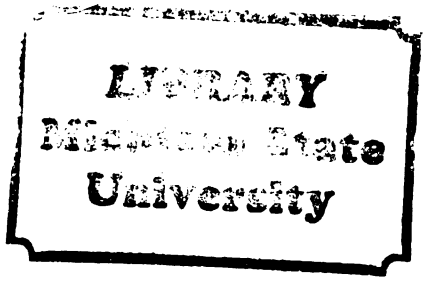

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GENETIC VARIATION FOR THE DURATION OF GRAIN-FILLING IN A SAMPLE OF THE WHEAT GERMPLASM POOL

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Susan L. Neuhausen

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GENETIC VARIATION FOR THE DURATION OF GRAIN-FILLING IN A SAMPLE OF THE WHEAT GERMPLASM POOL

By

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ABSTRACT

GENETIC VARIATION FOR THE DURATION OF GRAIN-FILLING IN A SAMPLE OF THE WHEAT GERMPLASM POOL

By

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Variation in the grain-filling period was examined in a diverse sample of the wheat germplasm pool in field studies in 1981 and 1982. Significant differences were found for the grain-filling period among accessions and species in both spring and winter growth habits. Repeatability measures over replications and years indicated that a large proportion of the phenotypic variation observed was due to additive genetic variation. Genotypic correlations indicated that, in general, accessions with long grain-filling periods were early pollinators and that the duration of grain-filling was determined largely by a developmental sequence. Generation means analysis for grain-filling period for two sets of spring wheat crosses indicated that for these two crosses, additive gene action was important and that in one of the crosses, dominance gene action was also important. Based on the repeatability estimates and on the wide range of variation found for grain-filling period, selection on a mean basis could be effective.

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TABLE OF CONTENTS

LIST OF TABLES

Page

CHAPTER 3

APPENDIX A

INTRODUCTION

Wheat breeders generally are concerned with increasing and protecting current yield levels. One component of yield which deserves study is the duration of the grain-filling period. A positive relationship has been found to exist between the grain-filling period in wheat and yield, through its positive association with kernels per spike and kernel weight (Gebeyehou et al., 1982a). Extending the duration of the grain-filling period to achieve larger seeds should be possible as grain size in wheat is only loosely restricted (Yoshida, 1972). The grain-filling period may be extended by having an earlier anthesis date or a later maturity date.

Before being able to adequately evaluate the impact of grain-filling period duration on wheat yields, a wide range of genetic variability must be obtained. Successful evaluation and development of improved varieties is dependent upon the availability of genetic variation for the desired character. An extensive survey of the germplasm pool may therefore expose the range of variability which exists for these characters.

Before developing an effective breeding strategy, an understanding of the genetic control of the trait is necessary. In pure-line varietal development, only the

additive and additive x additive types of gene action may be efficiently utilized. It is therefore important to determine the types of gene action inherent in the character as well as the proportion of additive genetic variance in relation to the phenotypic variance. Only when the underlying genetics are known can an intelligent decision be made as to the rate and type of selection necessary to perform varietal improvement for the trait.

The objectives of my thesis research were 1) to determine the range of variation in the duration of the grain-filling period, days to anthesis, and physiological maturity date, both within and between species in a diverse sample of the germplasm pool of wheat, 2) to use this variation to determine the inheritance pattern of the grain-filling period, anthesis date, and maturity date, and 3) to use this information to ascertain the feasibility of selecting for a longer grain-filling period in a breeding program.

LITERATURE REVIEW

Lengthening of the grain-filling period may be one means of increasing grain yield (Daynard et al., 1971) for it is a determinant of kernel weight which is a major yield component (Gebeyehou et al., 1982a). Grain size in wheat is loosely restricted by the lemma and palea, so extending the duration of grain-filling to achieve larger seeds and therefore higher yields may be possible (Yoshida, 1972). Duration of grain-filling is the period between anthesis and physiological maturity. As this character is measured by the difference between anthesis and maturity, factors affecting maturity and anthesis will affect the duration of grain-filling. As with all physiological traits, the underlying physiology and genetics need to be understood.

Since the majority of grain growth is supported by concurrent photosynthesis rather than by stored reserves, discussions of source and sink limits on the final stage of the life cycle, the grain filling phase, are necessary (Yoshida, 1972). Therefore, the first portion of the literature review focuses on the source and sink sites, and their limitations due to internal mechanisms.

The effects of variation in the environment on components of yield in wheat are well-documented (Evans et al., 1975) and play an important role in the phenotypic expression of the grain-filling period. The middle portion of this review pertains to environmental effects of light, temperature, and drought, as well as diseases which affect the duration and rate of grain-filling.

The final portion of the literature review is focused on the characterization of the duration of grain-filling and its two related factors, anthesis date and physiological maturity date. Before the impact of filling period duration can be evaluated on wheat yields, information must be obtained on the genetic variability available for the character. Once genetic variability is ascertained, it is then necessary to determine the mode of inheritance. After the range of genetic variability and the mode of inheritance are known, an appropriate breeding and selection strategy can then be instituted to evaluate these traits in relation to yield. The final section discusses the relationship to yield of the grain-filling period, the variability for the trait, and some reports on the genetics underlying the duration of grain-filling and its related traits, anthesis date and physiological maturity date.

Source Sites and Limitations

Final grain weight is determined by the rate and the duration of grain-filling. Both rate and duration of grain

filling are determined by genetic components, by the amount of assimilate translocated into the developing grain, and by the conversion of assimilates to storage products within the grain. It is not clear whether differences in the duration of photosynthetic activity cause or are caused by differences in the duration of grain-filling (Evans et al., 1975). The availability of assimilates to the developing grain is directly related to the photosynthetic supply as well as to the partitioning of the assimilate pool to grain growth. The possible contribution of photosynthate of different plant parts to the grain is based on a) potential photosynthetic activity, b) longevity of the tissue during the maturing process, and c) the light intensity in a crop canopy (Yoshida, 1972).

The contribution of pre-anthesis stored assimilates to final grain weight is small; the amount of photosynthate produced after anthesis is most important. Under most circumstances, 90-95% of the carbohydrate in the grain is derived from CO_2 fixation after anthesis (Evans et al., 1975). However, growth before ear emergence does indirectly affect grain growth by affecting the photosynthetic surface area after the ears emerge and the number and size of sink sites (Thorne, 1966). The assimilates produced both before and during anthesis are stored in the second internode (Wardlaw and Porter, 1967) and a proportion of these assimilates are shown to be relocated to the grain late in the

grain-filling period (Stoy, 1979). The percentage of final grain weight attributed to stored stem reserves has been shown to vary from 5% to 27%; Lupton (1969) observed that approximately 12% was attributed to stored stem reserves, Wardlaw and Porter (1967) observed 5-10%, Austin et. al. (1977) observed 7%. The contribution of stem reserves to grain growth depends on growing conditions (Spiertz, 1974). Bidinger et al. (1977) determined the contribution of stored pre-anthesis assimilates to final grain weight under drought and irrigated conditions. They found that under irrigated conditions, 13% of the final grain weight was due to stored assimilates, whereas under drought conditions, it accounted for 37% of the final grain weight. However, in the actual amount of grain dry weight (grams) contributed to the grain, the stem contribution was the same under both irrigated and drought conditions. It appears that the contribution of stored stem assimilates toward final grain weight should be expressed in grams rather than as a percentage of final grain weight. From the aforementioned studies, it can be concluded, that in wheat, the majority of final grain weight is due to assimilates produced after anthesis.

Therefore, the knowledge of which organs and to what extent they contribute post-anthesis assimilates to the grain is important. The flag leaf and plant parts above it are of primary importance in current assimilate production (Simpson, 1968; Stoy, 1965; Wardlaw and Porter, 1967; McNeal and Berg, 1977). Wardlaw and Porter (1967) observed that the

assimilates from the organs below the flag leaf are primarily translocated to the newly developing tillers, with the leaves, sheaths, and stems below the flag-leaf node contributing approximately 15% of the final grain weight (including the contribution of the pre-stored assimilates).

Photosynthesis by the ear and flag leaf (including the sheath, blade, and peduncle) alone can meet the needs of the ear, and grain growth does not appear to be limited by the supply of assimilates; photosynthesis by the stems and leaf sheaths appear to provide spare capacity (Rawson and Evans, 1971). The stem acts as a pool of available carbohydrate which increases with a surplus of photosynthates under optimal conditions and decreases with the consumption of carbohydrates under adverse conditions (Spiertz, 1974). Spiertz and Ellen (1978) observed that the stem weight increased for two weeks after anthesis, then sharply declined when the temperature increased; this indicated that initially the production of assimilates by current photosynthesis was greater than the demand for grain growth, and when the grain growth rate was accelerated due to higher temperatures, the need for more assimilates was satisfied by mobilization from the stem.

For the first week after anthesis, the expanding top internode acts as a sink for assimilates from both the flag leaf and the ear; thus under certain limiting conditions (i.e., low light intensity), stem growth may compete with the

grain for photosynthetic assimilates during the early period of grain differentiation (Carr and Wardlaw, 1965).

The contribution of ear photosynthesis to grain yield varies from 10 to 50% depending on the measurement technique and the environment. Ear photosynthesis is composed of two processes: (a) the assimilation of atmospheric CO_2; and (b) the photosynthetic refixation of the ear's respiratory CO_2. Both dry weight data and measurements of CO_2 exchange indicate that the refixation of respiratory CO_2 can make a significant contribution to grain dry weight. It was found that a high rate of CO_2 fixation can occur even when the ear is deprived of atmospheric CO_2. Under normal conditions, the CO_2 refixing activity is relatively stable with approximately 65% of the respiratory CO_2 refixed during the first thirty days after anthesis. The CO_2 refixation therefore is important for it reduces the respiratory loss under light (Kriedemann, 1966).

Using grain dry weight data to calculate the relative contribution to grain yields, Kriedemann (1966) found that, averaged over experiments, net atmospheric photosynthesis of the ear was 9% and CO_2 refixation of the ear was 20.6%, for a total CO_2 fixation of the ear and grains of 29.6%. Translocation of flag leaf assimilates to the ear was therefore 70.4%. DeVos (1979) observed that the flag leaves contributed 50-60% of the daily rate of CO_2 uptake. Thorne (1965) found that the CO_2 fixed by the ear was 17 to 30% of the final grain weight and Buttrose and May (1965) found that

the contribution of ear photosynthate to final grain weight was 51%. Carr and Wardlaw (1965) found that with a light intensity of 1200 foot candles, ear photosynthesis equalled that of a leaf blade in the non-awned variety and was considerably higher in the awned variety with the awns of the awned variety contributing approximately half of the total ear photosynthate. Over the whole period of grain development, Evans and Rawson (1970) observed that contribution to grain requirements by ear photosynthesis was 33% in the awned variety and 20% in the non-awned variety. The differences observed in ear photosynthetic contribution to grain weight is attributable to differing light intensities in Australia and Europe (Buttrose and May, 1965) and to the use of awned and awnless varieties.

Sink demand for carbohydrates can affect assimilate translocation (Thorne, 1966). By shading the ear, demand for translocated assimilate will be increased due to less photosynthate available from ear photosynthesis; by removing some spikelets, the demand will be decreased (Thorne, 1966). The demand for assimilates influences the rate of photosynthesis of the flag leaf (Evans and Rawson, 1970). King et al. (1967) observed that as assimilate demand decreased, more assimilate remained in the flag leaf and the photosynthetic rate of the flag leaf decreased. They found the reverse to be true also: as assimilate demand increased, more assimilates were transported from the flag leaf and the

photosynthetic rate of the flag leaf increased. The rate of photosynthesis by the leaves declined steadily after anthesis (Lupton, 1968; Carr and Wardlaw, 1965).

Stoy (1963) found that labelled carbon from the flag leaf was preferentially transported to those parts of the reproductive organs which were rapidly growing during the translocation period. He found no differences in translocation patterns of three varieties, but the time period of translocation from the leaves to the ears did differ in length between the varieties which had differing yields. Stoy (1963,1965) concluded that a variety which has the ability to maintain a sufficient rate of photosynthesis in the upper parts of the plant for a relatively long period after flowering will obtain a high yield providing that other conditions are favorable. Welbank et al. (1966) observed that the grain yields of three wheat varieties were nearly proportional to their leaf area duration with the duration from anthesis to maturity being more closely correlated to yield than the duration from ear emergence to maturity; Spiertz et al. (1971) observed the opposite result, however both agree that duration of the green area is important in obtaining higher yields. DeVos (1979) is in agreement with these results; but he has also observed that in many cases, the flag leaves were still green when the ears and peduncles had yellowed. This led him to hypothesize that kernel growth duration may be more limiting to grain yield than duration of photosynthetic activity.

In conclusion, final grain weight is mostly dependent on current assimilate during the time of grain-filling rather than on stored reserves. The majority of the current assimilate is from the plant parts above the flag leaf node. The estimates of ear photosynthate contribution to grain weight vary from 30 to 50% depending on the variety and the environment. The indication is that higher final grain weight is dependent on a sufficient rate of photosynthesis for a long duration. Rate of photosynthesis varies with assimilate demand so it appears that both sink demand and source duration are important determinants of final grain weight.

Sink Limitation

Devos (1979) stated that kernel growth duration may be more limiting than photosynthetic supply. Other researchers agree and believe that sink capacity is the limiting factor for yield due to a) size limitation determined early in grain development (Brocklehurst, 1977); b) biochemical processes operating within the grain (Jenner and Rathjen, 1975); c) physical barriers operating within the grain (Zee and O'Brien, 1970); and d) hormonal effects within the grain (Radley, 1976).

Brocklehurst (1977) indicated that the cell number in the endosperm is a major factor controlling the final grain weight such that the number of endosperm cells determines the maximum potential size of the grain sink. Assimilate supply is therefore important during the first two weeks after

anthesis when endosperm cell division is occurring, however, it is rarely limiting then (Asana and Basu, 1963). Therefore, Brocklehurst (1977) believes that the maximum potential grain size is a function of the number of cells in the endosperm and not a function of the duration of photosynthetic supply.

Jenner and Rathjen (1975), Zee and O'Brien (1970), and Radley (1976) believe that factors operating within the grain itself cause the cessation of starch accumulation and that it is not due to a reduction in assimilate supply. Working with dissected grain, Jenner and Rathjen (1975) found that there was a fall in the capacity of the endosperm to synthesize the sucrose to starch as shown by a reduction in starch and a build-up of sucrose in the grain. They concluded that the onset of the declining phase of the accumulation of starch was caused by a fall in the synthetic capacity of the endosperm, and not by a reduction in the supply of sucrose to the sites of starch synthesis. Zee and O'Brien (1970) found that a major function of the pigment strand, extending from the base of the wheat grain crease through its length, was to control and eventually stop the development of the grain by physically blocking the transport of water and solutes between the pericarp and endosperm. Thus, no assimilate can enter the endosperm even though assimilate is still being supplied from the photosynthetic sources. Radley (1976) observed that the loss in water from the grain, which signifies the cessation of grain dry matter accumulation, was

preceded by an increase in ABA content and that following dehydration of the endosperm, the starch-synthesizing enzymes were inactivated.

From the work of these researchers, it appears that the maximum potential size of the grain is fixed long before the cessation of starch synthesis by the amount of cell division (Brocklehurst, 1977; Radley, 1976) and that the cessation of starch synthesis is due to factors operating within the grain itself (Jenner and Rathjen, 1975; Zee and O'Brien, 1970; Radley, 1976). However, under adverse environmental conditions, i.e., drought, high temperature, and low light intensity, the maximum potential size of the grain may not be reached due to source limitations. Due to adverse conditions, Brocklehurst (1978) observed that shrivelled grain resulted from a failure of the endosperm cells to fill completely. In conclusion, it appears that under optimal conditions, sink capacity limits grain size when assimilate supply is not limiting, whereas, under adverse environmental conditions, source capacity limits grain size due to a lack of available assimilate to fill the grain to its maximum potential.

Environmental Effects

Environmental conditions which affect grain set and therefore grain number indirectly affect grain-filling due to the inverse correlation between grain number and grain weight (Wardlaw, 1970; Rawson and Evans, 1971; Fisher et al., 1977;

Evans et al., 1975; Evans and Wardlaw, 1976). Grain set is maximal when temperature is low and light intensity is high (Wardlaw, 1970). High temperatures (Warrington et al., 1977; Bagga and Rawson, 1977) and drought (Asana and Saini, 1958; Asana et al., 1958) reduce the grain numbers per head.

Once grain number is set, cereal grain yields are proportional to grain weight. Thus, environmental effects on grain size are important determinants of final grain yield (Wiegand and Cuellar, 1981). Environmental effects vary greatly depending on the stage of development of the crop. This discussion will focus on environmental conditions during the grain growth phase of development. Duration of grain growth is influenced by environmental effects involved in processes governing the ripening of the grain and the senescence of the vegative organs (Spiertz, 1977). The main environmental effects influencing final grain weight are temperature, which has been found to affect mainly duration and rate of grain-filling, and drought and light intensity which primarily affect rate of grain filling.

Temperature has a very pronounced effect on duration of grain-filling and a lesser effect on rate of filling. Nanda and Chinoy (1958) found a highly significant inverse correlation between duration of grain filling and maximum temperature. In wheat, high temperatures decrease the duration of filling and increase the growth rate (Sofield et al., 1974; Spiertz, 1974,1977; Yoshida, 1972). Because overall grain growth is a product of rate of grain filling and

duration of grain-filling, and since duration is more affected by temperature than is growth rate, high temperatures usually result in decreased growth (Yoshida, 1972). The rate of grain growth increases under higher temperatures (Asana and Joseph, 1964). Sofield et al. (1977) observed that rates of grain growth were at an upper limit at 21/16^{o} C and that at temperatures below 21^{o} C, the lower rate of grain filling balanced out the increased duration of filling. At temperatures above 21/16^{o} C, the rate of growth did not compensate for the shorter duration of filling and final grain weight was reduced. Both day and night temperatures appear to play a role (Wardlaw et al., 1980).

Wheat shows a clear and well-separated optimum temperature for individual kernel weight of 15/10^{o} C (Chowdhury and Wardlaw, 1978). Wardlaw (1970) observed that dry weight accumulation in the stem of cv. Gabo was highest at 15/10^{o} C. Increasing temperature sharply decreased the duration of filling and reduced grain size proportionately (Sofield et al., 1974,1977). The range of temperatures observed in studies of temperature effects on duration of grain filling was 15/10^{o} C to 30/25^{o} C. (Marcellos and Single, 1972; Spiertz, 1974; Bagga and Rawson, 1977). Asana and Williams (1965) reported small effects of temperature on the rapidity of post anthesis development, however, Marcellos and Single (1972) explain those results as an effect of the temperatures all being above 25^{o} C which is in the region where the response curve becomes asymptotic to the

temperature axis. Wiegand and Cuellar (1981) determined that for every 1^{o} C increase in mean temperature, there was a decrease in grain filling of 3.1 days for their study and that averaging the results of ten studies performed by other researchers gave a determination of a 3.3 day decrease in grain filling for every 1^{o} C increase in mean daily temperature. The kernel weight decrease for each degree centigrade increase, averaged across the same ten studies, was 1.5 mg/kernel. The temperature differences, despite initial differences in rates of cell division, did not affect the final number of cells per grain (Wardlaw, 1970).

Spiertz (1977) concluded that final grain weight depends on the balance between carbohydrate supply and ear capacity. At low temperatures and high light intensity, there is an excess of carbohydrates; whereas at high temperatures with hastened green tissue senescence, there can be a lack of available carbohydrates. He calculated grain growth per unit of degree day and found that it was the same with all temperatures until 300 degree days at which point the decline in the growth curve was highest with high temperature. He concluded that at high temperatures there was a more rapid senescence of the green tissue and a higher respiration rate and that these two factors caused a shortage of carbohydrates which reduced the growth rate towards the end of kernel filling. At low temperatures, it appears that grain maturation and leaf senescence are largely independent whereas at high temperatures, senescence of the leaves precedes ripening

of the grains (Spiertz, 1979). Ford et al. (1976) observed that the effects of changing the ear temperature were independent of that of the rest of the plant and that grain yield decreased progressively with duration of warm period on the ear. Wardlaw et al. (1980) believe that the independent effect of temperature on the ear is due to a direct effect of temperature on the grain and not due to a lack of assimilate. Part of the temperature effect on the grain is due to increased respiration, but they believe other factors are involved. They observed that by decreasing the demand for photosynthate by removing one-third of the grains in an ear, there was little effect on the temperature response of the remaining grain. There is controversy over where temperature exerts its effects on grain growth, whether on the sink, source, or sink and source. Nevertheless, these researchers all agree that temperature does influence the duration of grain filling.

Sofield et al. (1977) stated that the pronounced effect of high temperatures in reducing the duration of grain growth must be a major factor in reducing grain yields in wheat ripening at high temperatures. Wiegand and Cuellar (1981) concluded that at temperatures in excess of 15^{o} C, temperature effects determine plant senescence and that shortening of the duration of grain-filling is the result. They believe that temperatures above the optimum of 15-18^{o} C. dominate the duration of grain filling and that under temperature stress kernel weight will be dependent on duration of grain

filling. That duration of filling is dominated by temperature is also supported by evidence of other researchers. With a delay in flowering and thus increasingly higher temperatures during grain growth, the duration of grain-filling was shortened and grain weight was diminished (Nanda and Chinoy, 1958; Chinoy, 1947).

Whereas temperature has a very pronounced effect on duration of grain-filling and a lesser effect on rate of grain growth, drought and light conditions affect the rate of growth but do not appear to affect the duration of filling. The effects of drought and reduced illuminance on the rate of grain filling are quite similar since both conditions lower the rate of dry matter accumulation in the grain. Drought after ear emergence affects the size of grains, mainly due to reduced accumulation of dry matter in the grain.

In a study by Asana and Basu (1963), intermittent drought during the first two weeks after anthesis hastened the yellowing of the leaves and stems, decreased stem dry weight, and caused no reduction in grain dry weight. They concluded that the surplus of assimilates produced without water stress accumulated in the stem, whereas under water stress, all the assimilate produced was needed. Following the initial two weeks after anthesis, the rate of increase in grain weight was larger under normal water supply conditions than under drought conditions; this larger rate of increase in grain weight of the control ears was attributed to slower yellowing of the ear (Asana and Basu, 1963; Asana and Saini,

1958). Asana et al. (1958) reported that variation in green leaf area and stem surface, during the grain-filling period, had little influence on rate of increase in grain growth so long as the ear remained green.

Brocklehurst et al. (1978) found no interaction between illuminance and water supply effects on the two grain growth phases. During Phase I (cell division phase), the main effects of drought and reduced illuminance (caused by 50% shading) were a decrease in cell number caused by a decrease in the rate of cell division. The final weight per grain was proportional to the number of endosperm cells when Phase II (cell expansion phase) assimilate supply was held constant. However, if more assimilate was supplied during Phase II, the decrease in cell number did not affect final grain yield. Reducing water or illuminance during Phase II decreased the rate of dry matter accumulation in the grain with a resultant decrease in final grain weight. There was a larger decrease in final grain weight due to shading during Phase II than during Phase I and this was attributed to no compensatory movement of assimilate from the stem to the grain in Phase II. Neither drought nor shading in either phase of growth affected the duration of the phase, only the rate of grain growth was affected.

The findings of Sofield et al. (1977) on the effects of illuminance agree with those of Brocklehurst et al. (1978). There was a close relation between leaf photosynthetic rate as influenced by illuminance, the rate of grain growth per

ear, and final grain yield per ear; the duration of linear grain growth was not affected.

Both reduced illuminance (Spiertz, 1977) and drought (Brocklehurst et al., 1978) decreased grain growth rate at either phase of grain growth by decreasing photosynthesis and thus the supply of assimilate. This reduction in rate of growth significantly reduced grain weight at maturity (Wardlaw, 1970).

As shown by these researchers, environmental effects do cause changes in the duration and rate of grain filling. Oftentimes, the effects of drought, temperature, and illuminance act in unison, rather than singly. In any combination, the effects of temperature will be greatest on the duration of grain-filling and the effects of drought and illuminance will be greatest on the rate of grain-filling.

Disease Effects

Diseases affecting the flag leaf, sheath, peduncle, and head of wheat may cause significant yield losses due to damage to the photosynthetic source or sink. The yield losses will vary depending on the variety and on the severity of infection. The severity of disease is often associated with environmental conditions; fungal diseases are favored by moist conditions. The five most common diseases which affect grain yield through an effect on grain-filling are the fungal diseases: Fusarium graminearum (head blight or scab), Septoria nodorum (glume blotch), Septoria tritici (leaf

blotch), Puccinia recondita (leaf rust), and Erysiphe graminis f.sp. tritici (powdery mildew). A sixth important disease is barley yellow dwarf virus.

Scab causes significant yield losses due to floret sterility and poorly-filled grain in the florets above the point of fungal infection (Wiese, 1977). The grains of blighted wheat are so light that many are blown out during threshing (Bruehl, 1967). The scab infections occur most frequently at anthesis, so that the grain never develops properly.

Glume blotch reduces grain quality through a reduction in grain size and weight and through poor grain color (Shipton et al., 1971). The main result of glume blotch is shrivelled grain (Shipton et al., 1971; Rosen, 1921; Scharen and Krupinsky, 1969). Glume blotch is especially devastating for it causes blotches on the glumes as well as internodes and leaves (Bruehl, 1967; Wiese, 1977). Changes in photosynthetic ability of the infected plants were correlated with reductions in seed yield (Scharen and Krupinsky, 1969). Infection commencing at ear emergence accounts for the most severe reductions in yield (Shipman et al., 1971; Holmes and Colhoun, 1974).

Leaf blotch is essentially confined to the leaves and the sheaths and causes a reduction in the photosynthetic surface area of these organs. It results in a reduction in yield from shrivelled grain due to an impairment of seed-filling (Shipton et al., 1971; Wiese, 1977). Caldwell and

Narvaes (1960) reported that the plants ripened prematurely and that head size and straw strength were reduced due to a severe infection.

Leaf rust seldom causes shrivelling of the kernels but it does result in smaller kernels (Johnston, 1967) which leads to reduced yield. The damage due to leaf rust is most severe at the early dough stage (Burleigh et al., 1972). Heavy leaf rust infestations increase transpiration and decrease photosynthesis (Johnston, 1967), thereby reducing seed filling and plant vigor (Wiese, 1977).

Yield losses due to powdery mildew occur in relation to the intensity of the infection and are measurable as decreases in kernel weight (Wiese, 1977). Powdery mildew alters the physiology of the diseased leaves for it utilizes the nutrients of the host, increases the respiration and transpiration of the host, and reduces the surface area for photosynthesis (Wiese, 1977; Bruehl, 1967; Last, 1962), so that less assimilates are available for transport to the grain. The net result is that the plants lose vigor and seed filling is impaired (Wiese, 1977).

Barley yellow dwarf virus, the only non-fungal disease discussed, can also significantly reduce grain yield (Price and Stubbs, 1963). The two main symptoms of the virus are stunting and leaf yellowing (Suneson and Ramage, 1957) although there can be very light or varying symptom expression which then makes it difficult to know if the plants do have the virus (Gill, 1967). It is therefore often

diagnosed by the presence of aphid vectors (Wiese, 1977). Barley yellow dwarf virus tends to predispose plants to early senescence with consequent premature ripening of heads and thus to a reduction of yield through reduced kernel weight or sterile florets (Price and Stubbs, 1963; Suneson and Ramage, 1957).

All six of these diseases can affect grain yield depending on the severity of infection, and in combination, the effects may be additive. As final grain yield is primarily a function of the current photosynthate of the portion of the plant above the flag leaf node, and the duration over which it remains photosynthetically active (Thorne, 1966), the larger the photosynthetic surface diseased, the greater the impairment in grain-filling and therefore the greater reduction in yield. The impairment of grain-filling can be due to a reduction in rate of grain-filling or in duration of grain-filling or both. When a disease causes a reduction in photosynthetic surface area so that less assimilates are produced, it would seem that rate of grain-filling would decrease. When the disease becomes more severe and destroys more and more photosynthetic surface area, then duration of grain filling would also be affected along with the rate of grain-filling to lead to premature senescence.

Duration of Grain-Filling: Relation to Yield and Phenotypic Variation

The rate and length of grain filling must be important determinants of yield because most of the dry matter in small grain seeds is the product of concurrent photosynthesis during the grain-filling period (Evans and Wardlaw, 1976). Gebeyehou et al. (1982a), using path coefficient analysis, determined that in durum wheat, duration of grain-filling was positively associated with kernels per spike, with kernel weight, and with yield through its positive association with kernels per spike and kernel weight. In a later study (1982b), they determined that rate, as well as duration, of grain-filling was positively associated with final grain weight (mg/grain). Nass and Reiser (1975) and Pinthus and Sar-Shalom (1978) found a significant correlation between grain-filling rate and final grain yield in spring wheat. Nass and Reiser (1975) suggested that the observed lack of a correlation between duration of grain-filling and final grain yield may have been due to the variability in the amount of leveling off of filling rates at the end of the grain-filling period. Simmons and Crookston (1979) studied differences in kernel weight within spikelets and observed that differences in kernel growth rate during the linear phase of grain-filling were of major importance in accounting for the basal weight, but that these differences did not entirely account for the weight difference, so that differences in filling-period duration must also play a role.

Positive associations between yield and grain-filling period have also been found in other grains. In oats, McKee et al. (1979) found that grain yield was significantly correlated with both rate of grain-fill and duration of grain-fill. In corn, Cross (1975) and Daynard et al. (1971) observed that a significant portion of yield differences among corn genotypes was attributable to differences in the duration of grain-filling, whereas little of the yield differences could be explained by differences in the rate of grain-filling. Daynard and Kannenberg (1976) observed a positive relationship in corn between yield and duration of grain-filling. However, they also found a high-yielding, high rate, short grain-filling period variety which could indicate that the general relationship between duration of grain-filling and yield are only related through common relationships to other more basic factors, i.e., kernel volume, rather than directly related as indicated by the data. Daynard and Kannenberg (1976) noted that both the actual and effective filling periods were positively correlated with yield and that either measurement could be used when making associations with yield. In soybeans, Dunphy et al. (1979), Egli and Leggett (1973), and Hanway and Webber (1971) concluded that the differences in yield between the soybean varieties tested were due to differences in the duration of the grain-filling period rather than to differences in the rate of accumulation.

All of the previously mentioned researchers observed that durations of grain-filling and/or rate of grain-filling were positively associated with grain yields. These positive associations do not delineate which is the cause and which is the effect. Three hypotheses are possible: 1) final grain weight depends on the duration of grain-filling (Gebeyehou et al., 1980b) or the rate of grain filling (Pinthus and Sar-Shalom, 1978); 2) duration of grain-filling (Gebeyehou et al., 1982b) or the rate of grain-filling (Pinthus and Sar-Shalom, 1978) is dependent on the sink capacity of the grain; 3) under optimal conditions, the sink capacity of the grain is the causal factor and duration and rate of grain-filling are the effects, whereas under sub-optimal conditions, i.e., environmental factors affecting rate or duration directly or indirectly through photosynthetic sources, duration and rate of grain-filling are causal factors and final grain weight is the effect.

If hypothesis one or three is correct, then it is to the advantage of breeders to strive for increased duration and/or rate of grain-filling under normal conditions where environmental conditions are not optimal. It appears that the opportunity would exist for improving yield through altering the length of this period in a breeding program if sizeable, heritable differences occur within a species in the duration of the grain-filling period (Rasmusson et al., 1979).

To determine the importance and usefulness of these kernel characteristics, genetic variations should be

investigated (Poneleit and Egli, 1979). Identifying and characterizing the variation that may exist is an essential first step in determining if higher grain yields can be obtained by optimizing the duration of the grain-filling period (Rasmusson et al., 1979). Differences in the duration of grain-filling have been found in many of the small grains.

Significant differences were found to exist in the duration of grain-filling in rice (Jones et al., 1979), oats (McKee et al., 1979), barley (Rasmusson et al., 1979), and soybeans (Dunphy et al.,1979; Reicosky et al.,1982). In corn, significant differences in duration of grain-filling were found within hybrids (Cross, 1975; Daynard et al., 1977), within inbreds (Carter and Poneleit, 1973), between inbreds and hybrids (Poneleit and Egli, 1979) and within and between synthetic populations (Poneleit et al., 1980). In wheat, significant differences were found among Durum wheats (Gebeyehou et al., 1982b) and among Triticum aestivum wheats (Asana and Joseph,1964; Nass and Reiser,1975; Rawson and Evans,1971; Sofield et al., 1977).

Within the germplasm pool of each species of small grain, it may be possible to find larger differences in duration of grain-filling than within the range of the current varieties examined. Within the soybean germplasm, Reicosky et al. (1982) found strains that had longer seed filling periods than most current cultivars. With the knowledge that there are significant differences in duration of grain-filling and that duration of grain-filling is

positively associated with yield, selection for a longer grain-filling period may represent one possible means of breeding for increased yield.

Germplasm Evaluation

Successful development of improved varieties is dependent upon the availability of genetic variation for the desired character. It is now generally agreed that a broad genetic base is essential, particularly as breeding objectives become more complex and demanding (Hawkes, 1981). For the duration of grain-filling, genetic variation has been found; however, to accurately assess the potential use of the character, it is more readily facilitated by using extreme types (Sprague, 1969). An extensive survey of the germplasm of a species should therefore be undertaken to identify the range of variability which exists. Allard (1970) noted that the genetic variability on which the improvement of domestic plants depends is to be found in the advanced and primitive cultivars and in the wild relatives.

Hawkes (1977) believes that the breeder when looking for genetic variability should first look at working collections of old and current cultivars and breeding stock, then look at primitive cultivars, and lastly look at the wild species. In the case of wheat, it may be beneficial to explore all three avenues at once as it is clear that the wild relatives (Feldman and Sears, 1981) and the primitive wheats (Kuchuk, 1970) comprise rich pools of genetic variability and carry

many genes of great economic potential. The diploid species of wheat may contain genes not found in the polyploids because little of the allelic polymorphism of the evolving diploid wheats was transmitted to their amphiploid derivatives (Johnson, 1972). The genetic structure of the polyploids allows for a rapid build-up of genetic diversity due to hybridization or mutation which is tolerated more than in a diploid organism because the loci are present in four or six doses (Feldman and Sears, 1981). The evolutionary advantage of the polyploids over the diploid is reflected in the wide morphological and ecological variation of the polyploids (Feldman and Sears, 1981). The hexaploids are even more variable and adaptable than the tetraploid due to the addition of the D genome (Kuckuck, 1970). In summation, in the wild and primitive wheats, there are available sources of variability for immediate screening and exploitation (Zohary, 1970) as shown by the adaptation of the various forms to very different environments (Feldman and Sears, 1981; Kuckuck, 1970). It would appear to be important to screen all species of wheat for variability in the duration of grain-filling.

For the variation in the germplasm to be successfully utilized, the breeder must know what trait is desired and then screen or evaluate the collection for that trait (Krull and Borlaug, 1970; Hawkes, 1981). In wheat, phenotypic variation has been found for the duration of grain-filling, as indicated earlier, however, the range of genetic variation may not be sufficient to encourage the breeder to select for

the trait. It would therefore be beneficial to screen the germplasm pool of wheat for evidence of greater durations of grain-filling in order to successfully select for the trait within a wide range of variation.

Genetics

Once significant genetic variation is found for a character, it is necessary to perform genetic analyses to determine the mode of inheritance so that the breeder can determine the best breeding procedure to use for the improvement of the character. In wheat, genetic analysis is difficult because of the variation in genome number in Triticum and its related genera; as an example, in the hexaploid group there are three genomes so there may be three pairs of "effective factors" for a trait (Ausemus et al., 1946). A difficulty in the interpretation of quantitative genetic analyses is that the nature of gene action will differ depending on the environment and on the genotypes of the two parents comprising the cross (Ausemus et al., 1967). Therefore, types of gene action and genetic variances can only be accurately discussed for each cross; inferences about the mode of inheritance of a character not in the reference population can only be made with caution. With these difficulties in mind, results of genetic studies on heading date, anthesis date, maturity date, and grain-filling period will be summarized.

Heading date in wheat is composed of two phases: 1) the phase from seedling emergence to spike initiation and 2) the phase from spike initiation to ear emergence and both phases are determined by responses to vernalization and to daylength (Pinthus, 1963). Pinthus (1963) observed that earliness was dominant to lateness for both the spike initiation phase and the head emergence phase. These gene factors were presumed to govern the response to daylength for the parents did not have vernalization requirements. The two gene pairs were found to be linked which may explain why some researchers only consider time to heading as one character. Klaimi and Qualset (1973) determined that, in general, daylength insensitivity is dominant over daylength sensitivity and that minor genes govern the degree of daylength insensitivity. Daylength insensitivity generally results in earlier heading. Klaimi and Qualset (1974) and Gotoh (1977) observed that vernalization response which determines spring/winter growth habits was controlled by several major genes and minor genes (as demonstrated by intermediate growth habit types) and that spring habit was dominant to winter habit. Spring habit or lack of vernalization response results in earlier heading.

As these studies have shown, whether dividing the genetics of heading into two developmental phases or into photoperiodic and vernalization responses, earliness exhibits a degree of dominance over lateness with minor genes contributing to a continuum. These results are further borne out in genetic studies of heading date as a single character

using spring or winter and hexaploid or tetraploid wheats (Edwards et al., 1976; Crumpacker and Allard, 1962; Bhatt, 1972; Anwar and Chowdhry, 1969; Amaya et al., 1972; Johnson et al., 1966; Avey and Ohm, 1979). Bhatt (1972) and Amaya et al. (1972) found that additive gene action was significant and that other types of gene action were not. Edwards et al. (1976) determined that there were no significant deviations from the additive-dominance model. Anwar and Chowdhry (1969) observed non-additive gene effects. Klaimi and Qualset (1973) found that epistasis did play a role. These researchers all came to the conclusion that earliness was dominant to lateness for heading date, but their conclusions as to the reasons underlying the observation varied, possibly due to the use of different parental material, environments, and experimental techniques.

For days to anthesis, Walton (1971) found that phenotypic dominance was nearly complete for earliness of flowering. Fonesca and Patterson (1968) found a narrow-sense heritability of 0.80 ± 0.07 for earliness of flowering. It was observed by Walton (1971) and Sharma and Ahmad (1979) that both additive and dominance variances were significant, whereas Kandola and Anand (1974) observed that only additive variance was significant.

Fewer studies have been performed on the genetics of maturity and on the grain-filling period in wheat. For days to maturity, Walton (1971) and Sharma and Ahmad (1979) found that additive and dominance played a significant role in its

inheritance. Avey (1981) observed that maturity was mainly determined by additive effects but that dominance may have been of some consequence. For the inheritance of the grain-filling period, Singh et al. (1977) observed largely additive gene effects. Walton (1971) found that both additive and dominance variances played a role and that over-dominance was present for the length of grain-filling.

In general, the researchers concurred on the visual results, i.e. earliness is dominant to lateness for heading, but they found differences in the underlying genetic mechanisms. As these results indicate, the type of gene action and genetic variances found for a particular trait depend on the parents comprising the crosses and on the location of the experiments. For this reason, it would be prudent to evaluate the genetic potential of desirable parents for the character and then use this information to determine the best breeding procedure for those particular lines.

Conclusions

From this review, it can be concluded that the duration of the grain-filling period in wheat is a quantitative genetic trait modified by the environment. There is limited information on the extent of genetic variation for the grain-filling period. Although genotype-environment interaction has been indicated, it may still be possible to select successfully for a longer grain-filling period with the

expectation of increasing yield. The range of the grain-filling period in wheat needs to be further investigated to determine adequately the potential of utilizing this trait in a breeding program.

There is still controversy as to whether final grain weight and thus the duration of grain-filling is limited by sink or source capacity. The environmental interactions during the grain-filling phase of growth dramatically affect the grain-filling process. Under optimal conditions, e.g., sufficient water, high irradiance, moderate temperatures, and low disease incidence, the sink capacity may be limiting as assimilates are still reaching the grain but they are not converted to starch. Under adverse conditions, e.g., restricted water, low light intensity, and high temperatures, photosynthetic supply may be limiting as the grains do not fill to their full potential which leads to decreased kernel weight. Under conditions where rate of grain-filling is decreased due to lower light intensities and lack of water, an extension of the grain-filling period may be able to compensate for the decreased rate. Under conditions of high temperatures, where the rate reaches an optimum and the duration decreases, temperature insensitive types may be the answer. The genetic variation within the wheat species possibly may be successfully utilized to diminish the environmental interactions.

CHAPTER 2

GENETIC VARIATION IN THE DURATION OF GRAIN-FILLING

Abstract

Lengthening of the grain-filling period has been suggested as a means of increasing yield. Only if there are sizeable, heritable differences can the opportunity exist for possibly increasing yield through lengthening the grain-filling period. The objectives of this study were: 1) to determine the range of variation for the grain-filling period within and between species within and between winter and spring growth habits in a diverse sample of the wheat germplasm pool; and 2) to determine what proportion of the observed variation was due to genetics.

Accessions were planted in the field in 1981 and 1982. A significant range of variability was found among accessions within either growth habit. Repeatability estimates indicated that approximately 70% of the observed phenotypic variation was due to additive genetic variance. Based on the wide range of variability and the high repeatability estimates for grain-filling, selection should be effective.

Genotypic correlations indicated that accessions with long grain-filling periods were generally early pollinators

and that an underlying developmental sequence largely determined the duration of grain-filling.

Introduction

Breeders generally are concerned with increasing and protecting present yield levels. One component of yield which has been identified to have potential for increasing yield is the duration of grain-filling. Gebeyehou et al. (1982a), using path coefficient analysis, determined that duration of grain-filling in durum wheat (Triticum turgidum durum) was positively associated with yield through its positive association with kernels per spike and kernel weight (mg/grain). Positive associations between yield and grain-filling period have also been reported by McKee et al. (1979) in oats (Avena sativa L.), by Cross (1975) and Daynard et al. (1971) in corn (Zea mays L.), and by Dunphy et al. (1979), Egli and Leggett (1973), and Hanway and Webber (1971) in soybeans (Glycine max (L.) Merr.). This positive relationship implies that selection for a longer grain-filling period may represent one means of breeding for increased yield. Extending the duration of the grain-filling period to achieve heavier grains should be possible as grain size in wheat is only loosely restricted by the lemma and palea (Yoshida, 1972).

The duration of grain-filling in wheat (Triticum spp.) is very subject to environmental effects of temperature (Wiegand and Cuellar, 1981; Sofield et al., 1974, 1977; Spiertz, 1975). Therefore, only if sizeable, heritable differences

occur for duration of grain-filling does the opportunity exist for possibly improving yield through altering the length of this period. Thus, identifying and characterizing existing genotypic variation is an essential first step in determining if higher grain yields can be obtained by optimizing the duration of the grain-filling period (Rasmusson et al., 1979).

Differences in the duration of grain-filling have been found in many of the small grains, although only small numbers of lines have been examined. Differences have been found within rice (Oryza sativa L.)(Jones et al., 1979), oats (McKee et al., 1979), barley (Hordeum vulgare L.)(Rasmusson et al., 1979), soybeans (Reicosky et al., 1982; Dunphy et al., 1979), corn (Carter and Poneleit, 1973; Poneleit and Egli, 1979; Poneleit et al., 1980), durum wheat (Gebeyehou et al., 1982b), and Triticum aestivum wheats (Asana and Joseph, 1964; Nass and Reiser, 1975 ; Rawson and Evans, 1971; Sofield et al., 1977). Allard (1970) noted that the genetic variability on which the improvement of domestic plants depends is to be found in the advanced and primitive cultivars and in the wild relatives. An extensive survey of the germplasm pool to screen for duration of grain-filling may therefore expose the range of variability necessary for genetic improvement of this trait.

The objectives of this research were 1) to determine the range of variation in the duration of the grain-filling period in a diverse sample of the wheat germplasm pool; 2) to

determine the extent of variation within and between winter and spring growth habit and within and between species; and 3) to determine what proportion of the variation was due to genetics.

Materials and Methods

A random sample of accessions from the wheat germplasm collection was obtained from Dr. D. Smith, curator of the U.S.D.A. Wheat Germplasm Collection housed at Beltsville, Maryland. An additional twenty-five winter Triticum aestivum L. em Thell lines from Dr. E. Everson's wheat breeding program were used. The sample of the germplasm pool included winter growth-habit and spring growth-habit accessions from around the world and contained ten species comprising six genomes and three ploidy levels (Table 1).

Field studies were conducted in the 1981 and 1982 growing seasons at the Michigan State University field facilities in East Lansing, Michigan. Accessions of winter growth habit numbering 501 were planted on October 23, 1980 and 365 accessions of spring growth habit were planted on April 21, 1981. Spring accessions and winter accessions were planted in separate randomized block designs with 2 replications with each plot as a 1 meter row spaced 0.33 meters apart. Two hundred and fifty pounds per acre of 5-20-20 fertilizer were applied to both the winter and spring plots before planting each experiment. For further study in 1982, 106 winter accessions and 80 spring accessions from the 1981 experiment were selected. The 1981 accessions were rank

Table 1. Number of Accessions Within Species for Winter and Spring Growth Habits

	Genome*	1981	1982
Winter Growth Habit			
Triticum aestivum	ABD	295	60
Triticum turgidum durum	AB	121	27
Triticum turgidum dicoccum	AB	26	5
Triticum timopheevi araraticum	AG	5	2
Triticum monococcum	A	5	2
Triticum monococcum urartu	A	12	2
Triticum monococcum boeoticum	A	9	2
Triticum longissimum	B	1	1
Triticum speltoides	B	17	3
Triticum tauschii	D	10	2
Total		501	106
Spring Growth Habit			
Triticum aestivum	ABD	60	21
Triticum turgidum durum	AB	173	41
Triticum turgidum dicoccum	AB	50	9
Triticum monococcum	A	92	9
Total		365	80
Grand Total		866	186

* Reported genome of the species

ordered within growth habit and species by duration of the grain-filling period. Every sixth accession, as well as several of the longest and shortest grain-filling period accessions within each species and growth habit were chosen. The 106 winter types were planted on October 13, 1981 and fertilized with 350 lbs. of 6-24-24 per acre. The 81 spring types were planted on April 20, 1982 and fertilized with 300 lbs. of 6-24-24 per acre. The 9 spring Triticum monococcum accessions were replanted on May 4, 1982 due to mechanical problems during the first planting. In 1982, spring accessions and winter accessions were planted separately in randomized block designs with 5 replications with each plot as a 1 meter row spaced 0.33 meters apart. In 1982, both spring and winter plots were sprayed with four ounces of Bayleton per acre to control the spread of powdery mildew and leaf rust.

Data was collected every Monday, Wednesday, and Friday. Anthesis date was recorded when 50% of the heads within a plot showed anther extrusion and physiological maturity date was recorded when 50% of the heads and peduncles within a plot had lost their green color. Reicosky et al. (unpublished) have shown that the loss in color of the head and peduncle coincides with maximum grain dry matter accumulation. The duration of the grain-filling period was calculated as the difference in days between physiological maturity and anthesis.

Winter and spring accessions were analyzed separately by growth habit and combined over growth habits for grain-filling period. Analyses of variances were calculated for ploidy groups, genomes, species, and accessions. Genotypic correlation coefficients were determined for grain-filling period, anthesis date, and physiological maturity date separately for spring accessions and for winter accessions. Repeatability measures were calculated using the narrow sense heritability formula on an experiment basis (progeny mean basis, Hallauer and Miranda, 1981). The estimates of the standard errors of the genotypic correlations and of the repeatability measures were calculated as described by Dickerson (1969).

At harvest in 1982, a sample of 500 seeds for each of five reps for 30 accessions of winter wheat were taken. These samples were weighed and the simple correlation of duration of grain-filling to final grain weight (mg/grain) was determined.

Growing degree days were calculated by taking the mean daily temperature in degrees Celcius and subtracting 1^{o} C. These daily growing degree days were then summed over the duration of the grain-filling period for each accession. The weather data, used to calculate growing degree days and daily, biweekly, and monthly mean temperatures, was recorded at the Crops Barn in East Lansing, Michigan and was obtained from the Michigan Department of Agriculture Climatology Service.

Results and Discussion

Growth habit differences

Significant differences for the grain-filling period were found among accessions of both winter and spring growth habit in 1981 (Table 2). There was no meaningful difference for mean duration of grain-filling between the winter (28.8 days) and spring (28.1 days) growth habits in 1981. The 1981 range of the spring accessions was longer than that of the winter accessions due to one spring accession with a mean duration of 44.5 days; the next longest spring accession was 36 days. Both spring and winter accessions in 1981 had a minimum grain-filling period of 19 days and an approximate range of 18 days if the 44.5 day spring accession is ignored.

In 1982, significant differences for the grain-filling period were found among accessions of both winter and spring growth habits (Table 2). The range in winter growth habit in 1982 was longer than the range in spring growth habit. However, the variability was sufficiently wide in either growth habit such that selection for duration of grain-filling could occur. The 1982 grain-filling period means were significantly different between growth habit. The winter growth habit mean was 36.4 days versus the spring growth habit mean of 30.9 days (Table 2). The mean daily temperatures during the range of the grain-filling period were 17^{o} C for winter accessions and 19.7^{o} C for spring accessions (Table 3). Studies have shown that temperature has a pronounced effect on duration of grain-filling with lower

Table 2. Grain-Filling Period Minimum, Maximum, Mean, Range, and Standard Error in Days of Accessions within Growth Habit

	Winter Habit		Spring Habit	
	1981 (n=501)	1982 (n=106)	1981 (n=365)	1982 (n=80)
Minimum	19.0	25.0	19.0	21.0
Maximum	37.5	47.0	44.5	39.6
Mean	28.8	36.4	28.1	30.9
Range	18.5	22.0	25.5	18.6
$s_{\bar{x}}$	0.11	0.10	0.14	0.12

Table 3. Mean Temperature During the Range of Grain-Filling Periods in Spring and Winter Wheats Grown in 1981 and 1982

	1981 C°	1982 C°
Grain-filling period of winter wheats	19.8	17.0
Grain-filling period of spring wheats	20.5	19.7

temperatures resulting in a longer grain-filling period (Wiegand et Cuellar, 1981; Sofield et al., 1974, 1977; Marcellos and Single, 1972). The effect of temperature may explain the six-day discrepancy in grain-filling period between the two growth habits in 1982.

The temperature effect on grain-filling period may also explain the increased mean of both the winter and spring growth habit accessions from 1981 to 1982 (Table 2-3). The mean temperature during the range of the grain-filling period for winter wheat was 19.8^{o} C in 1981 and 17.0^{o} C in 1982 and for spring wheat was 20.5^{o} C in 1981 and 19.7^{o} C in 1982. The mean increase in duration of grain-filling was greater in the winter wheats from year to year than in the spring wheats which corresponded to the greater variation in mean temperature from year to year in the winter wheats than in the spring wheats.

Analyses of variance for growing degree days of the grain-filling period of each accession within each year were done in the hope that the growing degree day calculations would reduce the environmental influence of temperature as reflected in calendar days. However, the analysis using degree days did not represent an improvement over using the actual calendar days. Therefore analyses are presented with calculations using calendar days. The lack of a better fit when converting to growing degree days was in agreement with the results of Daynard (1972) and Johnson and Tanner (1972) with corn where they found that converting grain-filling

period into growing degree days did not change the differences between cultivars.

The wide variation exhibited in the germplasm pool for grain-filling period in both spring accessions and winter accessions indicated that selection for a longer grain-filling period should be possible in either growth habit. The choice of growth habit to select in will depend on the growth habit of the wheat common to the specific environment.

Species and ploidy comparisons

Analyses performed within and between species were calculated separately for winter growth habit and for spring growth habit. There were two reasons. 1) All the species were not common to both growth habits. This resulted in unbalanced data so that computer analysis became impossible due to the large data set and the nested and crossed experimental design. 2) Both growth habits exhibited wide variation for the duration of grain-filling such that selection could be effectively done in the growth habit common to the environment. Therefore, the two growth habits did not need to be analyzed together in order to obtain a broad range of variability.

Significant differences for grain-filling period were found in Triticum aestivum and in Triticum turgidum durum in both the winter and spring growth habits, in Triticum turgidum dicoccum in the spring growth habit, and in the diploid species in the winter growth habit and less so in the

spring diploids in both 1981 and 1982 (Table 4). The range in variation in the winter Triticum turgidum dicoccum species was minimal in 1982; however the sample size was small (Table 4). Considering the small sample, the range in the winter diploid species was quite wide. The species comprising the diploid ploidy group are discussed as a diploid group rather than as individual species because of the small sample size within these species. In 1981, the range and minimum and maximum values were very similar in Triticum aestivum for both growth habits and in Triticum turgidum durum (if the 44.5 day spring outlier is ignored) in both growth habits. In 1982, in Triticum aestivum, the range in days is the same in the spring and winter growth habits, but the minimum and maximum values are very different, possibly due to different temperatures during their grain-filling periods (Table 3-4).

In the winter types, there were no significant differences between Triticum aestivum, Triticum turgidum durum, and Triticum turgidum dicoccum means for grain-filling period in either year or combined over years (Table 5). The diploid species, in general, exhibited significantly lower means than the other species. One reason may be that the diploids have much smaller grains due to their generally uncultivated nature. Therefore they may need less time in order to fill those grains to their maximum potential. The screened hexaploids and tetraploids contain more cultivated and therefore improved accessions than do the diploids. As a consequence, the hexaploids and non-primitive tetraploids

Table 4. Duration of Grain-Filling in Days: Minimum, Maximum, Mean, and Range for Accessions Planted in Both Years, Within Species Within Growth Habit

	Minimum	Maximum	Mean	Range
Triticum aestivum				
Winter 1981 (n=60)	24.0	37.5	30.1	13.5
Winter 1982 (n=60)	32.8	47.0	36.9	14.0
Spring 1981 (n=21)	23.0	36.0	29.8	13.0
Spring 1982 (n=21)	24.2	39.6	32.6	15.0
Triticum turgidum durum				
Winter 1981 (n=27)	24.5	35.5	29.2	11.0
Winter 1982 (n=27)	34.6	43.4	37.6	9.0
Spring 1981 (n=41)	23.0	44.5	30.6	21.5
Spring 1982 (n=41)	25.6	38.0	31.8	12.5
Triticum turgidum dicoccum				
Winter 1981 (n=5)	24.5	33.0	28.3	8.5
Winter 1982 (n=5)	34.6	36.4	35.5	2.0
Spring 1981 (n=9)	19.5	32.0	26.4	13.5
Spring 1982 (n=9)	24.0	34.8	29.6	11.0
Combined diploids				
Winter 1981 (n=12)	17.5	31.5	25.2	14.0
Winter 1982 (n=12)	25.0	42.0	33.0	17.0
Spring 1981 (n=9)	21.0	29.5	25.9	8.5
Spring 1982 (n=9)	21.0	27.5	24.3	6.5

Table 5. Grain-Filling Period Species Means of Winter Wheats Planted in Both Years

Winter Growth Habit	1981	1982	Combined
Triticum aestivum (n=60)	30.1 a	36.9 a	33.5 a
Triticum turgidum durum (n=27)	29.2 ab	37.6 a	33.4 a
Triticum turgidum dicoccum (n=5)	28.3 abc	35.5 ab	31.9 ab
Triticum monococcum (n=2)	26.2 abcd	33.5 bc	29.9 bc
Triticum monococcum urartu (n=2)	25.0 bcd	32.7 bc	28.8 bcd
Triticum monococcum boeoticum (n=2)	23.5 cd	30.0 cd	26.8 cd
Triticum longissimum* (n=1)	30.0	42.0	36.0
Triticum speltoides (n=3)	26.0 bcd	32.6 bc	29.3 bcd
Triticum tauschii (n=2)	22.2 d	32.0 bc	27.1 cd
Triticum timophevii araraticum (n=2)	25.2 bcd	25.7 d	25.4 d
Max Tukey's .05	6.89	5.61	4.02
Min Tukey's .05	1.59	1.00	0.85

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* Because there was only one line, it was not included in Tukey's test for significant differences between means

could have evolved longer grain-filling periods. Another reason may be that the diploids are less adapted to this environment than the hexaploids and tetraploids so that they are less able to express their maximum potential due to environmental effects. The hexaploids and tetraploids may be better buffered than the diploids due to possessing more sets of homoeologous chromosomes (Feldman and Sears, 1981). However, regardless of what occurred, within this germplasm sample, Triticum aestivum and Triticum turgidum durum had longer grain-filling period means than the diploid species.

When comparing the duration of the grain-filling of the winter species between years, one can see that most of the species means were higher in 1982 than in 1981 (Table 5). In 1982 there was a very warm spring so the plants flowered earlier probably due to an increased rate of development. Then the temperatures cooled to below normal temperatures during the grain-filling period (Table 3, Table 6) which would result in longer grain-filling periods as discussed previously. There was not a significant species x year interaction in the winter wheats.

In the spring types, Triticum aestivum and Triticum turgidum durum means did not differ in either year or combined over years; the Triticum turgidum dicoccum mean was significantly less than that of Triticum aestivum and Triticum turgidum durum, and the diploid, Triticum monococcum, mean was even lower than that of Triticum turgidum dicoccum (Table 7). The lower mean of the Triticum monococcum

Table 6. Minimum, Maximum, and Mean Anthesis Date and Range and Standard Error of Accessions Within Growth Habit Within Year

	Winter Habit		Spring Habit	
	1981 (n=501)	1982 (n=106)	1981 (n=365)	1982 (n=80)
Minimum	June 4	May 28	June 17	June 14
Maximum	July 2	June 26	July 24	July 13
Mean	June 14	June 8	June 28	June 28
Range	28 days	26 days	37 days	29 days
$s_{\bar{x}}$	0.07	0.09	0.11	0.10

Table 7. Grain-Filling Period Species Means of Spring Accessions Planted in Both Years

	1981	1982	Combined
Triticum aestivum (n=21)	29.8 a	32.6 a	31.2 a
Triticum turgidum durum (n=41)	30.6 a	31.7 ab	31.2 a
Triticum turgidum dicoccum (n=12)	26.4 ab	29.6 b	28.0 b
Triticum monococcum (n=9)	25.9 b	24.3 c	25.1 c
Max Tukey's .05	5.19	3.70	2.96
Min Tukey's .01	1.80	1.14	0.96

subsample in the spring wheats in 1982 than in 1981 may be due to the later second planting of the accessions within that species. These accessions were growing in a different environment with slightly higher temperatures and more disease than the other accessions and both of these conditions may have caused a decrease in the grain-filling period. Due to the lower mean of Triticum monococcum in 1982, there was a species x year interaction in the spring wheats because all the other species' means increased from 1981 to 1982. There was less of a difference in the means of the spring wheats from 1981 to 1982 (Table 7) than there was in the winter wheats (Table 5). This could be due to temperature effects being fairly similar over the 1981 and 1982 range of the grain-filling period of the spring wheats (Table 3).

Whether the results were analyzed as accessions grouped within ploidy, within genome, or within species, the results were basically the same within either growth habit. There were significant differences both within groups and between groups. However, there was less variation between groups than within groups and because there was less variation between groups, the year x group interactions were less than the accessions within group x year interactions. There were highly significant interactions between years and accessions within groups. The significant accession by environment interaction suggests that selection should be done on lines tested over replications and years in the environment under

which the crop will be grown in order to properly select the longest or shortest grain-filling period.

Wide variation was found within both spring and winter Triticum aestivum and Triticum turgidum durum. Selection should therefore be possible in either species in either growth habit. Wide variation was also found in the primitive diploid species. However, hybridization between diploids and tetraploids or hexaploids is difficult; therefore it is more practical to select within the readily crossable germplasm. Depending on which type of wheat is grown in a region, crosses can be readily made using the selected accession within a species and growth habit common to the region. In Michigan, the common varieties are soft, white winter Triticum aestivum wheats. Therefore, for this project selection would be made within those accessions. If selections are to be made in another environment, the germplasm sample of interest should be rescreened for performance in that environment. However, in order to determine how effective selection will be, a measure of the additive genetic variance or the repeatability of the pure lines should be calculated.

Additive genetic variance

To determine the proportion of genetic variation within the phenotypic variation, variance components were calculated. Repeatability measures were calculated over replications and years using the same formula as narrow-sense

heritability estimates. The repeatability measures can be considered narrow sense rather than broad sense because the accessions being analyzed were all homozygous lines. Because they are inbred lines, there are only additive effects and no dominance effects; therefore, variance among lines will be due only to additive effects (Hallauer and Miranda, 1981). The repeatability measures were calculated over all accessions within the hexaploid and tetraploid species rather than within species in order to obtain better estimates from a larger sample size. The estimates were quite similar between the winter accessions and the spring accessions (Table 8). The repeatability estimates for grain-filling period of 0.69 in the winters and 0.78 in the springs were indicative that a large proportion of the phenotypic variation observed for the grain-filling period may be attributed to genotypic variation and more precisely, to additive genetic variance. These results indicate that selection for the grain-filling period can be readily done. However, the significant genotype by environment interaction of accessions by years suggests that selection should be done over replications and years. Otherwise, what is the longest grain-filling period accession in one environment may not be the longest in the desired environment.

Anthesis date and physiological maturity date

Anthesis date and physiological maturity date were not the main points of the study, but they are important in terms

Table 8. Repeatability Estimates Over Replications and Years

	Winter Accessions (n=94)	Spring Accessions (n=71)
Grain-Filling Period	0.69 ± 0.16	0.78 ± 0.17
Anthesis Date	0.94 ± 0.15	0.90 ± 0.17
Maturity Date	0.83 ± 0.15	0.83 ± 0.14

Table 9. Minimum, Maximum, and Mean Physiological Maturity Date and Range and Standard Error of Accessions Within Growth Habit Within Year

	Winter Habit		Spring Habit	
	1981 (n=501)	1982 (n=106)	1981 (n=365)	1982 (n=80)
Minimum	June 27	July 5	July 13	July 22
Maximum	July 27	July 28	Aug. 17	Aug. 10
Mean	July 13	July 15	July 26	July 30
Range	30 days	23 days	34 days	20 days
$s_{\bar{x}}$	0.08	0.10	0.12	0.10

of their relationships to grain-filling period. Significant variation was found for both these traits in both growth habit types (Table 6,9) and between and within all the species (data not presented). The ranges of variation for anthesis date and for physiological date were similar. There were accession by environment interactions, but the magnitude of the interaction was much smaller than that of only accessions in the analysis of variance for both anthesis date and physiological maturity date. The repeatability measures of anthesis date and physiological maturity date (Table 8) were very high, especially that of anthesis date. These results were in agreement with the analysis of variance which showed more genotypic variation (accessions) than genotype by environment variation (accessions x year).

Genotypic correlations

There was a significant negative genotypic correlation between the grain-filling period and anthesis date (Table 10) and a significant positive genotypic correlation between anthesis date and physiological maturity date for both spring and winter growth habit (Table 10). The negative genotypic association between grain-filling period and physiological maturity date was significant (Table 10), but it was not as strong a correlation as the others.

The high genotypic correlation of anthesis date and physiological maturity date (Table 10) suggested that an underlying developmental sequence may play a role in

Table 10. Genotypic Correlations of Grain-Filling Period, Anthesis Date, and Physiological Maturity Date

	Winter Habit (n=94)	Spring Habit (n=71)
Grain-Filling : Anthesis Date	-0.77 + 0.07	-0.76 + 0.07
Grain-Filling : Maturity Date	-0.46 + 0.15	-0.26 + 0.15
Anthesis Date : Maturity Date	+0.92 + 0.01	+0.83 + 0.05

determining the duration of the grain-filling period. Anthesis date and physiological maturity are on a "time line" and anthesis date can never occur after the maturity date for a given accession. The similarity in the range of variation for anthesis date and physiological maturity date also give credence to an underlying developmental sequence associating anthesis date and physiological maturity date rather than to a linkage of genes for anthesis date and physiological maturity date.

The high negative correlation of grain-filling period and anthesis date (Table 10) can be explained when placed in the context of environmental conditions. The grain-filling period has a large genetic component as indicated by the repeatability measure (Table 8), but it is also subject to environmental influences as shown by the significant accession x year interaction. The earlier the anthesis date, the earlier the start of the grain-filling period. In general, the environmental conditions are more favorable early in the season than later in the season: temperatures are more moderate, moisture is adequate, diseases are less prevalent, and daylength is at its longest. The plant is therefore growing under conditions where lower temperatures favor longer durations of grain-filling (Sofield et al., 1974, 1977), and adequate moisture and less disease favor longer maintenance of photosynthesizing tissue which then prolongs the period for photosynthetic supply. Therefore, the early-pollinating, long grain-filling period accessions

may be more capable than late-pollinating accessions of expressing their maximum genetic potential for final grain weight because these accessions fill their grain during the more favorable environmental conditions.

The poor correlation of grain-filling period to maturity date (Table 10) may be explained on the basis of environmental conditions affecting expression of the duration of grain-filling. Accessions which pollinate in mid-season and which are less able to withstand unfavorable environmental conditions may quit filling their grains and mature at an earlier time than other more environmentally-adapted lines, thus they will have shorter grain-filling periods. Therefore, the lack of a stronger genotypic correlation between days to maturity and grain-filling period may be explained as due to modifying effects of environment, especially high temperatures which shorten the duration of grain-filling (Wiegand and Cuellar, 1981; Sofield et al., 1974, 1977; Spiertz, 1975). High temperatures mainly occur late in the grain-filling phase which can then interact with the genotype to hasten maturity. This supposition also explains the even lower correlation between maturity date and grain-filling period in the spring wheats. Spring wheats, in general, pollinate between two weeks and a month after winter wheats in Michigan, so the environment under which they fill is one of more unfavorable conditions.

As mentioned previously, there appears to be an underlying developmental sequence determining the duration of

grain-filling as shown by the high genotypic correlation of anthesis date and physiological maturity date. In general, the long grain-filling period accessions pollinate early and are therefore able to take advantage of the more favorable growing conditions found earlier in the season. There are accessions, however, which are late pollinators with long grain-filling periods which may be better able to withstand higher temperatures and other unfavorable environmental conditions.

Reason to select for a longer grain-filling period

The main reason one would want to select for a longer grain-filling period would be to achieve a higher final grain weight or to obtain a higher number of filled grain which should result in a higher yield. The correlation between final grain weight and duration of grain-filling was 0.19 which was significant at the 5% level. However, the low magnitude of the correlation coefficient indicates that it is not the only factor involved. This evidence suggests that some gain in final grain weight may be made by selecting for longer grain-filling period but that there are other more important causal factors. It could be that the rate of grain-filling is more important to final grain weight than the duration of grain-filling. If duration of grain-filling also plays a part in determining number of grains per spike, as suggested by Gebeyehou et al. (1982a), then duration of grain-filling may play a significant role as a means of

increasing yields through both a modest gain in final grain weight and through increasing the final number of grains per spike. One reason why duration of grain-filling was poorly correlated with final grain weight (mg/grain) may be due to variability in the amount of leveling off of filling rates at the end of the grain-filling period as reported by Nass and Reiser (1975). It may be more appropriate to determine the effective filling period and correlate it to final grain weight in order to attain a higher correlation. Another reason for the poor correlation may be due to the unadapted nature of the accessions sampled in which case they are more susceptible to environmental effects. It might be prudent to incorporate the long duration of grain-filling trait into an adapted variety and then see how it affects final grain weight and grain yield.

Conclusion

Effective selection for a long grain-filling period should be possible in either growth habit and in either of the commonly cultivated species, Triticum aestivum and Triticum turgidum durum. The choice of the species and growth habit germplasm to be selected within will depend on the type of wheat grown in the environment of interest. The high repeatability measure of the grain-filling period should make for similar performance in similar environments. However, because of the significant genotype x environment interaction, selection of one accession to obtain a long

grain filling period in several different environments may not be possible.

The high positive genotypic correlation between anthesis date and physiological maturity date suggested that an underlying developmental sequence may be largely controlling the grain-filling period. For two common Michigan wheat cultivars, the average duration of grain-filling over 1981 and 1982 was 35 days. The longest winter accession averaged over 1981 and 1982 was 42 days, therefore, there is still room to lengthen the grain-filling period even with developmental sequence boundaries.

A large pool of genetic variability has been found for the duration of grain-filling period which can be exploited. The next step is to prove a cause and effect relationship between a longer grain-filling period and a higher yield. In order to do this, a backcross program should be instituted to obtain several long grain-filling period, well-adapted varieties. These "new" lines will then be compared with "old" varieties for final grain weight (mg/grain), number of grains, and yield. In this manner, a cause and effect relationship of duration of grain-filling and yield can be ascertained.

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CHAPTER 3

GENE ACTION IN TWO SPRING WHEAT CROSSES

Abstract

The choice of appropriate selection and breeding procedures depends largely on the type of gene action and genetic variance controlling the trait. The objective of this study was to determine the mode of inheritance of the grain-filling period, anthesis date, and physiological maturity date in three spring wheat crosses.

Three sets of spring wheat crosses comprising parents, F1's, F2's, and 2 backcrosses were hand-planted in the field in 1982. Generation means analyses were performed on two of the crosses for anthesis date and grain-filling period and on one of the crosses for physiological maturity date.

For anthesis date of the two crosses, it appeared that, overall, additive gene action was prevalent and that there was little or no dominance. In one cross, a heterotic effect in the F1 was due to partial dominance. For physiological maturity date, there were additive and dominance gene effects although the magnitude of the additive effects was double that of the dominance effects. For duration of grain-filling, in either cross, additive gene effects were

important. In one cross, dominance gene effects were equally important and in the other cross, additive x additive gene effects were important.

For crosses in which additive gene action was of primary importance, selection within the populations should be on a mean basis. For those crosses in which dominance gene effects were of equal importance, selection on a mean basis can be done, but it will not be as effective as when all the gene action is additive because dominance can not be utilized in a pure-line wheat breeding program.

Introduction

Lengthening the duration of grain-filling may be one possible means of increasing yields. A positive association has been shown to exist between the grain-filling period and yield in wheat (Triticum spp.) (Gebeyehou et al., 1982), oats (Avena sativa L.) (McKee et al., 1979), corn (Zea mays L.) (Cross, 1975; Daynard et al., 1971), and soybeans (Glycine max (L.) Merr.) (Dunphy et al., 1979; Egli and Leggett, 1973). A previous study indicated substantial genetic variation among wheat accessions randomly chosen from the wheat germplasm collection for duration of grain-filling period such that effective selection could be done (Neuhausen and Reicosky, unpublished).

The choice of an appropriate breeding procedure depends to a large extent on the type of gene action and genetic variance controlling a trait. In the development of improved

wheat lines, progress from selection depends primarily on additive gene action. It is therefore important to determine the types of gene action inherent in the trait as well as the proportion of additive genetic variance in relation to the phenotypic variance. Only when the underlying genetics are known can an intelligent decision be made as to the rate and type of selection necessary to improve the trait.

Little is known of the mode of inheritance of the grain-filling period in wheat. Working with wheat, Walton (1971) found that both additive and dominance variances were important and that over-dominance was expressed for a longer grain-filling period. Singh et al. (1977) using 36 one-way wheat crosses observed that more additive genetic variance than non-additive variance was involved in the expression of grain-filling period.

Anthesis date and physiological maturity date are visual indicators of the beginning and end of grain-filling in wheat. For this reason and because genotypic correlations indicated that there was an association between duration of grain-filling and anthesis date and an association between duration of grain-filling and physiological maturity date (Neuhausen and Reicosky, unpublished), the modes of inheritance of anthesis date and physiological maturity date may be important.

Few studies have been performed on the inheritance of anthesis date. Walton (1971) and Sharma and Ahmad (1979) found that both additive variance and dominance variance were

significant, whereas Kandola and Anand (1974) observed that only additive variance was significant. Fonesca and Patterson (1968) reported a narrow-sense heritability of 0.80 ± 0.07 for earliness of flowering.

Although few studies have been performed on the genetics of anthesis date, many studies have been performed to determine the inheritance of heading date; because they are both ruled by vernalization and photoperiodic responses and because anthesis date directly follows heading by approximately four days developmentally, the genetics of anthesis and heading date are similar if not the same. Heading time can be divided into two developmental phases (Pinthus, 1963) both having photoperiodic and vernalization requirements (Klaimi and Qualset, 1973, 1974). No matter how heading date genetics are classified, earliness exhibits a degree of phenotypic dominance over lateness with minor genes contributing to a continuum. Edwards et al. (1976), working with winter wheats, determined that there were no significant deviations from an additive-dominance model. Bhatt (1972) and Amaya et al. (1972) found that additive gene action was significant and that other types of gene action were absent. Anwar and Chowdhry (1969) observed non-additive gene effects. Klaimi and Qualset (1973) found that epistasis did play a role. These researchers all came to the conclusion that earliness was dominant to lateness for heading date, but

their conclusions as to the reasons underlying the observation varied, possibly due to the use of different parental material and environments.

For days to maturity, Walton (1971) and Sharma and Ahmad (1979) found that additive and dominance variances played a significant role in its inheritance. Avey (1981) observed that maturity was mainly determined by additive effects but that dominance may have been of some importance.

One difficulty in the interpretation of quantitative genetic analyses is that the nature of gene action may differ depending on the environment, on the method, and on the genotypes of the two parents comprising the cross (Ausemus et al., 1967). This concept was well-illustrated by the variable results obtained for these three characters. In general, the researchers concurred on visual results, e.g., earliness was dominant to lateness for heading, but they found some differences in the underlying genetic mechanisms. These varying observations are to be expected for gene differences for a trait vary from parent to parent and will be reflected in estimates of genic effects.

The purpose of this study was to determine the mode of inheritance of the grain-filling period, anthesis date, and physiological maturity date using widely differing parents.

Materials and Methods

Three sets of spring wheat crosses were made in the greenhouse during the winter of 1981-1982. The 6 parental

lines were selected based on 1981 field data. Cross 1, PI185841 (from Brazil) x CI17704 (from Montana, U.S.A.), was between a long grain-filling period line and a short grain-filling period line respectively. Cross 2, CI15556 (from Minnesota, U.S.A.) x CI07627 (from USSR) was between an early-pollinating,long grain-filling period line and an intermediate pollinating, short grain-filling period line respectively. Cross 3, CI14240 (from Colombia) x CI06591 (from Iran) was between an early pollinating, early maturing line and a late pollinating, late maturing line respectively. For each cross, reciprocal F1 seed (F11 and F12), reciprocal F2 seed (F21 and F22), backcross 1 seed (BC1), and backcross 2 (BC2) seed were generated.

On May 4, 1982, the progeny seeds and parental seeds were hand-planted in the Crop Sciences field in East Lansing. The seed from each cross was grown in a separate experiment in a completely randomized design with three replications. Each row was 12 feet long, with 36 seeds per row spaced 4 inches apart. Rows were spaced 1 foot apart. The plots were fertilized with 300 pounds per acre of 6-24-24 and sprayed with 4 ounces of Bayleton per acre to prevent powdery mildew and leaf rust.

The primary tiller on each plant was tagged so that anthesis date and physiological maturity date could be recorded on the same head. Data was collected every Monday, Wednesday, and Friday. Anthesis date was recorded on the day when the head was extruding pollen. Physiological maturity

was recorded on the day when the tagged head and the node below it had lost their green color. The grain-filling period was calculated as the period between physiological maturity date and anthesis date. For each cross, the number of seeds planted for each generation type was: 45 P1, 45 P2, 45 F11, 45 F12, 90 BC1, 90 BC2, 150 F21, and 150 F22. The number of plants measured varied per cross since there was not 100% germination (Table 1). There appeared to be a soil problem in one part of each range; however, soil and micronutrient testing did not delineate the problem.

Observed and expected progeny means were compared and genetic analyses of generation means were performed in order to determine the nature of gene action in the inheritance of duration of grain-filling, anthesis date, and physiological maturity date. For traits in which there was less than a four day difference between the parental means, no analysis was performed because the differences between the parents were not large enough to warrant analysis. For this reason, none of the material from Cross 1 was evaluated.

Generation means analysis was done to allow for estimates of gene action (Mather and Jinks, 1971). Using a least squares procedure, estimates of the three parameter model of gene effects were obtained using the population means of two inbred lines, F1, F2, and two backcross generations. In the three parameter model, the mean effect (m), the additive effects (a) and the dominance effects (d) were estimated. The coefficient of determination (R^2) was used as an

Table 1. Number of plants per generation per cross.

Cross 1	Cross 2	Cross 3	Generation Type
35	40	42	Parent 1
31	40	41	Parent 2
68	67	76	Backcross 1
60	64	74	Backcross 2
37	37	48	F1 with maternal parent 1 (F11)
30	42	44	F1 with maternal parent 2 (F12)
109	130	124	F2 - derived from F11 (F21)
89	127	152	F2 - derived from F12 (F22)

indication of goodness of fit of the additive-dominance model. When the three-parameter model was inadequate to explain the variation exhibited, the model was expanded to a six parameter model. In the six parameter model, the parameters represent mean effects (m), additive effects (a), dominance effects (d), additive x additive effects(a x a), additive x dominance effects (a x d), and dominance x dominance effects (d x d). The relative importance of the different gene effects can be evaluated from the magnitude and significance of the estimates (E.E. Gamble, 1961). The analysis was performed for grain-filling period and anthesis date in crosses 2 and 3 and for physiological maturity date in cross 3.

One cause of non-significant differences between parents may have been an infestation of aphids which transmitted barley-yellow dwarf virus to these plots. Parents planted in field plots in 1981 and on April 24, 1982 exhibited larger differences (Table 2). The hand-planted plots for this experiment were planted two weeks later than machine-planted accessions which also included the parents in these crosses. The later planting date made them more susceptible to an aphid infestation because they were in a more succulent stage of growth at the time of aphid infestation. The later heading plants in crosses 1 and 2 were especially effected. Barley yellow dwarf has been shown to predispose plants to early senescence with consequent premature ripening of heads (Price and Stubbs, 1963; Suneson and Ramage, 1957). This

Table 2. Anthesis Date, Physiological Maturity Date, and Grain-Filling Period Means for Parents in 1981, 1982A*, and 1982B**

	Cross 1: Parent 1			Cross 1: Parent 2		
	1981	1982A	1982B	1981	1982A	1982B
GFP (Days)	35.0	34.0	26.1	25.0	27.6	24.2
Anthesis	6-24	6-28	7-11	6-25	6-30	7-10
Maturity	7-29	8-01	8-06	7-20	7-27	8-04

	Cross 2: Parent 1			Cross 2: Parent 2		
	1981	1982A	1982B	1981	1982A	1982B
GFP (Days)	33.0	37.4	29.1	23.5	28.8	25.1
Anthesis	6-17	6-18	7-02	6-30	6-30	7-07
Maturity	7-21	7-26	8-01	7-24	7-29	8-02

	Cross 3: Parent 1			Cross 3: Parent 2		
	1981	1982A	1982B	1981	1982A	1982B
GFP (Days)	29.0	37.8	30.7	27.5	26.6	25.5
Anthesis	6-17	6-14	6-27	7-07	7-06	7-14
Maturity	7-16	7-22	7-28	8-04	8-02	8-08

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* = April 24, 1982 machine-planted plots
** = May 4, 1982 hand-planted plots

resulted in the reduction of differences for some of the characters in some of the crosses and as a result, those characters were not analyzed.

Variance component analysis was performed in order to calculate narrow-sense heritabilities (Warner, 1952). Using a perfect fit solution, estimates of A (additive variance), D (dominance variance), and E (error variance) were obtained. The average degree of dominance ($\bar{a}$) was estimated by the formula $\sqrt{D/A}$ (Mather and Jinks, 1971). Analyses were only done for anthesis date, physiological maturity date, and grain-filling period in cross 3. No variance component analyses were done for any characters in cross 2 or cross 1 because the parental variances were equal to or greater than the F2 and backcross variances.

Results and Discussion

No reciprocal F1 or F2 differences were found so the reciprocal F1's and reciprocal F2's were pooled for the analyses.

Anthesis date

In cross 2, the mean difference between parents for anthesis date was 5 days (Table 3). The generation means analysis and estimates of gene effects (Table 4) results indicated that only additive effects were significant (-2.65 ± 0.40) in this model. The sign was negative because parent 2 pollinated later. The dominance gene effects were negligible (0.21 ± 0.63). The additive dominance model

Table 3. Means and Standard Errors for Grain-filling Period, Anthesis Date, and Physiological Maturity Date for Each of Two Crosses

Grain-filling period means

Generation	Cross 2	Cross 3
Parent 1	29.08 ± .55	30.69 ± .28
Parent 2	25.13 ± .35	25.51 ± .32
F1	29.15 ± .38	29.24 ± .31
Backcross 1	29.58 ± .34	28.95 ± .36
Backcross 2	27.76 ± .32	27.62 ± .42
F2	28.61 ± .18	27.37 ± .21

Anthesis Date Means
(Days after January 1)

Generation	Cross 2	Cross 3
Parent 1	183.80 ± .36	179.57 ± .26
Parent 2	189.26 ± .38	195.73 ± .24
F1	186.87 ± .19	183.63 ± .27
Backcross 1	187.16 ± .17	183.79 ± .21
Backcross 2	188.86 ± .27	191.53 ± .52
F2	187.69 ± .15	187.52 ± .28

Physiological Maturity Date Means
(Days after January 1)

Generation	Cross 2	Cross 3
Parent 1	212.88 ± .49	210.26 ± .26
Parent 2	214.40 ± .47	221.24 ± .38
F1	216.01 ± .40	212.87 ± .32
Backcross 1	216.75 ± .36	212.74 ± .46
Backcross 2	216.62 ± .39	219.15 ± .59
F2	216.30 ± .20	214.89 ± .34

t.01 = 2.878
t.05 = 2.101
t.10 = 1.734

Table 4. Analyses of Variance, Coefficients of Determination (R^2), and Estimates of Gene Effects (m,a,d) in a 3 Parameter Model for Anthesis Date in Cross 2 and Cross 3

Source	DF	Cross 2 MS	Cross 3 MS
Generations	5		
Additive	1	52.679**	479.232**
Dominance	1	.129	46.091**
Dev. from model	3	3.300	8.169*
Error	18	2.145	1.892
R^2 =		0.68	0.89
m =		187.23 ± 0.38	187.72 ± 3.23
a =		-2.65 ± 0.40	-7.99 ± 0.61
d =		0.21 ± 0.63	-3.92 ± 0.96

**significant at 1% level.
*significant at 5% level.

accounted for 68% of the variation exhibited by the generations which indicated a good fit. Similarly, the observed values of the F1 and F2 did not differ significantly from the expected values indicating additive effects.

The mean difference between parents in cross 3 for anthesis date was 16 days (Table 3). The generation means analysis and estimates of gene effects (Table 3) results indicated mostly additive gene effects (-7.99 ± 0.61) with smaller dominance effects (-3.92 ± 0.96). The magnitude of the additive effects was double that of the dominance effects. The negative sign for additive gene action was because parent 2 pollinated later and the negative sign for dominance gene action indicated earliness was dominant for pollination date. The F1 mean was significantly different from the mid-parental value at the 5% level which indicated partial dominance for earliness of pollination. The F2 mean value exhibited no partial dominance when compared with the expected values. Therefore the heterosis in the F1 was due to partial dominance. The additive-dominance model accounted for 89% of the variation among the generations. There was a statistically significant deviation from the additive-dominance model. However, the R^2 value only increased by 5% when the model was expanded to six-parameters so that the three-parameter model was deemed adequate.

When observing the two crosses, it appeared that, overall, additive gene action was prevalent and that there was little to no dominance. The heterotic effect in the F1

in Cross 3 was due to partial dominance for earliness. The results of the generation means analysis for anthesis date in Cross 2 are in agreement with the results of Amaya et al. (1972) and Bhatt (1972) for heading date in which they found that additive gene action was significant and other types were absent. Results of generation means analysis for anthesis date in Cross 3 are in agreement with the results of Anwar and Chowdhry (1969) for heading date.

Physiological maturity date

In cross 3, there was an 11 day difference between the parents for physiological maturity date (Table 3). The generation means analysis and estimates of gene effects (Table 5) indicated partial dominance. Both additive and dominance effects were highly significant. The negative sign for additive effects was because parent 2 matured later and the negative sign for dominance effects was due to partial dominance of earliness for physiological maturity date. The magnitude of the additive gene effects (-5.68 ± 0.48) was double that of the dominance gene effects (-2.88 ± 0.76). The heterosis in the F1 was due to partial dominance. The additive dominance model accounted for 88% of the variation exhibited which indicated a good fit. Therefore, physiological maturity date appeared to be mainly controlled by genes with additive effects and some dominance effects. Avey (1981) observed similar gene effects.

Table 5. Analysis of Variance, Coefficient of Determination (R^2), and Estimates of Gene Effects (m,a,d) in a 3 Parameter Model for Physiological Maturity Date in Cross 3

Source	DF	MS
Generations	5	
Additive	1	241.820**
Dominance	1	24.929**
Dev. from model	3	3.814
Error	18	1.379

R^2 =	0.88
m =	216.31 ± 0.46
a =	-5.68 ± 0.48
d =	-2.88 ± 0.76

**significant at 1% level.
*significant at 5% level.

Grain-filling period

In Cross 2, there was a significant 4 day difference between the parental means; this was a large enough difference that generation means analysis could be adequately performed (Table 3). The generation means analysis and estimates of gene effects (Table 6) indicated that dominance effects (2.26 ± 0.62) and additive effects (2.06 ± 0.39) were of equal importance. Both the F1 and F2 exhibited dominance for a long grain-filling period when compared with the expected values. The additive-dominance model was a good fit accounting for 66% of the variation; there were no significant epistatic effects.

In cross 3, there was a five day difference between the parental means for the grain-filling period (Table 3). The generation means analysis and estimates of gene effects (Table 6) indicated that gene effects were mainly due to additive gene action (2.32 ± 0.38). The additive-dominance model accounted for 65% of the variation exhibited. However, the deviations from the model were significant at the 5% level so that it was necessary to fit a 6-parameter model. The significant deviation was due to additive x additive gene action (3.48 ± 2.08). The six-parameter model (R^2 = 0.78) was a better fit than the three-parameter model (R^2 = 0.65). The F1 exhibited a heterotic effect due to partial dominance for a long grain-filling period. The F2 value indicated no dominance.

Table 6. Analyses of Variance, Coefficients of Determination (R^2), and Estimates of Gene Effects (m,a,d) in a 3 Parameter Model in Cross 2 and in a 3 and 6 Parameter Model in Cross 3 for Grain-filling Period

Source	DF	Cross 2 MS	Cross 3 MS	Cross 3 MS
Generations	5			
Additive	1	31.761**	40.208**	40.208**
Dominance	1	15.382**	3.225	3.225
Dev. from model	3	0.397	2.936*	
Add x Add	1			6.478*
Add x Dom	1			2.110
Dom x Dom	1			0.215
Error	18	1.271	0.807	0.807
R^2 =		0.66	0.65	0.78
m =		27.26 ± 0.38	27.70 ± 0.37	24.65 ± 2.11
a =		2.06 ± 0.39	2.32 ± 0.38	2.58 ± 0.37
d =		2.26 ± 0.62	1.04 ± 0.61	6.29 ± 5.42
aa =				3.48 ± 2.08
ad =				-2.65 ± 1.64
dd =				-1.78 ± 3.44

**significant at 1% level.
*significant at 5% level.

In either cross 2 or cross 3, additive gene action was extremely important in the determination of the duration of the grain-filling period.

An additive-dominance model was adequate to explain the variation among generations in most cases with the exception of the grain-filling period in Cross 3. The adequacy of the model was indicated by the low incidence of meaningful epistatic effects and by the high coefficient of determination. The large additive effects are indicative that selection on a mean basis could be effective for grain-filling period or anthesis date in a breeding program. However, it is impossible to predict gain from selection based on gene effects. Failure to detect epistasis or dominance does not mean they do not exist, for balancing of plus and minus effects can result in epistatic and/or dominance effects which are not significant (Hayman, 1958).

Variance analysis

Variance analyses to derive estimates of A, D, and E were performed on anthesis date, physiological maturity date, and grain-filling period in Cross 3 (Table 7) in order to determine narrow-sense heritabilities.

Variance analysis for anthesis date indicated that the additive variance was small in relation to total phenotypic variance which resulted in a narrow-sense heritability of 0.32. The dominance variance was much larger than the

Table 7. Variance Components for Cross 3 for Anthesis Date, Physiological Maturity Date, and Grain-Filling Period

Generation	Anthesis Variance	Maturity Variance	GFP Variance
Parent 1	2.88	2.78	3.34
Parent 2	2.30	5.99	4.31
F1	6.80	9.24	8.65
F2	21.51	17.14	11.62
BC1	15.96	15.98	10.08
BC2	20.25	25.94	13.01
A	13.63	-7.63	0.31
D	40.00	17.97	20.91
E	4.70	6.81	6.24
h^2	0.32	---	0.01
$\bar{a}$	1.71	---	8.27

additive variance which resulted in an appearance of over-dominance when the average degree of dominance was calculated.

For physiological maturity date, the estimate of additive variance was negative which can only be explained as a sampling deviation (Dudley and Moll, 1969). The estimate of additive variance was 0.

For grain-filling period, the estimate of additive genetic variance was small such that only 1% of the phenotypic variation could be explained as due to additive variance. The low additive variance estimate and high dominance variance estimate therefore gave a high estimate of over-dominance when calculating the average degree of dominance.

These variance estimates were not in agreement with the results of the generation means analysis. The generation means analysis results were probably more reliable because they were based on first degree statistics rather than the second degree statistics of the variance analysis, such that the error terms are smaller. There are several possible reasons why the variance analysis results were so different. 1) There may have been epistasis which is a violation of one of the assumptions of the variance analysis. In this case, data transformation would have had little effect because the frequency distributions overlap in which case narrow-sense heritability estimates would have changed little with a change in scale (Warner, 1952). 2) There was a large amount

of environmental variance as indicated by the large F1 variances; because these were second order statistics, the error term would be even larger than for first order statistics. 3) Spring wheats are ill-adapted agronomically to Michigan summers as illustrated by the barley-yellow dwarf virus invasion. For this reason, environmental effects due to disease and higher temperatures may have masked or distorted the genetics of these traits. 4) The adequacy of the model in respect to A, D, and E can not be tested because they are estimated as perfect fit solutions. Therefore, if A is underestimated, then D will be overestimated.

Conclusions

Grain-filling period, for the two crosses examined, was controlled largely by additive effects with dominance effects being of equal importance in Cross 2. These results indicate that this trait could be improved through selection on a mean basis in a wheat breeding program, although without variance estimates, advance from selection can not be predicted.

For the two crosses examined, anthesis date was determined mainly by additive effects although some dominance effects were exhibited towards earliness of flowering in Cross 3. In a pure-line breeding program, dominance effects can not be utilized; however, the magnitude of the additive effects were large such that it may be possible to select for early flowering types by selecting on a mean basis.

For the one cross examined, physiological maturity date was governed by both additive and dominance effects with additive effects of a larger magnitude.

The reference population only contained four lines. Therefore, the results of the limited data obtained in this study could not be generalized to include other samples. However, from this data and the studies of other researchers (previously cited), it appears that additive gene effects play a role; depending on the magnitude of the additive gene effects, they may or may not be of primary importance.

The variances were of unexpected magnitude so that narrow-sense heritabilities could not be estimated for all three crosses and all three traits. The genetic variance data are too limited and possibly too error-prone to make any generalizations about narrow-sense heritabilities. In order to be able to test the parameters for goodness of fit, more generations should be grown from each cross.

Based on the results of the mean analysis, grain-filling period could be improved within the reference or similar populations. For further work, long grain-filling period winter accessions should be crossed with Michigan varieties and the mode of inheritance should be determined in order to select the best breeding procedure to incorporate longer grain-filling periods into Michigan varieties.

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SUMMARY AND RECOMMENDATIONS

Summary

There was significant variation both within and between species for duration of grain-filling, anthesis date, and physiological maturity date.

The range of variability for grain-filling period was such that selection could occur in most of the species screened within either growth habit. Approximately 70% of the observed phenotypic variation was attributed to additive genetic variance in both spring and winter accessions based on a measure of repeatability over replications and years. Because of significant year x accession interactions, selection should be over replications and years in the environment in which the crop will be grown.

Genotypic correlations of -0.77 for grain-filling period and anthesis for both spring and winter accessions indicated that early pollinating accessions generally have long grain-filling periods. The high genotypic correlation of anthesis date and physiological maturity date (0.92 in winter accessions and 0.83 in spring accessions) suggested that an underlying developmental sequence largely determined the duration of grain-filling.

Gene action was determined for duration of grain-filling, anthesis date, and physiological maturity date in two spring wheat crosses. Duration of grain-filling was determined predominantly by additive gene effects in one cross and by both additive and dominance gene effects in the other cross. In the cross with large additive gene effects, selection on a mean basis would be effective. This concurs with the repeatability estimates using mean values.

The duration of grain-filling period may not be as important as other characters in determining final grain weight as demonstrated by the correlation of 0.19 between grain-filling period and final grain weight. However, if the duration of grain-filling does affect the number of grains, then it may be more important to yield through an increase in number of grains filled than it is to final grain weight.

Recommendations

There are two main recommendations on how my field studies could have been improved: 1) ensure that all possible disease and insect preventative measures have been employed; and 2) check the field location before planting by conferring with the researcher of the preceding year to ascertain if there were abnormal spots in the area.

There are several ways in which the genetic analysis experiment could have been improved, only one of which I could have done and still have been able to plant the experiment. The experiment should have been planted at the

same time as the other spring experiment; two weeks appeared to make a large difference in the results, mostly due to the onset of barley yellow dwarf virus. In order to have planted earlier, I should have imposed a stressful condition on the greenhouse plants so that they would have matured earlier.

A second recommendation for this experiment is that another generation such as the F3 should have been grown. This would have allowed for a best-fit model of genetic variances rather than a perfect fit solution which could not be tested for goodness of fit. However, there was not time over one fall and winter in the greenhouse to attain another generation.

A third recommendation would be to use winter wheat lines rather than spring lines for they are better adapted agronomically for Michigan climate. Lines with long and short grain-filling periods could have been selected and crossed with common Michigan varieties. This method would have given specific information on how to best incorporate the trait within Michigan varieties. Because of vernalization requirements, the necessary generations could not be obtained in time for me to use winter wheat lines.

Another possibility for future work would be to cross many parents, e.g., 20 parents, in various combinations and form the same generations as I did and an F3 generation. The lines could be chosen either randomly or selected. Because of the large number of lines, the results could be generalized more easily than those using only four parents.

It would be best to use randomly selected lines for then the information would be pertinent to the entire population from which the lines were selected.

An experiment to discern the correlations between final grain-weight (mg/grain), rate of grain-filling, effective filling period, and actual grain-filling period has already been planted for 30 winter wheat accessions. The results of this study will indicate whether duration of grain-filling is an important determinant of final grain weight.

As mentioned in Chapter 2, a long-term option is to develop lines with long grain-filling periods, short grain-filling periods, and medium grain-filling periods in the background of one or more of the well-adapted Michigan varieties. Measurements could be taken for rate of grain-filling, effective filling period, actual grain-filling period, number of grains per head, number of tillers, grain weight, and yield. Then the effects of grain-filling period on yield can be adequately proven or disproven.

Temperature differences appeared to affect some accessions more than others. Accessions could be grown in different temperature regimes to determine if some lines are temperature insensitive or if their threshold level is different from other lines. This information could help to stabilize g x e interactions.

The lack of larger differences between parents for pollination date in Cross 2 of the genetic study may have been due to photoperiodic effects. An experiment could be

done to mimic the photoperiodic conditions during the summer and determine what effect it has on flowering and maturity dates and on durations of grain-filling. This experiment could be run in conjunction with the temperature sensitivity experiment.

APPENDIX A

Table A1. Grain-Filling Period Analyses of Winter and Spring Wheats Grouped by Species, Genome, and Ploidy

Grouped by Species

Source	DF	MS	F-test
Species	10	556.52	36.29**
Growth Habit	1	17.42	1.13
Species x Growth Habit	3	40.20	2.62*
Accessions(Spec x Grth Hab)	851	15.33	2.25**
Error	864	6.80	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Genome

Source	DF	MS	F-test
Genome	5	827.77	48.98**
Growth Habit	1	20.45	1.21
Genome x Growth Habit	2	28.86	1.70
Accessions(Geno x Grth Hab)	857	16.92	2.49**
Error	864	6.80	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Ploidy	2	1,941.62	113.38**
Growth Habit	1	33.26	1.94
Ploidy x Growth Habit	2	54.18	3.17*
Accessions(Ploid x Grth Hab)	860	17.08	2.51**
Error	864	6.80	

* = SIG. AT .05
** = SIG. AT .01

Table A2. Grain-Filling Period Analyses of Spring Wheat Grouped by Species and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	426.29	
Reps(Years)	5	27.95	
Species	3	492.19	3.80*
Species x Years	3	57.54	3.88*
Accessions(Species)	76	75.92	5.12**
Accessions(Species) x Years	76	14.83	2.97**
Error	368	4.99	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	426.29	
Reps(Years)	5	27.95	
Ploidy	2	544.72	3.89
Ploidy x Years	2	63.95	4.20*
Accessions(Ploidy)	77	79.96	5.25**
Accessions(Ploidy) x Years	77	15.22	3.05**
Error	368	4.99	

* = SIG. AT .05
** = SIG. AT .01

Table A3. Grain-Filling Period Analyses of Winter Wheat Grouped by Species, Genome, and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	8,228.92	
Reps(Years)	5	72.06	
Species	9	220.38	3.10**
Species x Years	9	24.75	1.85
Accessions(Species)	96	50.67	3.78**
Accessions(Species) x Years	96	13.39	2.66**
Error	497	5.03	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Genome

Source	DF	MS	F-test
Years	1	8,228.92	
Reps(Years)	5	72.06	
Genome	5	329.39	3.85**
Genome x Years	5	37.20	2.69*
Accessions(Genome)	100	51.99	3.76**
Accessions(Genome) x Years	100	13.83	2.75**
Error	497	5.03	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	8,228.92	
Reps(Years)	5	72.06	
Ploidy	2	437.13	5.12*
Ploidy x Years	2	30.35	2.14
Accessions(Ploidy)	103	57.84	4.07**
Accessions(Ploidy) x Years	103	14.21	2.82**
Error	497	5.03	

* = SIG. AT .05
** = SIG. AT .01

Table A4. Anthesis Date Analyses of Spring Wheat Grouped by Species and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	1,525.28	
Reps(Years)	5	39.25	
Species	3	948.31	2.61
Species x Years	3	163.02	10.06**
Accessions(Species)	76	206.72	12.76**
Accessions(Species) x Years	76	16.20	4.78**
Error	368	3.39	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	1,525.28	
Reps(Years)	5	39.25	
Ploidy	2	1,369.35	3.70
Ploidy x Years	2	169.84	9.47**
Accessions(Ploidy)	77	205.41	11.46**
Accessions(Ploidy) x Years	77	17.93	5.29**
Error	368	3.39	

* = SIG. AT .05
** = SIG. AT .01

Table A5. Anthesis Date Analyses of Winter Wheat Grouped by Species, Genome, and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	4,770.42	
Reps(Years)	5	41.03	
Species	9	985.99	4.15**
Species x Years	9	97.26	10.58**
Accessions(Species)	96	142.48	15.50**
Accessions(Species) x Years	96	9.19	2.14**
Error	497	4.29	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Genome

Source	DF	MS	F-test
Years	1	4,770.42	
Reps(Years)	5	41.03	
Genome	5	1,260.76	4.26**
Genome x Years	5	135.99	12.50**
Accessions(Genome)	100	162.28	14.92**
Accessions(Genome) x Years	100	10.88	2.54**
Error	497	4.29	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	4,770.42	
Reps(Years)	5	41.03	
Ploidy	2	2,166.21	7.17**
Ploidy x Years	2	127.47	8.62**
Accessions(Ploidy)	103	176.59	11.94**
Accessions(Ploidy) x Years	103	14.79	3.45**
Error	497	4.29	

* = SIG. AT .05
** = SIG. AT .01

Table A6. Physiological Maturity Date Analyses of Spring Wheat Grouped by Species and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	3,564.30	
Reps(Years)	5	15.70	
Species	3	432.08	3.65*
Species x Years	3	30.97	2.26
Accessions(Species)	76	91.17	6.64**
Accessions(Species) x Years	76	13.73	3.55**
Error	368	3.87	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	3,564.30	
Reps(Years)	5	15.70	
Ploidy	2	198.64	1.60
Ploidy x Years	2	31.14	2.23
Accessions(Ploidy)	77	101.66	7.29**
Accessions(Ploidy) x Years	77	13.95	3.60**
Error	368	3.87	

* = SIG. AT .05
** = SIG. AT .01

Table A7. Physiological Maturity Date Analyses of Winter Wheat Grouped by Species, Genome, and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	468.51	
Reps(Years)	5	60.13	
Species	9	584.12	3.82**
Species x Years	9	61.82	3.61**
Accessions(Species)	96	95.76	5.59**
Accessions(Species) x Years	96	17.14	3.51**
Error	497	4.88	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Genome

Source	DF	MS	F-test
Years	1	468.51	
Reps(Years)	5	60.13	
Genome	5	768.78	3.95*
Genome x Years	5	93.21	5.30**
Accessions(Genome)	100	105.84	6.02**
Accessions(Genome) x Years	100	17.58	3.60**
Error	497	4.88	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	468.51	
Reps(Years)	5	60.13	
Ploidy	2	776.69	2.68
Ploidy x Years	2	171.68	9.45**
Accessions(Ploidy)	103	125.10	6.89**
Accessions(Ploidy) x Years	103	18.17	3.72**
Error	497	4.88	

* = SIG. AT .05
** = SIG. AT .01

Table A8. Growing Degree Day Analyses of Winter Wheat Grouped by Species, Genome, and Ploidy

Grouped by Species

Source	DF	MS	F-test
Years	1	799,477	
Reps(Years)	5	28,147	
Species	9	52,554	2.23*
Species x Years	9	10,449	1.69
Accessions(Species)	96	15,932	2.57**
Accessions(Species) x Years	96	6,195	3.17**
Error	497	1,954	

* = SIG. AT .05
** = SIG. AT .01

Grouped by Genome

Source	DF	MS	F-test
Years	1	799,477	
Reps(Years)	5	28,147	
Genome	5	83,006	0.50
Genome x Years	5	18,287	3.05*
Accessions(Genome)	100	158,480	2.64**
Accessions(Genome) x Years	100	5,999	3.07**
Error	497	1,954	

* = SIG. AT .05
** = SIG. AT .10

Grouped by Ploidy

Source	DF	MS	F-test
Years	1	799,477	
Reps(Years)	5	28,147	
Ploidy	2	57,417	1.19
Ploidy x Years	2	35,015	5.76**
Accessions(Ploidy)	103	18,259	3.00**
Accessions(Ploidy) x Years	103	6,0749	3.11**
Error	497	1,954	

* = SIG. AT .05
** = SIG. AT .01

Table A9. Grain-Filling Period Analysis of Spring Wheat for Accessions Comprising Species 2-4: For Use in Repeatability Measure and for Genotypic Correlation

Source	DF	MS
Years	1	1,445.15
Reps(Years)	5	0.74
Accessions	71	218.78
Accessions x Years	71	18.93
Error	350	3.29

Table A10. Cross-Product Analysis Comprising Species 2-4 of Grain-Filling Period and Anthesis Date of Spring Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	
Reps(Years)	5	
Accessions	70	-99.30
Accessions x Years	70	-10.13
Error	350	-2.12

Table A11. Cross-Product Analysis Comprising Species 2-4 of Grain-Filling Period and Maturity Date of Spring Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	
Reps(Years)	5	
Accessions	70	-12.29
Accessions x Years	70	6.19
Error	350	2.57

Table A12. Anthesis Date Analysis of Spring Wheat for Accessions Comprising Species 2-4: For Use in Repeatability Measure and for Genotypic Correlation

Source	DF	MS
Years	1	1,445.15
Reps(Years)	5	0.74
Accessions	70	218.78
Accessions x Years	70	18.93
Error	350	3.29

Table A13. Maturity Date Analysis of Spring Wheat for Accessions Comprising Species 2-4: for Use in Repeatability Estimate and for Genotypic Correlation

Source	DF	MS
Years	1	3,230.59
Reps(Years)	5	12.03
Accessions	70	107.19
Accessions x Years	70	14.99
Error	350	3.74

Table A14. Cross-Product Analysis Comprising Species 2-4 of Anthesis Date and Maturity Date of Spring Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	
Reps(Years)	5	
Accessions	70	119.48
Accessions x Years	70	8.80
Error	350	1.17

Table A15. Grain-Filling Period Analysis of Winter Wheat for Accessions Comprising Species 1-4: for Use in Repeatability Measure and for Genotypic Correlation

Source	DF	MS
Years	1	7,156.09
Reps(Years)	5	40.68
Accessions	93	49.08
Accessions x Years	93	13.39
Error	465	4.10

Table A16. Cross-Product Analysis Comprising Species 1-4 of Grain-Filling Period and Anthesis Date of Winter Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	-5,809.76
Reps(Years)	5	12.72
Accessions	93	-60.79
Accessions x Years	93	-3.89
Error	465	-1.25

Table A17. Cross-Product Analysis Comprising Species 1-4 of Grain-Filling Period and Maturity Date of Winter Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	1,346.33
Reps(Years)	5	53.40
Accessions	93	-11.71
Accessions x Years	93	9.34
Error	465	2.85

Table A18. Anthesis Date Analysis of Winter Wheat for Accessions Comprising Species 1-4: for Use in Repeatability Measure and for Genotypic Correlation

Source	DF	MS
Years	1	4,716.72
Reps(Years)	5	19.83
Accessions	93	178.82
Accessions x Years	93	9.72
Error	465	3.18

Table A19. Maturity Date Analysis of Winter Wheat for Accessions Comprising Species 1-4: for Use in Repeatability Estimate and for Genotypic Correlation

Source	DF	MS
Years	1	253.30
Reps(Years)	5	85.95
Accessions	93	106.32
Accessions x Years	93	15.18
Error	465	4.78

Table A20. Cross-Product Analysis Comprising Species 1-4 of Anthesis Date and Maturity Date of Winter Wheat for Use in Genotypic Correlation

Source	DF	MCP
Years	1	-1,093.03
Reps(Years)	5	32.55
Accessions	93	118.02
Accessions x Years	93	5.82
Error	465	1.93

Table A21. Phenotypic Correlations with Accessions Combined Over Years

	Winter Habit	Spring Habit
Grain-filling period : Anthesis date	-0.65	-0.72
Grain-filling period : Maturity date	-0.16	-0.13
Anthesis date : Maturity date	+0.86	+0.78

Table A22. Correlations of Grain-Filling Period, Anthesis Date, and Physiological Maturity Date for 1981:1982.

	Winter habit	Spring habit
Grain-filling period	0.65	0.67
Anthesis date	0.86	0.82
Maturity date	0.70	0.71

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