.
- Ketata, H., L.H. Edwards, and E.L. Smith. 1976. Inheritance of eight agronomic characters in a winter wheat cross. *Crop Sci.* 16: 19-22.
- Mather, K.. 1949. *Biometrical Genetics*. Dover Publication, Inc.. New York.
- Mather, K. and J.L. Jinks. 1982. *Biometrical genetics. The study of continuous variation*. Third edition. Chapman and Hall Ltd., London.

- Metz, G.L., D.E. Green, and R.M. Shibles. 1985. Reproductive duration and date of maturity in populations of three wide soybean crosses. *Crop Sci.* 25: 171-176.
- Pfeiffer, T.W. and D.B. Egli. 1988. Heritability of seed-filling period estimates in soybean. *Crop Sci.* 28: 921-925.
- SAS Institute Inc.. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, NC: SAS Institute Inc..
- Smith, D.H. and K.J. Donnelly. 1991. Visual markers of maximum grain dry weight accumulation in winter wheat. *Crop Sci.* 31: 419-422.
- Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4: 785-797.
- Sun, P.L.F., H.L. Shands, and R.A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. *Crop Sci.* 12: 1-5.
- Van Sanford, D.A.. 1985. Variation in kernel growth characters among soft red winter wheats. *Crop Sci.* 25: 626-630.
- Wardlaw, I.F.. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Aust. J. Biol. Sci.* 23: 765-774.
- Wiegand, C.L. and J.A. Cuellar. 1981. Duration of grain filling and kernel weight as affected by temperature. *Crop Sci.* 21: 95-101.

CHAPTER III

Genetic Estimates of Grain Filling Parameters in Selected Winter Wheat Populations

ABSTRACT

After flowering the grain yield of wheat (*Triticum aestivum* L.) is largely determined by kernel weight which is a function of the rate and duration of grain fill. The lack of information regarding the inheritance of grain filling rate and duration prompted this study. Parents and F_1 s resulting from a 4X4 diallel cross were grown in space-planted experiments for two years and the plots were sampled at 2-3 day intervals to obtain grain filling parameters. Significant genotypic variation for grain filling rate, duration, and kernel weight was observed in both seasons. Genotype X year interaction was not significant for any of the grain filling traits. General combining ability effects for grain filling rate, duration, and kernel weight were much larger than specific combining ability effects. The results of combining ability analyses were in agreement with estimates of the genetic components from the diallel which indicated that the additive gene action made the major contribution to the inheritance of the grain filling traits. However, dominance effects appeared also involved in the genetic control of grain filling duration and

kernel weight. Narrow sense heritability estimates were high for all three traits of grain fill. Results indicated that early generation selection for both duration and rate of grain fill and kernel weight should be effective in these populations.

INTRODUCTION

Grain yield of wheat depends on number of kernels per unit area and kernel weight. Kernel weight relies, in turn, on rate and duration of grain filling period. A better understanding of the genetic control and environmental influences on the duration and rate of grain fill and kernel weight would help wheat breeders and agronomists to increase and stabilize grain yield.

Grain filling period is the duration from anthesis to physiological maturity (beyond which there is no significant increase in kernel dry matter). Grain filling rate is the result of the translocation of photosynthate from source to sink. Eighty to ninety percent of the carbohydrate for grain growth are from photosynthesis after anthesis, whereas 10-20 % of the carbon are from available reserves (Spiertz and Vos, 1985).

Research results indicated that genetic differences among wheat cultivars exist for kernel weight and both rate and duration of grain filling (Gebeyehou et al., 1982; Van Sanford, 1985; Bruckner and Frohberg, 1987; Darroch and Baker, 1990). Grain filling in wheat is also known to be influenced by environmental factors, such as temperature and light (Wardlaw, 1970; Sofield et al., 1977; Wiegand and Cuellar, 1981; Grabau et al., 1990).

Bhatt (1972) and Ketata et al. (1976) reported that the nature of gene action involved in the inheritance of kernel weight was predominantly of the additive type

in two spring wheat crosses and a winter cross, respectively. Sun et al. (1972) found evidence of nonallelic interactions but indicated that additive and dominance effects made the major and most consistent contributions to the expression of kernel weight in six spring wheat crosses. However, there is a lack of information regarding the inheritance of grain filling rate and duration in wheat. In a diallel analysis of seven inbred lines of corn, Cross (1975) reported that the general combining ability effects for duration and rate of grain fill were larger than specific combining ability effects. In soybean, Metz et al. (1985) estimated the realized heritabilities of seed-filling period ranging from 0.40 to 1.02 except for indeterminates, but Pfeiffer and Egli (1988) found nonsignificant heritability estimates for effective filling period which was calculated by dividing the final kernel weight by the dry matter accumulation rate of the seed during the linear phase of kernel growth.

In order to exploit different types of gene action involved in inheritance of the grain filling traits, information regarding the relative magnitude of genetic components and estimates of combining ability are essential. Such information will help wheat breeders in their identification of parents and selection strategies. This study was undertaken to determine the mode of inheritance, genotype X year interaction, and combining ability and heritability estimates for the duration and rate of grain filling and kernel weight in selected winter wheat populations.

MATERIALS AND METHODS

A 4X4 diallel cross, excluding reciprocals, was developed to produce six F_1 populations. Two winter wheat cultivars developed by Oregon State University, 'Stephens' and 'Yamhill Dwarf', and two Chinese winter cultivars, 'AI Feng 2' and 'CB 83-52', were the parental material. These cultivars differ in many traits including heading, flowering and maturity time, and the components of yield.

Seeds of the parents and F_1 populations were planted at the Crop Science Field Laboratory, Corvallis, Oregon in October in both the 1986-87 and 1987-88 growing seasons. The soil type at the experiment site is a fine silty mixed mesic Aquultic Argixeroll. A randomized complete block design with four replications was employed. Plots consisted of four rows for each parent and F_1 population per replication. Rows were 4.5 m in length with 30 cm between rows and 15 cm between plants within the row allowing for a total of 30 plants/row. Before planting, the plots received 56 kg/ha and 45 kg/ha of N as ammonium nitrate in 1986-87 and 1987-88 growing seasons, respectively. An additional 90 kg/ha of N broadcast were split equally in late February and late April in both years. Fungicide "Tilt", at the rate of 0.22 l/ha, was applied once a month from March to June to control leaf diseases. The experiment sites were boarded by barley plants.

At anthesis, 140 flowering primary spikes were randomly selected and tagged in each plot. The terminal plants from each end of the plot were avoided to minimize border effects. Five tagged spikes were collected from each plot at 2-3

day intervals from 3 days after anthesis to past harvest maturity. Samples were oven-dried at 70°C for 24 hours. Subsequently, 20 kernels from each spike were separated from the two basal florets of the middle spikelets. Kernels were redried at 70°C for 20 hours and weighed immediately.

A polynomial model was fitted to the dry weight data from each plot using SAS statistical package (SAS Institute Inc., 1987). Stepwise variable selection method was used to select the best equation for each plot. Data fit the models well; r^2 values generally ranged from 0.97 to 0.99, and exceeded 0.94 in all cases. The date of physiological maturity was determined by taking the derivative of the equation, setting $dy/dx = 0$, and solving for independent variable time. The estimate of grain filling duration was the time from anthesis to physiological maturity. Mean grain filling rate for each plot was estimated as predicted maximum grain dry weight divided by grain filling duration.

Data obtained for each trait were subjected to analyses of variance for each growing season and, because error variances were homogeneous, over growing seasons. Estimates of general and specific combining ability were derived by the method 2, model I of the diallel cross analyses provided by Griffing (1956) using both the parents and F_1 populations and assuming a fixed model.

Possible additive and dominant gene actions involved in the inheritance of the traits were analyzed using Hayman's approach (Singh and Chaudhary, 1979). To exam whether the populations meet the assumptions postulated by Hayman (1954), the covariance between parents and F_1 , W_r values, were plotted against the

corresponding variance V_r . In the absence of non-allelic interaction and with independent distribution of genes among the parents, W_r is related to V_r by a straight regression line of unit slope. The validity of the assumptions was further tested using the formula by Hayman (1954):

$$t^2 = \frac{n - 2}{4} \left[\frac{(\text{Var } V_r - \text{Var } W_r)^2}{\text{Var } V_r \times \text{Var } W_r - \text{Cov}^2(V_r, W_r)} \right]$$

which follows a F distribution with 4 and $(n - 2)$ degree of freedom.

Significance of the test indicates failure of the hypotheses.

Narrow sense heritability for the grain filling characters was also estimated from the diallel following Mather and Jinks' (1982) formula:

$$h^2 = \frac{1/2D + 1/2H_1 - 1/2H_2 - 1/2F}{1/2D + 1/2H_1 - 1/4H_2 - 1/2F + E}$$

where the genetic parameters are: D, additive effect; H_1 , dominant effect; H_2 , dominant effect adjusted by gene frequency; F, covariance of additive and dominance effects; E, error.

RESULTS AND DISCUSSION

Significant genotypic variation existed for grain filling rate and duration and for kernel weight across both seasons (Table 1). However, genotype X year interaction was not significant for any of the grain filling parameters. This suggests that selection for grain filling traits in these populations would not be influenced by the year environments. Van Sanford (1985) found a significant genotype X environment interaction which, however, was not of a magnitude that would preclude identification of superior genotypes in a selection program.

Both the rate of grain fill and kernel weight were reduced in 1987-88 season, but grain filling duration was not affected by different environment (Table 2). Mean daily air temperatures during grain filling period were higher in 1986-87 than in 1987-88 season (14.6 vs 12.2 °C in May and 17.5 vs 15.6 °C in June), which may partially account for the higher grain filling rate and subsequent heavier kernel weight in the first season. Sofield et al. (1977) also found that rate of grain filling in common wheat was higher at higher temperatures.

Rate of grain fill ranged from 1.16 mg/kernel/day in AI Feng 2 to a high of 1.56 mg/kernel/day in Stephens (Table 2). Variation in grain filling duration was of a similar magnitude, ranging from 41 day in Yamhill Dwarf to 50 day in AI Feng 2 X CB 83-52. Stephens had the highest rate of grain filling and kernel weight, while AI Feng 2 was the lowest for both traits. These data indicate that there is substantial genotypic variation for grain filling traits in these materials. Significant differences

Table III.1. Summary of analyses of variance in and across environments for estimated grain fill (GF) parameters of parents and F₁s in the diallel grown at the Hyslop Crop Science Field Lab, Corvallis, Oregon for two seasons.

Trait	Season		Combined analyses		
	1986-87	1987-88	Year	Genotype	G X Y
Rate of GF mg/kernel/day	**	**	**	**	NS
Duration of GF day	**	**	NS	**	NS
Kernel weight mg	**	**	**	**	NS

**** Significant differences among genotypes at individual seasons and significant year (Y), genotype (G), and G X Y variation in the combined analysis at the 0.01 probability level.**

Table III.2. Means and F₁-midparent(MP) values of estimated grain fill (GF) parameters for the genotypes in the diallel cross evaluated in two seasons at the Hyslop Crop Science Field Lab, Corvallis, Oregon.

Genotype	GF rate, mg/kernel/day				GF duration, day				Kernel weight, mg			
	1986-87		1987-88		1986-87		1987-88		1986-87		1987-88	
	Mean	F ₁ -MP	Mean	F ₁ -MP	Mean	F ₁ -MP	Mean	F ₁ -MP	Mean	F ₁ -MP	Mean	F ₁ -MP
AI Feng 2	1.158	----	1.155	----	48.0	----	47.5	----	55.6	----	54.9	----
CB 83-52	1.276	----	1.172	----	48.5	----	48.1	----	61.9	----	56.9	----
Stephens	1.563	----	1.456	----	44.8	----	46.9	----	69.9	----	68.4	----
Yamhill Dwarf	1.511	----	1.406	----	41.1	----	41.3	----	61.9	----	57.9	----
AI Feng 2 X CB 83-52	1.273	0.056*	1.188	0.025	49.4	1.2	50.5	2.7**	63.0	4.3**	60.0	4.1**
AI Feng 2 X Stephens	1.360	-0.001	1.323	0.018	48.1	1.7	47.3	0.1	65.3	2.6*	62.5	0.9
AI Feng 2 X Yamhill Dw.	1.317	-0.018	1.280	-0.001	46.3	1.8*	44.0	-0.4	60.9	2.2	56.3	-0.1
CB 83-52 X Stephens	1.439	0.020	1.353	0.039	48.6	2.0*	48.5	1.0	69.8	3.9**	65.5	2.9**
CB 83-52 X Yamhill Dw.	1.428	0.035	1.327	0.038	44.8	0.0	45.8	1.1	63.9	2.0	60.6	3.2**
Stephens X Yamhill Dw.	1.541	0.004	1.422	-0.009	42.7	-0.3	42.8	-1.3	65.9	0.0	60.8	-2.4**
Mean	1.387	0.016	1.308	0.018	46.2	1.1	46.3	0.5	63.8	2.5	60.4	1.4
CV %	2.6	----	3.2	----	3.1	----	2.7	----	3.0	----	2.4	----
LSD _{0.05}	0.053	0.046	0.060	0.052	2.1	1.8	1.8	1.6	2.8	2.4	2.1	1.8

*,** Significant from zero at 0.05 and 0.01 probability levels, respectively.

between F_1 and midparent value were found for rate and duration of grain fill and kernel weight in specific crosses, suggesting that nonadditive gene action was influencing the expression of these traits.

Since differences among genotypes were found for all three grain filling traits, combining ability analyses were conducted (Table 3). General combining ability (GCA) effects were highly significant for all three traits in both seasons. Significant specific combining ability (SCA) was consistently observed for kernel weight, while SCA effect was significant for grain filling duration only in 1987-88 season. In comparing the relative magnitude of general versus specific combining ability, the major part of the total genetic variability was associated with general combining ability for all traits. The largest GCA to SCA ratio was noted for grain filling rate, followed by duration of grain fill and kernel weight. General combining ability is recognized as primarily a measure of additive gene action, while specific combining ability is regarded as an estimate of the effects of non-additive gene action. Therefore, the grain filling traits seem mainly under additive type of genetic control in these crosses. This agrees with the gene actions of grain filling rate and duration in corn reported by Cross (1975). However, non-additive gene action may play an important role in certain crosses, especially for kernel weight.

Direct comparisons of GCA performances of individual cultivars with the corresponding standard errors for each trait are presented in Table 4. Stephens and Yamhill Dwarf displayed significant positive GCA effects for grain filling rate, while the two Chinese cultivars, AI Feng 2 and CB 83-52, had significant negative GCA

Table III.3. Mean squares for general combining ability (GCA) and specific combining ability (SCA) effects for grain filling parameters of the 4X4 diallel grown at the Hyslop Crop Science Field Lab, Corvallis, Oregon in 1986-87 and 1987-88 seasons.

Source	d.f.	<u>Grain fill rate</u>		<u>Grain fill duration</u>		<u>Kernel weight</u>	
		1986-87	1987-88	1986-87	1987-88	1986-87	1987-88
GCA	3	0.0513**	0.0339**	21.710**	21.450**	46.761**	45.480**
SCA	6	0.0005	0.0004	0.996	1.254*	3.690**	4.892**
Error	27	0.0003	0.0004	0.482	0.367	0.903	0.593
GCA/SCA		95.46	90.49	21.80	17.11	12.67	9.30

*, ** Significant from zero at 0.05 and 0.01 probability levels, respectively.

Table III.4. Estimates of general combining ability effects for grain filling traits for four parents grown at the Hyslop Crop Science Field Lab, Corvallis, Oregon in 1986-87 and 1987-88 seasons.

Parents	Grain fill rate		Grain fill duration		Kernel weight	
	1986-87	1987-88	1986-87	1987-88	1986-87	1987-88
AI Feng 2	-0.11**	-0.07**	1.46**	0.92**	-3.09**	-2.17**
CB 83-52	-0.04**	-0.05**	1.46**	1.58**	0.22	-0.49
Stephens	0.09**	0.08**	-0.38	0.21	3.63**	4.00**
Yamhill Dwarf	0.06**	0.05**	-2.54**	-2.71**	-0.77*	-1.34**
SE($g_i - g_j$)	0.01	0.01	0.40	0.35	0.55	0.44

*, ** Significant from zero at 0.05 and 0.01 probability levels, respectively.

effects for this trait in both seasons. In contrast, the two Chinese genotypes showed significant positive GCA effects for the duration of fill with Yamhill Dwarf consistently reflecting significant negative effects. Stephens was the only cultivar which invariably provided significant positive GCA effect for kernel weight, while AI Feng 2 always generated large negative GCA effects. Since the major part of genetic variability associated with the grain filling traits was a result of additive gene action in these populations, crossing the two parents having the highest GCAs would have the greatest possibility of producing the best performing progeny.

Estimation of effects for SCA involving each F_1 mean along with the corresponding standard errors for the three grain filling traits are shown in Table 5. The only significant SCA effect for grain fill rate was observed in AI Feng 2 X CB 83-52 during 1986-87 season. Significant positive SCA effect was found in CB 83-52 X Stephens for duration of grain fill in 1986-87, but it was only found to be significant in AI Feng 2 X CB 83-52 in 1987-88. Significant positive SCA effects for kernel weight were detected in two crosses in 1986-87 and in three crosses in 1987-88, while significant negative SCA effect was found only in Stephens X Yamhill Dwarf in 1987-88 season. This again suggests that non-additive gene actions are more important for kernel weight than for grain filling rate and duration.

Hayman (1954) outlined several conditions that must be met for the genetic interpretation of statistics obtained from diallel analysis, including the independent distribution of genes in parents and no epistasis. There is general agreement that failure to meet the assumption that genes are independently distributed in the parents

Table III.5. Estimates of specific combining ability effects for grain filling traits from the 4X4 diallel grown at the Hyslop Crop Science Field Lab, Corvallis, Oregon in 1986-87 and 1987-88 seasons.

F ₁ s	Grain fill rate		Grain fill duration		Kernel weight	
	1986-87	1987-88	1986-87	1987-88	1986-87	1987-88
AI Feng 2 X CB 83-52	0.037*	0.008	0.383	1.750**	2.008*	2.360**
AI Feng 2 X Stephens	-0.005	0.010	0.717	-0.125	0.935	0.366
AI Feng 2 X Yamhill Dwarf	-0.022	-0.005	1.133	-0.458	0.961	-0.489
CB 83-52 X Stephens	0.004	0.022	1.217*	0.458	2.103**	1.705**
CB 83-52 X Yamhill Dwarf	0.019	0.023	-0.367	0.625	0.632	2.145**
Stephens X Yamhill Dwarf	0.003	-0.014	-0.533	-1.000	-0.784	-2.222**
SE (S _{ij} - S _{ik})	0.023	0.027	0.897	0.783	1.227	0.994
SE (S _{ij} - S _{kl})	0.021	0.024	0.802	0.700	1.098	0.889

*,** Significant from zero at 0.05 and 0.01 probability levels, respectively.

of the diallel will often result in overestimation of the average level of dominance. There are however conflicting reports as to whether or not failure of this assumption will result in biased estimates of GCA and SCA components of variance (Baker, 1978). Estimates of additive and dominance genetic variances can be obtained from a diallel cross only in the absence of epistasis. The slopes of the regression of (V_r , W_r) for the grain filling traits in this diallel ranged from 0.835 to 1.210 with an average of 1.021, all of which differed significantly from a slope $b=0$ but not from $b=1$. Furthermore, the t^2 tests for the traits were all non-significant. Therefore, there is no evidence implying the invalidity of the hypotheses for the grain filling traits in this study.

The estimates of genetic components from the diallel cross for grain filling rate, duration, and kernel weight are listed in Table 6. The relative magnitude of the additive components was much larger than dominant components for all three grain filling parameters. Dominant effects were significant for grain filling duration and kernel weight, but not for the rate of grain fill. The sign of F is an indicator of the relative frequencies of dominant and recessive alleles in the parents. F value was positive for grain filling rate and kernel weight, indicating that there is an excess of dominant alleles over the recessive alleles in the parents for these traits. In contrast, F value was negative for the duration of grain fill, suggesting that recessive genes were in excess over the dominant ones contributed by the parents for this trait. The degree of dominance, $\sqrt{H_1/D}$, was less than one for all three traits, indicating average partial dominance in the experiment materials. The average degree of

Table III.6. Estimates of genetic components and narrow sense heritability for grain filling traits from a four-parent diallel grown at Corvallis, Oregon in 1986-87 and 1987-88 seasons.

Components	Grain fill rate		Grain fill duration		Kernel weight	
	1986-87	1987-88	1986-87	1987-88	1986-87	1987-88
D	0.0362**	0.0239**	11.536**	9.500**	33.337**	37.169**
H ₁	0.0011	0.0003	2.233**	4.330**	9.522**	17.971**
H ₂	0.0009	0.0001	2.094**	2.576*	8.252**	12.903**
F	0.0035**	0.0022**	-3.912**	-5.865**	4.843*	14.259**
E	0.0018	0.0011	0.960	0.931	1.212	0.741
$\sqrt{H_1/D}$	0.1772	0.1172	0.440	0.675	0.535	0.695
h ² _{N.S.}	0.890	0.904	0.840	0.844	0.814	0.779

*, ** Significant from zero at 0.05 and 0.01 probability levels, respectively.

partial dominance was intermediate for duration of fill and kernel weight but low for grain filling rate. The narrow sense heritability estimates were relatively high for all the grain filling parameters, especially for the rate of grain fill. This indicates again that additive gene action made the main contributions to the inheritance of the grain filling traits. These findings are consistent with the result of the combining ability analyses. This also agrees with results reported by Sun et al. (1972) which indicated that additive and dominance effects were the major and most consistent contributors to the expression of kernel weight. Metz et al. (1985) also found relatively high estimates of realized heritability (0.40 - 1.02) for seed filling period in soybean.

It would be desirable for wheat breeders to manipulate grain filling parameters in order to develop cultivars suitable to different growing areas and management systems. Results obtained indicate that the additive gene action played the major role in the genetic control of the grain filling parameters. Coupled with the genetic variability detected and the high heritability estimates, it follows that selection for the grain filling traits in early generations should be effective in these populations. Combining ability analyses can also help breeders in choosing those parental lines which when crossed will result in the highest proportion of desirable segregates. The similarity of the estimates of the various genetic parameters over two years, together with the non-significant genotype X year interaction (Table 1), again suggests that selection for these grain filling traits would not be interfered by different environments.

If male sterility or chemical gametecides can be utilized for the commercial

production of hybrids, the wheat breeder will be able to take advantage of the non-additive as well as the additive portion of the total genetic variability. Under this circumstance, there would appear to be merit in selecting lines on the basis of high GCA effects, either for one or perhaps more of these grain filling traits which respond primarily to additive gene action, and desired SCA effect for kernel weight which also seems to react to non-additive gene action. With only two of the six possible F_1 crosses consistently displaying a significant SCA in this study, a large number of potential parental combinations might have to be tested to obtain a acceptable level of hybrid vigor in wheat.

REFERENCES

- Baker, R.J.. 1978. Issues in diallel analysis. *Crop Sci.* 18: 533-536.
- Bhatt, G.M.. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. *Crop Sci.* 12: 95-98.
- Bruckner, P.L. and R.C. Frohberg. 1987. Rate and duration of grain fill in spring wheat. *Crop Sci.* 27: 451-455.
- Cross, H.Z.. 1975. Diallel analysis of duration and rate of grain filling of seven inbred lines of corn. *Crop Sci.* 15: 532-535.
- Darroch, B.A. and R.J. Baker. 1990. Grain filling in three spring wheat genotypes: statistical analysis. *Crop Sci.* 30: 525-529.
- Gebeyehou, G., D.R. Knott, and R.J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. *Crop Sci.* 22: 337-340.
- Grabau, L.J., D.A. Van Sanford, and Q.W. Meng. 1990. Reproductive characters of winter wheat cultivars subjected to postanthesis shading. *Crop Sci.* 30: 771-774.
- Griffing, B. 1956. Concept of general and specific combining ability in relation of diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463-493.
- Hayman, B.I.. 1954. The theory and analysis of diallel crosses. *Genetics* 39: 789-809.
- Ketata, H., L.H. Edwards, and E.L. Smith. 1976. Inheritance of eight agronomic characters in a winter wheat cross. *Crop Sci.* 16: 19-22.
- Mather, K. and J.L. Jinks. 1982. *Biometrical genetics. The study of continuous variation.* Third edition. Chapman and Hall Ltd., London.
- Metz, G.L., D.E. Green, and R.M. Shibles. 1985. Reproductive duration and date of maturity in populations of three wide soybean crosses. *Crop Sci.* 25: 171-176.
- Pfeiffer, T.W. and D.B. Egli. 1988. Heritability of seed-filling period estimates in soybean. *Crop Sci.* 28: 921-925.

- SAS Institute Inc.. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, NC: SAS Institute Inc..
- Singh, R.K. and B.D. Chaudhary. 1979. Biometrical methods in quantitative genetic analysis. Second edition. Kalyani Publishers, Ludhiana, India.
- Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4: 785-797.
- Spiertz, J. H. J. and J. Vos. 1985. Grain growth of wheat and its limitation by carbohydrate and nitrogen supply. *In* W. Day and R. K. Atkin (eds.), *Wheat Growth and Modelling*, Plenum Press, pp. 129-141.
- Sun, P.L.F., H.L. Shands, and R.A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. *Crop Sci.* 12: 1-5.
- Van Sanford, D.A.. 1985. Variation in kernel growth characters among soft red winter wheats. *Crop Sci.* 25: 626-630.
- Wardlaw, I.F.. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Aust. J. Biol. Sci.* 23: 765-774.
- Wiegand, C.L. and J.A. Cuellar. 1981. Duration of grain filling and kernel weight as affected by temperature. *Crop Sci.* 21: 95-101.

CHAPTER IV

Associations between the Rate and Duration of Grain Filling and the Kernel Protein Content in Winter Wheat

ABSTRACT

Understanding the relationship and interaction of dry matter and nitrogen accumulation in wheat (*Triticum aestivum* L.) grain would aid in the improvement in both grain protein and grain yield. Information is lacking regarding the influence of the duration and rate of grain filling on subsequent grain protein content. In this study, parents, F₁s, and selected F₂ genotypes from a 4X4 diallel cross were evaluated for the rate and duration of grain filling, grain protein content, and other agronomic traits in Oregon for two years. Plots were sampled at 2-3 day intervals to obtain grain filling parameters. Significant genotypic differences for the traits measured were observed in both seasons. Genotype X environment interactions were not significant for grain filling traits and protein content. Anthesis date was negatively associated with the duration, but positively correlated with the rate of grain filling. Rate, but not duration of grain fill was closely associated with kernel weight. There was a inverse relationship between duration and rate of grain filling. Kernel protein percentage was positively associated with duration, but negatively related to rate of the grain filling. Results suggest that starch and protein

accumulations in the kernel are two highly independent process and may not necessarily compete for assimilates or energy. It may be necessary under the environments of this study to increase the duration of the grain fill to obtain high protein content and acceptable grain yield.

INTRODUCTION

As wheat is a staple food for more than one-third of the world's population, its grain protein is important to human nutrition and acceptable end product uses. Thus protein quantity and quality receive considerable attention in wheat improvement programs. However, increasing grain yield and grain protein concentration simultaneously has been difficult because of the well documented negative association between these two economically significant traits (Terman et al., 1969; McNeal et al., 1972; Loffler and Busch, 1982; Cox et al., 1985).

The process of dry matter (carbohydrate) and protein accumulation in the cereal grain may compete for assimilates and energy (Bhatia and Rabson, 1976). According to Penning de Vries et al. (1974), 1 g of glucose produced by photosynthesis can be used by the crop to produce 0.83 g of carbohydrate or 0.40 g of protein (assuming nitrate to be the N source). This implies that increases in protein content would use more photosynthate thus decreasing carbohydrate content and thus ultimately leading to decreases in dry matter yield. However, Brunori and Micke (1979) found no clear reduction of the grain dry weight and a dramatic increase of the nitrogen content in some genotypes upon a late application of nitrogen fertilizer. They therefore concluded that dry matter and N accumulation do not necessarily compete for the same resources.

Grain filling period is the duration from anthesis to physiological maturity (beyond which there is no significant increase in kernel dry matter). It was found

that complete loss of green color from the glumes occurred close to physiological maturity in wheat (Hanft and Wych, 1982; Singh et al., 1984; Smith and Donnelly, 1991). Research results indicated that genetic differences among wheat cultivars exist for kernel weight and both rate and duration of grain filling (Gebeyehou et al., 1982; Van Sanford, 1985; Bruckner and Frohberg, 1987; Darroch and Baker, 1990). Grain filling in wheat is also known to be influenced by environmental factors, such as temperature and light (Wardlaw, 1970; Sofield et al., 1977; Wiegand and Cuellar, 1981; Grabau et al., 1990).

Bauer et al. (1987) found that N uptake by kernels closely paralleled the kernel dry matter assimilation, and peak N content occurred about 2 days after maximum assimilation of kernel dry matter. Decline in kernel N concentration after anthesis, followed by near-constant concentrations thereafter has been reported for winter and spring wheat (Spiertz and Ellen, 1978; Bauer et al., 1987). However, Karlen and Whiney (1980) observed no change in kernel N concentration during grain filling of hard red winter wheat, while in spring wheat, McNeal et al. (1968) observed increases in concentration after the dough stage of about 1.0 and 3.0 g/kg under dryland and irrigation management, respectively.

Understanding the relationship and interaction of the dry matter and nitrogen accumulation in wheat grain would aid in the improvement in both grain protein and grain yield. However, there is no report regarding the influence of grain filling duration and rate on grain protein content. This experiment was designed to provide such information using four cultivars and their diallel cross progenies.

MATERIALS AND METHODS

Two winter wheat cultivars developed by Oregon State University, 'Stephens' and 'Yamhill Dwarf', and two Chinese winter cultivars, 'AI Feng 2' and 'CB 83-52', were the parental material. These cultivars differed in many traits including heading, flowering and maturity time, kernel protein content, and the components of yield. A 4X4 diallel cross, excluding reciprocals, was made to produce six F_1 populations for this investigation.

Seeds of the parents and F_1 populations were planted at the Crop Science Field Laboratory, Corvallis, Oregon in October in both the 1986-87 and 1987-88 growing seasons. The soil type at the experiment site is a fine silty mixed mesic Aquultic Argixeroll. A randomized complete block design with four replications was employed. Plots consisted of four rows for each parent and F_1 population per replication. Rows were 4.5 m in length with 30 cm between rows and 15 cm between plants within the row allowing a total of 30 plants/row. Five rows of F_2 plants from the cross of CB 83-52 X Yamhill Dwarf were also planted in 1987-88 season. Before planting, the plots received 56 kg/ha and 45 kg/ha of N as ammonium nitrate in 1986-87 and 1987-88 growing seasons, respectively. An additional 90 kg/ha of N broadcast were split equally in late February and late April. Fungicide "Tilt", at the rate of 0.22 l/ha, was applied once a month from March to June to control foliar pathogens. The experiment sites were boarded by barley plants.

At anthesis, 140 flowering main spikes were tagged for each parental and F_1 plot. The terminal plants from each end were avoided to minimize border effects. Five tagged spikes were collected from each plot at 2-3 day intervals from 3 days after anthesis to past harvest maturity. Samples were oven-dried at 70°C for 24 hours, subsequently 20 kernels from each spike were separated from the two basal florets of the middle spikelets. Kernels were redried at 70°C for 20 hours and weighed immediately.

A polynomial model was fitted to the dry weight data from each plot using SAS statistical package (SAS Institute Inc., 1987). Stepwise variable selection method was used to select the best equation for each plot. Data fit the models well; r^2 values generally ranged from 0.97 to 0.99, and exceeded 0.94 in all cases. The date of physiological maturity was determined by taking the derivative of the equation, setting $dy/dx = 0$, and solving for independent variable time. The estimate of grain filling duration was the time from anthesis to physiological maturity. Mean grain filling rate for each plot was estimated as predicted maximum grain dry weight divided by grain filling duration.

Five main tillers of each F_2 plant were tagged at anthesis and the time of green color disappearance from the glume of each tagged tiller was recorded. The grain filling duration for each F_2 plant was obtained by averaging the time periods from anthesis to complete loss of green color from glume of the five main tillers. After harvest, 20 kernels from each of the five spikes were separated from the two basal florets of the middle spikelets. The 100 seeds from each F_2 plant were oven-dried

and weighed. The kernel weight was divided by the grain filling duration to give the grain filling rate for each F_2 plant.

Agronomic data were collected from ten plants from each parental and F_1 plot and every F_2 plant for fertile tiller number, anthesis date, biological yield, main spike length, seed number of main spike, and grain yield. Seed samples from each parental and F_1 plot and each F_2 plant were ground in a Udy cyclone mill using a 0.5 mm mesh sieve. The wholemeal flour produced was utilized to determine the grain protein percentage by near-infrared reflectance spectroscopy using a Technicon InfraAlyser 400. Protein per kernel was calculated as grain protein percentage X average kernel weight of main spikes. Grain protein yield was determined as grain yield X grain protein percentage.

Data obtained for each trait were subjected to analyses of variance for each growing season and over growing seasons, and simple correlation coefficients among all traits were computed on plot mean basis using Statgraphics procedures (STSC Inc., 1991). Genotypic correlation was calculated as $r_g = G_{ij} / [(G_{ii})(G_{jj})]^{0.5}$, where r_g = genotypic correlation coefficient, G_{ij} = genotypic covariance, and G_{ii} and G_{jj} = genotypic variances for characters i and j , respectively. Environmental correlations were estimated as $r_e = E_{ij} / [(E_{ii})(E_{jj})]^{0.5}$, where r_e = environmental correlation coefficient, E_{ij} = error mean cross product, and E_{ii} and E_{jj} = error mean squares for characters i and j , respectively.

RESULTS AND DISCUSSION

The analyses of variance for grain filling parameters, protein content, and agronomic traits within each year indicated differences among genotypes except protein yield per plant (Table 1). When analyses were conducted over environments, differences between years were observed for all traits except grain filling duration. Genotypic differences in the combined analyses were significant for most traits except tiller number, plant yield, and protein yield per plant. This may be partly due to the significant genotype X year interactions for these three traits. The lack of genetic variation for plant yield may also contribute directly to the nonsignificance for protein yield per plant. However, there was no significant genotype X year interaction for grain filling parameters and kernel protein content, suggesting that these traits may be insensitive to the year environments.

Stephens had the highest rate of grain filling and kernel weight, with AI Feng 2 being the lowest for these traits (Table 2). As indicated by low coefficients of variation, grain filling parameters were estimated with good precision. Genotype with highest kernel protein percentage may not have the highest amount of protein per kernel. In addition, genotypes with higher kernel protein percentage or protein per kernel may not have higher protein yield per plant. For example, the kernel protein percentage or protein per kernel was lower than the average for AI Feng 2 X Yamhill Dwarf, but it had the highest protein yield per plant. These data indicate that there is substantial genetic difference for grain filling and protein traits in these populations.

Table IV.1. Summary of analyses of variance in and across environments for grain filling (GF) parameters, protein content, and associated agronomic traits of parents and F_1 s grown in the Hyslop Crop Science Field Lab, Corvallis, Oregon during 1986-87 and 1987-88 seasons.

Trait	Season		Combined analyses		
	1986-87	1987-88	Year	Genotype	G X Y
Rate of GF	**	**	**	**	NS
Duration of GF	**	**	NS	**	NS
Kernel weight	**	**	**	**	NS
Kernel protein %	**	**	**	**	NS
Protein/kernel	**	**	**	**	NS
Protein yield/plant	**	NS	**	NS	**
Anthesis	**	**	**	**	**
Biological yield	**	**	**	*	*
Fertile tiller	**	*	**	NS	*
Kernels/spike	**	**	**	**	**
Spike length	**	**	**	**	**
Plant yield	**	**	**	NS	**

*,** Significant differences among genotypes at individual seasons and significant year (Y), genotype (G), and G X Y variation in the combined analysis at the 0.05 and 0.01 probability levels, respectively.

Table IV.2. Mean values of estimated grain fill (GF) parameters, protein content, and other agronomic characters for the parents, F₁s, and (CB 83-52 X Yamhill Dwarf)F₂ evaluated at the Hyslop Crop Science Field Lab, Corvallis, Oregon in 1986-87 and 1987-88.

Genotype	GF rate mg/kernel/day	GF duration day	Kernel weight mg	Kernel protein %	Protein /kernel mg	Protein yield/plant g
AI Feng 2	1.158	47.8	55.3	13.0	6.9	7.8
CB 83-52	1.224	48.3	59.1	13.8	7.8	7.4
Stephens	1.509	45.9	69.2	11.3	7.0	6.7
Yamhill Dwarf	1.459	41.1	59.9	11.4	6.1	7.5
AI Feng 2 X CB 83-52	1.231	50.0	61.5	12.9	7.6	7.9
AI Feng 2 X Stephens	1.342	47.6	63.9	12.4	7.8	7.9
AI Feng 2 X Yamhill Dwarf	1.299	45.1	58.6	11.8	6.5	8.9
CB 83-52 X Stephens	1.396	48.5	67.7	12.4	8.0	7.7
CB 83-52 X Yamhill Dwarf	1.378	45.3	62.3	11.5	6.7	8.3
Stephens X Yamhill Dwarf	1.482	42.8	63.3	11.1	6.4	7.7
Mean	1.348	46.2	62.1	12.1	7.1	7.8
CV %	2.9	2.8	2.8	4.4	5.9	9.5
LSD _{0.05}	0.039	1.3	1.7	0.5	0.4	0.7
F ₂ mean	1.257	44.7	55.9	12.2	6.8	5.2
S.D.	0.158	3.5	5.3	1.9	0.9	2.6
Range	0.852-1.867	36-54	45.2-74.4	8.9-19.5	5.4-11.4	1.2-17.4

Table IV.2 (continued). Mean values of estimated grain fill (GF) parameters, protein content, and other agronomic characters for the parents, F₁s, and (CB 83-52 X Yamhill Dwarf)F₂s evaluated at the Hyslop Crop Science Field Lab, Corvallis, Oregon in 1986-87 and 1987-88.

Genotype	Anthesis day	Biological yield g	Fertile tiller	Kernels /spike	Spike length cm	Plant yield g
AI Feng 2	131.0	131.0	17.7	112.8	12.0	59.2
CB 83-52	131.0	136.3	21.0	72.3	11.0	52.9
Stephens	140.6	148.6	19.5	90.8	14.7	59.6
Yamhill Dwarf	145.2	166.5	18.9	96.9	11.9	64.7
AI Feng 2 X CB 83-52	130.1	142.9	17.0	94.6	12.3	61.0
AI Feng 2 X Stephens	133.9	146.1	16.8	98.9	13.3	63.6
AI Feng 2 X Yamhill Dwarf	135.7	162.6	17.9	123.7	12.0	74.3
CB 83-52 X Stephens	134.9	150.6	20.6	77.2	12.9	61.6
CB 83-52 X Yamhill Dwarf	137.7	167.0	20.0	91.0	11.8	71.0
Stephens X Yamhill Dwarf	143.5	169.0	19.4	104.7	13.8	69.3
Mean	136.4	152.1	18.9	96.3	12.6	63.7
CV %	0.7	7.7	9.8	5.5	2.5	8.8
LSD _{0.05}	0.9	11.7	1.9	5.3	0.3	5.6
F ₂ mean	143.2	103.0	14.7	63.5	10.1	44.2
S.D.	4.4	44.9	5.7	15.8	1.1	21.9
Range	134-160	19-293	5-39	10-95	7.1-13.3	5.7-145.3

F₂ plants from the cross CB 83-52 X Yamhill Dwarf were evaluated in 1987-88, as the parents of this cross represented the extremes in the duration and rate of grain filling and kernel protein content in 1986-87 (Table 2). A wide range of variation in grain filling parameters and kernel protein contents as well as other agronomic traits was also observed within the F₂ population.

The associations among the estimated grain filling parameters, protein contents, and other agronomic characters were investigated by calculating correlation coefficients (Table 3). Anthesis date was negatively associated with the grain filling duration, but positively correlated with grain filling rate. Late flowering genotypes were exposed to relatively higher temperatures, so their kernel growth proceeded at a higher rate for a shorter duration (Table 2). This agrees with the observations of other researchers (Van Sanford, 1985; Bruckner and Froberg, 1987). There was a positive association between grain filling rate and biological yield, suggesting that a plant may need a large carbohydrate "source" potential to support the grain filling process.

Rate, but not duration of grain fill, was closely associated with kernel weight in these populations (Table 3 and 4). This suggests that grain filling rate was more important in contributing to kernel weight than duration of grain filling period under these environments. Grain filling duration and rate were found to be negatively associated in this experiment. High rate and short duration of grain fill may contribute to higher kernel weights and grain yields in early maturing cultivars suitable for double cropping systems, short growing seasons, and environments with

Table IV.3. Simple correlation coefficients between estimated grain filling (GF) parameters, protein content, and selected agronomic traits of parents and F₁s (N = 40) evaluated in two seasons and (CB 83-52 X Yamhill Dwarf)F₂ (N = 130) grown in 1987-88 at the Hyslop Crop Science Field Lab, Corvallis, Oregon.

Trait		GF duration	GF Rate	Kernel weight	Kernel protein %	Protein /kernel	Protein yield/plant
GF	86-87	----	-0.7022**	-0.0065	0.4822**	0.6157**	0.1447
Duration	87-88	----	-0.5661**	0.2619	0.6743**	0.8102**	-0.2102
	F ₂	----	-0.6595**	-0.0488	0.4422**	0.4739**	0.1238
GF	86-87	----	----	0.7147**	-0.5689**	-0.2450	-0.4263**
Rate	87-88	----	----	0.6419**	-0.7794**	-0.2517	0.1821
	F ₂	----	----	0.7744**	-0.6249**	-0.1411	0.1624
Kernel	86-87	----	----	----	-0.3389*	0.2592	-0.4447**
Weight	87-88	----	----	----	-0.2794	0.3492*	0.0024
	F ₂	----	----	----	-0.4824**	0.2055*	0.3301**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table IV.3 (continued). Simple correlation coefficients between estimated grain filling (GF) parameters, protein content and selected agronomic traits of parents and F₁s (N = 40) evaluated in two seasons and (CB 83-52 X Yamhill Dwarf)F₂s (N = 130) grown in 1987-88 at the Hyslop Crop Science Field Lab, Corvallis, Oregon.

Trait		Anthesis	Biological yield	Spike length	Seeds /spike	Fertile tiller	Plant yield
GF	86-87	-0.8740**	-0.5746**	-0.1423	-0.2624	-0.0250	-0.1002
Duration	87-88	-0.7468**	-0.4796**	-0.1279	-0.3536*	-0.2425	-0.5744**
	F ₂	-0.6099**	-0.0125	-0.0863	-0.3274**	0.2591**	0.0307
GF	86-87	0.8143**	0.3930*	0.5718**	-0.0697	0.0199	-0.1332
Rate	87-88	0.8246**	0.5694**	0.6193**	-0.1659	0.3651*	0.6000**
	F ₂	0.4740**	0.2729**	0.4195**	0.5398**	-0.0206	0.2851**
Kernel	86-87	0.2832	-0.0006	0.6656**	-0.3494*	0.0174	-0.2662
Weight	87-88	0.2734	0.2020	0.5958**	-0.5367**	0.1852	0.1553
	F ₂	0.0832	0.3655**	0.4592**	0.4452**	0.2010*	0.4083**

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table IV.4. Genotypic (G) and environmental (E) correlation coefficients among grain filling (GF) parameters, protein contents, and yield of parents and F₁ genotypes (N = 40) evaluated at the Hyslop Crop Science Field Lab, Corvallis, Oregon. (Data from 1986-87 season above diagonal, data from 1987-88 season below diagonal.)

Trait		GF duration	GF rate	Kernel weight	Kernel protein %	Protein /kernel	Plant yield
GF duration	(G)		-0.7522	-0.1571	0.8755	0.9001	-0.1598
	(E)		-0.4588	0.6012	-0.0522	0.0517	0.0452
GF rate	(G)	-0.5624		0.7683	-0.9028	-0.3232	-0.1739
	(E)	-0.6550		0.3275	-0.0189	-0.0682	0.1402
Kernel weight	(G)	0.2317	0.6733		-0.5126	0.3896	-0.3790
	(E)	0.3038	0.4859		-0.0886	-0.0322	0.1399
Kernel protein %	(G)	0.7684	-0.9865	-0.3739		0.5814	-0.4292
	(E)	0.1968	0.2585	0.2613		0.6542	-0.1014
Protein / kernel	(G)	0.9108	-0.3226	0.3264	0.7545		-0.4212
	(E)	0.4107	-0.1015	0.3453	0.7092		0.0564
Plant yield	(G)	-0.7399	0.8845	0.3742	-0.9537	-0.7432	
	(E)	-0.2826	0.1082	-0.2392	0.0935	0.2490	

postanthesis high temperature stress. This would be especially true in areas where late frost is a problem, as short grain filling period is required in developing cultivars with delayed flowering but early maturity. Genotypic correlation analysis suggests that there is no genetic barrier to hinder development of genotypes with high rate but short duration of grain fill and high yield potential (Table 4). Actually, Stephens X Yamhill Dwarf possesses such properties (Table 2).

Since kernel weight was associated with the rate, but not duration of grain fill, it may be feasible to increase kernel weight without lengthening grain fill duration by selecting high rate of grain filling. Conversely, kernel weight can be used as a marker for the selection of higher grain filling rate, as kernel weight is easier to identify than grain filling rate. Since spike length is also significantly correlated with the rate of grain fill (Table 3), selection of larger spikes may also lead to higher grain filling rate.

The relationships between grain filling parameters and protein contents are also shown in Table 3 and 4. Protein per kernel was highly correlated with grain filling duration, but not the rate of grain fill. The accumulation of nitrogen and dry matter may cease at nearly same time, or the accumulation of nitrogen may continue for a short while after the kernel has attained the maximum dry weight (Brunori et al., 1980; Bauer et al., 1987). Longer grain filling duration will provide the kernel a longer period to assimilate nitrogen, resulting higher protein content in the grain. As mentioned by Austin et al. (1977), photosynthesis is needed for several interrelated processes: 1) nitrogen uptake by the roots, 2) reduction of NO_3 to NH_4 , and 3)

maintenance of electro-neutrality to compensate nitrate reduction. An coincidence in time when grain filling ceased and chlorophyll in leaves was completely decomposed has been observed (Herzog, 1982; Chen et al., 1990). Therefore, a longer grain filling period will provide continued photosynthetic assimilate and energy for nitrogen absorption, reduction, and storage. This is supported by the observation that benzimidazole fungicides, which delay leaf senescence, increase the nitrogen content of wheat plants, especially in late grain filling stage (Ellen and Spiertz, 1975).

The fact that grain filling rate was correlated with kernel weight but not protein per kernel also support the hypothesis that starch and protein accumulation in the kernel are two highly independent processes and may not necessarily compete for assimilates or energy. Such competition would lead to significant negative association between grain filling rate and protein per kernel.

There was a negative correlation between kernel protein percentage and grain filling rate (Table 3 and 4). This implies that the amount of nitrogen may be "diluted" by the carbohydrate translocated into kernels. Kernel protein percentage was positively associated with grain filling duration. Genotypes with longer grain filling durations tended to have lower rate of grain fill as evidenced by the negative correlation between the two traits, therefore the kernel nitrogen was probably less diluted by the influx of carbohydrates.

Other researchers have reported a negative correlation between plant yield and grain protein content which was also observed in this study (Table 4). Such a

inverse relationship could be explained by the negative correlation between grain filling rate and grain protein percentage. However, in this investigation it was found that the processes of dry matter and protein accumulation may not necessarily compete for assimilates or energy. Therefore, simultaneous improvements of both traits should be possible. The successful breeding of "Lancota", a cultivar with large seed, improved protein percentage and high yield (Johnson et al., 1978), proves that increments of the protein content do not necessarily have to be at the expense of grain yield. Since both grain protein percentage and protein per kernel were highly correlated with grain filling duration, it may be necessary to increase the duration of the grain fill to achieve this goal. Such increase in duration of grain fill should not decrease kernel size, as these two traits were not associated. If early maturity is desired, growing stages before anthesis may have to be reduced to obtain a shorter life cycle. Data obtained indicate that large genetic differences of rate and duration of dry matter accumulation and protein content exist. This genetic variability may be explored for breeding programs where high protein content with acceptable grain yield is desired.

REFERENCES

- Austin, R.B., M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977. The nitrogen economy of winter wheat. *J. Agric. Sci., Camb.* 88: 159-167.
- Bauer, A., A. B. Frank and A. L. Black. 1987. Aerial parts of hard red spring wheat. III. Nitrogen and phosphorus concentration and content in kernels, anthesis to ripe stage. *Agron. J.* 79: 859-864.
- Bhatia, C.R. and R. Rabson. 1976. Bioenergetic considerations in cereal breeding for protein improvement. *Science* 194: 1418-1421.
- Bruckner, P.L. and R.C. Frohberg. 1987. Rate and duration of grain fill in spring wheat. *Crop Sci.* 27: 451-455.
- Brunori, A., H. Axmann, A. Figueroa, and A. Micke. 1980. Kinetics of nitrogen and dry matter accumulation in the developing seed of some varieties and mutant lines of *Triticum aestivum*. *Z. Pflanzenzuchtg.* 84: 201-218.
- Brunori, A. and A. Micke. 1979. Dry matter and nitrogen accumulation in the developing seed of *Triticum aestivum*. p. 156-160. *In* J.H.J. Spiertz and T. Kramer (ed.) Crop physiology and cereal breeding. Proc. EUCARPIA Workshop, Wageningen, the Netherlands.
- Chen, C., L.S. Daley, and W.E. Kronstad. 1990. Photosynthetic structure change in selected wheat cultivars during grain fill detected by *in vivo* spectroscopy. *Plant Physiol. Biochem.* 28 (2): 259-269.
- Cox, M.C., C.O. Qualset, and D.W. Rains. 1985. Genetic variation for nitrogen assimilation and translocation in wheat. I. Dry matter and nitrogen accumulation. *Crop Sci.* 25: 430-435.
- Darroch, B.A. and R.J. Baker. 1990. Grain filling in three spring wheat genotypes: statistical analysis. *Crop Sci.* 30: 525-529.
- Ellen, J. and J.H.J. Spiertz. 1975. The influence of nitrogen and benlate on leaf area duration, grain growth and pattern of N-, P-, and K-uptake of winter wheat (*Triticum aestivum*). *Zeitschrift fur Acker und Pflanzenbau* 141: 231-239.
- Gebeyehou, G., D.R. Knott, and R.J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. *Crop Sci.* 22: 337-340.

- Grabau, L.J., D.A. Van Sanford, and Q.W. Meng. 1990. Reproductive characters of winter wheat cultivars subjected to postanthesis shading. *Crop Sci.* 30: 771-774.
- Hanft, J.M. and R.D. Wych. 1982. Visual indicators of physiological maturity of hard red spring wheat. *Crop Sci.* 22: 584-587.
- Herzog, H.. 1982. Relation of source and sink during grain filling period in wheat and some aspects of its regulation. *Physiol. Plant.* 56: 155-160.
- Johnson, V. A., P. J. Mattern, K.D. Wilhelmi, and S. L. Kuhr. 1978. Seed protein improvement in common wheat (*Triticum aestivum* L.). In Seed protein improvement by nuclear techniques, IAEA, Vienna, 23-32.
- Karlen, D. L. and D. A. Whitney. 1980. Dry matter accumulation, mineral concentrations, and nutrient distribution in winter wheat. *Agron. J.* 72: 281-288.
- Loffler, C.M. and R.H. Busch. 1982. Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. *Crop Sci.* 22: 591-595.
- McNeal, F. H., M. A. Berg, and C. A. Watson. 1968. Nitrogen in plant parts of seven spring wheat varieties at successive stages of development. *Agron. J.* 58: 605-608.
- McNeal, F.H., M.A. Berg, C.F. McGuire, V. R. Stewart, and D.E. Baldrige. 1972. Grain and plant nitrogen relationships in eight spring wheat crosses, *Triticum aestivum* L.. *Crop Sci.* 12: 599-602.
- Penning de Vries, F.W.T., A.H.M. Brunsting, and H.H. van Laar. 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *J. Theor. Biol.* 45: 339-377.
- SAS Institute Inc.. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, NC: SAS Institute Inc..
- Singh, V.P., M. Singh, and M.S. Kairon. 1984. Physiological maturity in *aestivum* wheat: Visual determination. *J. Agric. Sci.* 102: 285-287.
- Smith, D.H. and K.J. Donnelly. 1991. Visual markers of maximum grain dry weight accumulation in winter wheat. *Crop Sci.* 31: 419-422.
- Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing

- the rate and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4: 785-797.
- Spiertz, J.H.J. and J. Ellen. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. *Neth. J. Agric. Sci.* 26: 210-231.
- STSC, Inc.. 1991. Statgraphics reference manual. Version 5. STSC, Inc., Rockville, Maryland.
- Terman, G.L., R.E. Ramig, A.F. Dreier, and R.A. Olson. 1969. Yield-protein relationships in wheat grain, as affected by nitrogen and water. *Agron. J.* 61: 755-759.
- Van Sanford, D.A.. 1985. Variation in kernel growth characters among soft red winter wheats. *Crop Sci.* 25: 626-630.
- Wardlaw, I.F.. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Aust. J. Biol. Sci.* 23: 765-774.
- Wiegand, C.L. and J.A. Cuellar. 1981. Duration of grain filling and kernel weight as affected by temperature. *Crop Sci.* 21: 95-101.

BIBLIOGRAPHY

- Allard, R. W. and J. Harding. 1963. Early generation analysis and prediction of grain under selection in derivatives of a wheat hybrid. *Crop Sci.* 3: 454-456.
- Amaya, A. A., R. U. Busch, and K. L. Lebsack. 1972. Estimates of genetic effects of heading date, plant height and grain yield in durum wheat. *Crop Sci.* 12: 478-481.
- Austin, R.B., M.A. Ford, J.A. Edrich, and R.D. Blackwell. 1977. The nitrogen economy of winter wheat. *J. Agric. Sci., Camb.* 88: 159-167.
- Avey, D. P. and H. W. Ohm. 1982. Advanced generation analysis of days to heading in three winter wheat crosses. *Crop Sci.* 22: 912-915.
- Axtell, J. D.. 1981. Breeding for improved nutritional quality. In K. J. Frey (eds.), *Plant Breeding II*, Iowa State University Press, pp.365-432.
- Baker, R.J.. 1978. Issues in diallel analysis. *Crop Sci.* 18: 533-536.
- Bauer, B., A.B. Frank, and A.L. Black. 1984. Estimation of spring wheat leaf growth rates and anthesis from air temperature. *Agron. J.* 76: 829-835.
- Bauer, A., A. B. Frank and A. L. Black. 1987a. Aerial parts of hard red spring wheat. I. Dry matter distribution by plant development stage. *Agron. J.* 79: 845-852.
- Bauer, A., A. B. Frank and A. L. Black. 1987b. Aerial parts of hard red spring wheat. II. Nitrogen and phosphorus concentration and content by plant development stage. *Agron. J.* 79: 852-858.
- Bauer, A., A. B. Frank and A. L. Black. 1987c. Aerial parts of hard red spring wheat. III. Nitrogen and phosphorus concentration and content in kernels, anthesis to ripe stage. *Agron. J.* 79: 859-864.
- Beuerlein, J.E. and H.N. Lafever. 1989. Row spacing and seeding rate effects on soft red winter wheat yield, its components and agronomic characteristics. *Appli. Agric. Res.* Vol. 4, No. 2, pp. 106-110.
- Bhatia, C.R. and R. Rabson. 1976. Bioenergetic considerations in cereal breeding for protein improvement. *Science* 194: 1418-1421.

- Bhatt, G.M.. 1972. Inheritance of heading date, plant height, and kernel weight in two spring wheat crosses. *Crop Sci.* 12: 95-98.
- Bingham, J.. 1969. The physiological determinants of grain yield in cereals. *Agric. Progress* 44: 30-41.
- Borlaug, N. E., J. Ortega, I. Narvaez, A. Garcia and Rodriquez. 1964. Hybrid wheat in perspective. pp. 1-19. Hybrid Wheat Seminar Report. Crop Quality Council. Minneapolis, Minnesota.
- Bruckner, P. L. and R. C. Frohberg. 1987. Rate and duration of grain fill in spring wheat. *Crop Sci.* 27: 451-455.
- Brunori, A., H. Axmann, A. Figueroa, and A. Micke. 1980. Kinetics of nitrogen and dry matter accumulation in the developing seed of some varieties and mutant lines of *Triticum aestivum*. *Z. Pflanzenzuchtg.* 84: 201-218.
- Brunori, A. and A. Micke. 1979. Dry matter and nitrogen accumulation in the developing seed of *Triticum aestivum*. pp.156-160. *In* J. H.J. Spiertz and T. Kramer (ed.) *Crop Physiology and cereal breeding: Proc. EUCARPIA Workshop*, Wageningen, the Netherlands.
- Busch, R. H. and D. D. Chamberlain. 1981. Effects of daylength response and semidwarfism on agronomic performance of spring wheat. *Crop Sci.* 21: 57-60.
- Chapman, S.R. and F.H. McNeal. 1971. Gene action for yield components and plant height in a spring wheat cross. *Crop Sci.* 11: 384-386.
- Chen, C. 1988. Identification and inheritance of factors influencing the rate and duration of grain fill in selected wheat populations (*Triticum aestivum* L. em Thell). Ph.D. thesis. Oregon State University.
- Chen, C., L.S. Daley, and W.E. Kronstad. 1990. Photosynthetic structure change in selected wheat cultivars during grain fill detected by *in vivo* spectroscopy. *Plant Physiol. Biochem.* 28 (2): 259-269.
- Choi, B. H.. 1982. Time and duration of growth stages and subsequent grain yield in selected wheat cultivars (*Triticum aestivum* L. em Thell). MS thesis. Oregon State University.
- Choi, B. H. 1983. Nature of inheritance and association of time, duration and rate of grain filling and subsequent grain yield in crosses of winter and spring wheat (*Triticum aestivum* L. em Thell). Ph.D. thesis. Oregon State University.

- Chujo, H.. 1970. Some observations on the reversal of vernalization effect of wheat. *Japan Journal Crop Sci.* 39: 451-456.
- Cisar, G. and H.L. Shands. 1978. Floral initiation and development in cultivars of oats. *Crop Sci.* 18: 461-464.
- Clarke, J. M.. 1983. Time of physiological maturity and post-physiological maturity drying rate in wheat. *Crop Sci.* 23: 1203-1205.
- Copeland, P. J. and R. K. Crookston. 1985. Visible indicators of physiological maturity in barley. *Crop Science*: 25: 843-847.
- Cox, M. C., C. O. Qualset and D. W. Rains. 1985. Genetic variation for nitrogen assimilation and translocation in wheat. I. Dry matter and nitrogen accumulation. *Crop Sci.* 25: 430-435.
- Cox, M. C., C. O. Qualset and D. W. Rains. 1986. Genetic variation for nitrogen assimilation and translocation in wheat. III. Nitrogen translocation in relation to grain yield and protein. *Crop Sci.* 26: 737-740.
- Cox, T. S.. 1981. In K. J. Frey (eds.), *Plant Breeding II*, Iowa State University, Chapter 10: Breeding for improved nutritional quality. Discussion, pp. 415-432.
- Cross, H. Z.. 1975. Diallel analysis of duration and rate of grain filling of seven inbred lines of corn. *Crop Sci.* 15: 532-535.
- Crumpacker, D. W. and R. W. Allard. 1962. A diallel cross analysis of heading date in wheat. *Hilgardia* 32: 275-318.
- Darroch, B.A. and R.J. Baker. 1990. Grain filling in three spring wheat genotypes: statistical analysis. *Crop Sci.* 30: 525-529.
- Daynard, T.B. and W.G. Duncan. 1969. The black layer and grain maturity in corn. *Crop Sci.* 9: 473-476.
- Downs, R. J. and H. Hellmers. 1975. In *Environment and Control of Plant Growth*. III. Light. pp. 60-82.
- Eguchi, T.. 1937-39. Effects of relative length of day and night before and after differentiation on formation and development of flower bud. *Jap. J. Bot.* 9: 100-101.
- Ellen, J. and J.H.J. Spiertz. 1975. The influence of nitrogen and benlate on leaf area

- duration, grain growth and pattern of N-, P-, and K-uptake of winter wheat (*Triticum aestivum*). *Zeitschrift fur Acker und Pflanzenbau* 141: 231-239.
- Evans, L. T.. 1975. Wheat, Crop Physiology. Cambridge Univ. Press. London. pp. 116-131.
- Fischer, R. A. and Z. Kertesz. 1976. Harvest index in spaced populations and grain weight in microplots as indicators of yielding ability in spring wheat. *Crop Sci.* 16: 55-59.
- Frederick, J.R. and H.G. Marshall. 1985. Grain yield and yield components of soft red winter wheat as affected by management practices. *Agron. J.* 77: 495-499.
- Frey, K. J.. 1977. Protein of oats. *Z. Pflanzenzuchtg* 78: 185-215.
- Friend, D. J., J. E. Fisher and V. A. Helson. 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. *Can. J. Bot.* 41: 1660-1673.
- Gebeyehou, G., D. R. Knott and R. J. Baker. 1982. Rate and duration of grain filling in durum wheat cultivars. *Crop Sci.* 22: 337-340.
- Gott, M.B.. 1961. Flowering of Australian wheats and its relation to frost injury. *Aust. J. Agric. Res.* 12: 547.
- Grabau, L.J., D.A. Van Sanford, and Q.W. Meng. 1990. Reproductive characters of winter wheat cultivars subjected to postanthesis shading. *Crop Sci.* 30: 771-774.
- Griffing, B. 1956. Concept of general and specific combining ability in relation of diallel crossing systems. *Aust. J. Biol. Sci.* 9: 463-493.
- Halse, N. J. and R. N. Weir. 1970. Effects of vernalization, photoperiod and temperature on phenological development and spikelet number of Australian wheat. *Aust. J. Agric. Res.* 21: 383-393.
- Hanft, J. M. and R. D. Wych. 1982. Visual indicators of physiological maturity of hard red spring wheat. *Crop Sci.* 22: 584-587.
- Hayman, B.I.. 1954. The theory and analysis of diallel crosses. *Genetics* 39: 789-809.

- Hayman, B.I.. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12: 371-390.
- Hayman, B.I. and K. Mather. 1955. The description of genetic interaction in continuous variation. *Biometrics* 11: 69-82.
- Herzog, H.. 1982. Relation of source and sink during grain filling period in wheat and some aspects of its regulation. *Physiol. Plant.* 56: 155-160.
- Hunter, J.L., D.M. TeKrony, D.F. Miles, and D.B. Egli. 1991. Corn seed maturity indicators and their relationship to uptake of carbon-14 assimilate. *Crop Sci.* 31: 1309-1313.
- Johnson, V. A., P. J. Mattern and S. L. Kuhr. 1979. Genetic improvement of wheat protein, pp. 165-78. *In* Proc. Symp. on Seed Protein Improv. in Cereals and Grain Legumes, Neuherberg, Fed. Repub. Ger., 4-8 Sept. 1978.
- Johnson, V. A., P. J. Mattern, J. E. Stroike, and K. D. Wilhelmi. 1975. Breeding for improved nutritional quality in wheat. *Proc. Int. Winter Wheat Conf.* 2nd, 1975. pp. 316-333.
- Johnson, V. A., P. J. Mattern, K.D. Wilhelmi, and S. L. Kuhr. 1978. Seed protein improvement in common wheat (*Triticum aestivum* L.). *In* Seed protein improvement by nuclear techniques, IAEA, Vienna, 23-32.
- Karlen, D. L. and D. A. Whitney. 1980. Dry matter accumulation, mineral concentrations, and nutrient distribution in winter wheat. *Agron. J.* 72: 281-288.
- Keim, D. L., J. R. Welsh and R. L. McConnell. 1973. Inheritance of photoperiodic heading response in winter and spring cultivars of bread wheat. *Can. J. Plant Sci.* 53: 247-250.
- Ketata, H., L.H. Edwards, and E.L. Smith. 1976. Inheritance of eight agronomic characters in a winter wheat cross. *Crop Sci.* 16: 19-22.
- Kiangsu Institute of Agricultural Sciences. 1976. Problems on breeding of earliness in wheat. *Acta Genetica Sinica*. Vol. 3, No. 1: 61-68.
- Kirby, E.J.M.. 1986. Significant stages of ear development in winter wheat. p. 7-24. *In* W. Day and R.K. Atkin (ed.) *Wheat growth and modelling*. Plenum Press, New York.
- Klaimi, Y. Y. and C. O. Qualset. 1973. Genetics of heading time in wheat (*Triticum*

- aestivum L.). I. The inheritance of photoperiodic response. *Genetics* 74: 139-156.
- Klaimi, Y. Y. and C. O. Qualset. 1974. Genetics of heading time in wheat (*Triticum aestivum* L.). II. The inheritance of vernalization response. *Genetics* 76: 119-133.
- Knott, D. R. and G. Gebeyehou. 1987. Relationships between the lengths of the vegetative and grain filling periods and agronomic characters in three durum wheat crosses. *Crop Sci.* 27: 857-860.
- Kolhe, A. K., B. S. Patil and A. N. Demanna. 1977. Influence of temperature on flowering of varieties grown under different spacing and seed rates. *In* *Genetics and Wheat Improvement*. pp. 178-179. Oxford & IBH Publishing Co., New Delhi.
- Large, E. C.. 1954. Growth stages in cereals. Illustration of the Feekes scale. *Plant Pathol.* 3: 128-129.
- Lee, H. J.. 1977. Determination of physiological maturity and rate and length of grain filling in *Avena sativa* L.. Ph.D. thesis. Pennsylvania state university.
- Lelley, J.. 1976. Quality improvement. *In* *Wheat Breeding, Theory and Practice*. Chapter 11. Akademiai Kiado, Budapest, pp. 138-165.
- Levy, J. and M. L. Peterson. 1972. Responses of spring wheat to vernalization and photoperiod. *Crop Sci.* 12: 487-490.
- Li, D.. 1976. Wheat Earliness. *In* *Wheat Breeding*. Science Publi., Beijing. pp. 193-201.
- Liu, N.. 1979. Thermal unit and flowering date in early-maturing wheat varieties. *In* *New Technology for Wheat Productivity*. Kiangsu Sci. and Tech. Pub. pp. 178-188.
- Loffler, C. M. and R. H. Busch. 1982. Selection for grain protein, grain yield, and nitrogen partitioning efficiency in hard red spring wheat. *Crop Sci.* 22: 591-595.
- Loffler, C. M., T. L. Rauch and R. H. Busch. 1985. Grain and plant protein relationships in hard red spring wheat. *Crop Sci.* 25: 521-524.

- Masle, J., G. Doussinault, and B. Sun. 1989. Response of wheat genotypes to temperature and photoperiod in natural conditions. *Crop Sci.* 29: 712-721.
- Mather, K.. 1949. *Biometrical Genetics*. Dover Publication, Inc.. New York.
- Mather, K. and J.L. Jinks. 1982. *Biometrical genetics. The study of continuous variation*. Third edition. Chapman and Hall Ltd., London.
- May, L. and D.A. Van Sanford. 1992. Selection for early heading and correlated response in maturity of soft red winter wheat. *Crop Sci.* 32: 47-51.
- McNeal, F.H., M.A. Berg, C.F. McGuire, V. R. Stewart, and D.E. Baldrige. 1972. Grain and plant nitrogen relationships in eight spring wheat crosses, *Triticum aestivum* L.. *Crop Sci.* 12: 599-602.
- McNeal, F. H., M. A. Berg, and C. A. Watson. 1968. Nitrogen in plant parts of seven spring wheat varieties at successive stages of development. *Agron. J.* 58: 605-608.
- Meredith, P. and L. D. Jenkins. 1976. The developing starch granule. 3. the filling of the wheat grain. *New Zealand Journal of Science* 11: 115-123.
- Metz, G.L., D.E. Green, and R.M. Shibles. 1985. Reproductive duration and date of maturity in populations of three wide soybean crosses. *Crop Sci.* 25: 171-176.
- Millet, E. and M. J. Pinthus. 1983. The association between grain volume and grain weight in wheat. *Journal of Cereal Science* 1: 1-5.
- Min, H. K.. 1981. Association between length of grain filling period and grain yield in two wheat populations (*Triticum aestivum* L. em Thell). MS thesis. Oregon State University.
- Mou, B.. 1985. 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). M.S. thesis. Oregon State University.
- Nass, H. G. and B. Reiser. 1975. Grain filling and grain yield relationships in spring wheat. *Can. J. Plant Sci.* 55: 673-678.
- Penning de Vries, F. W. T., A. H. M. Brunsting and H. H. van Laar. 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *J. Theor. Biol.* 45:339-377.

- Pfeiffer, T.W. and D.B. Egli. 1988. Heritability of seed-filling period estimates in soybean. *Crop Sci.* 28: 921-925.
- Pinthus, M. J. and Y. Sar-Shalom. 1978. Dry matter accumulation in the grains of wheat (*Triticum aestivum* L.) cultivars differing in grain weight. *Ann. Bot.* 42: 469-471.
- Pinthus, M. J. and H. Nerson. 1984. Effect of photoperiod at different growth stages on the initiation of spikelet primordia in wheat. *Aust. J. Plant Physiol.* 11: 000-00.
- Pirasteh, B. and J. R. Welsh. 1980. Effect of temperature on the heading date of wheat cultivars under a lengthening photoperiod. *Crop Sci.* 20: 453-456.
- Poehlman, J. M.. 1987. Breeding wheat and triticale. *In* Breeding Field Crops, AVI Publishing Company, Chapter 14, pp. 290-339.
- Pugsley, A. T.. 1963. The inheritance of a vernalization response in Australian spring wheats. *Aust. J. Agric. Res.* 14: 622-627.
- Pugsley, A. T.. 1971. A genetic analysis of the spring-winter habit of growth in wheat. *Aust. J. Agric. Res.* 22: 21-31.
- Purvis, O. N. and F. G. Gregory. 1952. Studies in vernalization. XII. The reversibility by high temperature of the vernalized condition in Petkus winter rye. *Annals of Botany (N. S.)* 16: 1-21.
- Rahman, M.S. and J.H. Wilson. 1977. Determination of spikelet number in wheat. I. effect of varying photoperiod on ear development. *Aust. J. Agric. Res.* 28: 565-574.
- Rao, K. P., D. W. Rains, C. O. Qualset and R. C. Huffaker. 1977. Nitrogen nutrition and grain protein in two spring wheat genotypes differing in nitrate reductase activity. *Crop Sci.* 17: 283-286.
- Rashid, A.H. and G.M. Halloran. 1984. Influence of photoperiod on culm elongation and apical development in semi-dwarf and standard-height wheats. *Ann. Bot.* 54: 375-382.
- Rawson, H.M.. 1970. Spiklet number, its control, and relation to yield per ear in wheat. *Aust. J. Biol. Sci.* 23: 1-15.
- Rawson, H. M. and L. T. Evans. 1970. The pattern of grain growth within the ear of wheat. *Aust. J. Biol. Sci.* 23: 753-764.

- Rickman, R. W. and B. L. Klepper. 1983. Using air temperature to anticipate wheat crop development. In Columbia Basin Agricultural Research. Special Report 680. Agri. Exp. Station, Oregon State University. pp. 28-36.
- Ross, W.M.. 1955. Associations of morphological characters and earliness in oats. *Agron. J.* 47: 453-457.
- SAS Institute Inc.. 1987. SAS/STAT guide for personal computers, version 6 edition. Cary, NC: SAS Institute Inc..
- Sayed, H. I. and A. M. Gadallah. 1983. Variation in dry matter and grain filling characteristics in wheat cultivars. *Field Crop Research* 7: 61-71.
- Simmons, S. R. and R. K. Crookston. 1979. Rate and duration of growth of kernels formed at specific florets in spikelets of spring wheat. *Crop Sci.* 19: 690-693.
- Singh, R. K. and B. D. Chaudhary. 1979. *Biometrical Methods in Quantitative Analyses*. Kalyani Publishers.
- Singh, V.P., M. Singh, and M.S. Kairon. 1984. Physiological maturity in *aestivum* wheat: Visual determination. *J. Agric. Sci.* 102: 285-287.
- Sisodia, N. S.. 1977. Photoinsensitivity in wheat breeding. In *Genetics and Wheat Improvement*. Oxford & IBH Publishing Co., New Delhi. pp. 172-174.
- Smith, D.H. and K.J. Donnelly. 1991. Visual markers of maximum grain dry weight accumulation in winter wheat. *Crop Sci.* 31: 419-422.
- Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4: 785-797.
- Spiertz, J.H.J. and J. Ellen. 1978. Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. *Neth. J. Agric. Sci.* 26: 210-231.
- Spiertz, J. H. J., B. A. Tennhag and L. J. P. Kupers. 1971. Relation between green area duration and grain yield in some varieties of spring wheat. *Neth. J. Agric. Sci.* 19: 211-222.
- Spiertz, J. H. J. and J. Vos. 1985. Grain growth of wheat and its limitation by carbohydrate and nitrogen supply. In W. Day and R. K. Atkin (eds.), *Wheat Growth and Modelling*, Plenum Press, pp. 129-141.

- STSC, Inc.. 1991. Statgraphics reference manual. Version 5. STSC, Inc., Rockville, Maryland.
- Stuber, C. W., V. A. Johnson and J. W. Schmidt. 1962. Grain protein content and its relationships to other plant and seed characters in the parents and progeny of a cross of *Triticum aestivum* L. *Crop Sci.* 2: 506-508.
- Sun, P.L.F., H.L. Shands, and R.A. Forsberg. 1972. Inheritance of kernel weight in six spring wheat crosses. *Crop Sci.* 12: 1-5.
- Syme, J. R.. 1968. Ear emergence of Australian, Mexican and European wheats in relation to time of sowing and their response to vernalization and daylength. *Austr. J. Exp. Agric. Ani. Husb.* 8: 578-581.
- Terman, G.L., R.E. Ramig, A.F. Dreier, and R.A. Olson. 1969. Yield-protein relationships in wheat grain, as affected by nitrogen and water. *Agron. J.* 61: 755-759.
- Upadhy, M. D., R. Chandra and T. R. Dayal. 1977. Differential photoperiodic response of spring wheat genotypes. *In* Genetics and Wheat Improvement. Oxford & IBH Publishing Co., New Delhi. pp.178-179.
- Van Sanford, D.A.. 1985. Variation in kernel growth characters among soft red winter wheats. *Crop Sci.* 25: 626-630.
- Waldren, R. P. and A. D. Flowerday. 1979. Growth stages and distribution of dry matter, N, P, and K in winter wheat. *Agron. J.* 71: 391-397.
- Wardlaw, I. F.. 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Aust. J. Biol. Sci.* 23: 765-774.
- Warrington, I. J., R. L. Dunstone and L. M. Green. 1977. Temperature effects at three development stages on the yield of wheat ear. *Aust. J. Agric. Res.* 28: 11-27.
- Wiegand, C. L. and J. A. Cuellar. 1981. Duration of grain filling and kernel weight as affected by temperature. *Crop Sci.* 21: 95-101.
- Wong, L. S. L. and R. J. Baker. 1986. Developmental patterns in five spring wheat genotypes varying in time to maturity. *Crop Science* 26: 1167-1175.
- Xue, S.. 1979. The analysis of late development stages in early maturing wheat. *In* New Technology for Wheat Productivity. Kiangsu Sci. and Tech. Pub., pp. 168-177.

- Yasuda, S.. 1968. Physiology and genetics of ear emergence in barley and wheat. VII. The mode of inheritance of spring and winter habit of growth in common wheat. *Nogaku Kenkyu* 52: 79-88.
- Yu, J.. 1982. Studies on the inheritance of earliness and its approaches of the selective breeding in wheat. MS thesis. Northwestern College of Agriculture, P. R. China.
- Zadok, J.C., T.T. Chang and C. F. Konzak. 1974. A decimal code for the growth stages of cereals. *Weed Research* 14: 415-421.

APPENDICES

Appendix Table 1. Pedigree and description of the genotypes used in the study.

AI Feng 2:	(Feng Chan 3//Xian Nong 39/Selection 58(18)2). A hard white winter 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 red winter wheat from Chinese Academy of Agriculture. 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 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 meteorological data on a per month basis for Hyslop Crop Science Field Laboratory at Corvallis, Oregon in 1986-87 and 1987-88 growing seasons.

Growing season	Month	Precipitation mm	Temperature °C		
			Average Max.	Average Min.	Mean
1986-87	October	71.12	18.50	7.22	12.86
	November	218.95	12.17	4.44	8.30
	December	88.90	7.78	0.28	4.03
	January	208.79	7.89	0.61	4.25
	February	114.30	10.89	2.56	6.73
	March	93.98	13.44	3.67	8.56
	April	39.64	18.50	4.61	11.56
	May	35.56	21.22	7.83	14.53
	June	7.37	25.44	9.56	17.50
	July	56.64	25.33	11.50	18.42
	Total	935.23			
1987-88	October	6.86	23.00	5.28	14.14
	November	99.06	12.11	4.89	8.50
	December	290.07	6.50	1.39	3.95
	January	180.84	7.06	0.67	3.86
	February	43.18	11.17	1.61	6.39
	March	99.06	13.50	2.50	8.00
	April	84.58	16.06	5.61	10.84
	May	97.54	17.89	6.56	12.23
	June	46.48	22.00	9.22	15.61
	July	2.29	28.00	11.00	19.50
	Total	949.95			