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Title: ASSOCIATION BETWEEN LENGTH OF GRAIN FILLING PERIOD AND GRAIN YIELD IN TWO WHEAT POPULATIONS (*TRITICUM AESTIVUM* L. EM THELL.)

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The objective of this study was to determine interrelationships among agronomic traits in early and late maturing populations.

Two populations were obtained from the crosses, Roussalka/Tesopaco 76 and Yamhill/Aspen. Seeds were space planted with split plot design and nine agronomic traits were observed.

In comparative studies between early and late populations, the early population was earlier in heading date, maturity date, longer maturity duration, heavier kernel weight, and higher harvest index. However, it was shorter in plant height, had fewer tillers, kernels and lower grain yield than the late population.

Grain filling duration expressed positive relationships with grain yield in both crosses, although the correlation coefficient with grain yield was very low compared to other agronomic traits.

Grain filling duration showed consistent positive relationships with kernel weight in both populations and with kernel number in the late population. No relationship was found between grain filling duration and tiller number.

Grain filling duration influenced grain yield mainly by the indirect effects of kernel weight and kernel number.

Yield components generally showed high positive relationships with grain yield; tiller number being the most important, followed by kernel number, and kernel weight. Competition among yield components was minimal in this space planted study.

Heading date showed a negative association while plant height and harvest index expressed high positive relationships with grain yield.

Association between Length of Grain Filling Period
and Grain Yield in Two Wheat Populations
(*Triticum aestivum* L. em Thell.)

by

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IN DEDICATION TO

my mother, brother

and my sisters

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ASSOCIATION BETWEEN LENGTH OF GRAIN FILLING PERIOD AND GRAIN YIELD IN TWO WHEAT POPULATIONS (*Triticum aestivum* L. em Thell.)

INTRODUCTION

In most areas of the world, there has been a growing concern to obtain stable food resources required to adequately feed the present and future population. To meet this challenge, available natural resources which are needed for production of edible crops must be developed and fully utilized for stable high yields of food products. Plant breeders around the world have played major roles in helping to solve the problems of increasing yield potential of food resources, by developing cultivars which are; widely adapted in different areas of the world; resistant to major disease and insect species; and of a plant architecture which can best utilize external factors such as light and soil fertility.

In some areas of the world, multiple cropping is practiced to maximize the use of limited arable land. A multiple cropping system is designed to grow two or three crops on the same land per year. The choice of crops which can best fit this system is one of the major problems confronting the scientists. Consideration must be given to adjustment of the total growing period of each crop, and the farmer's economics from the point of view of their input-output on the land. To avoid overlapping of crops in multiple cropping, it is necessary to reduce the total growing period of at least one of them. Higher yields are generally expected from longer growing periods, however, as far as total yield per unit area per year is concerned, minimum yield reduction of one crop would not be of major consequence to the producer.

In Korea, arable land area for food production is relatively small and production of cereal crops is far below demand. Wheat consumption has increased very rapidly during the last two decades, but wheat production was not enough to meet growing demands partly because a major portion of the land for cereal production has been occupied by paddy fields for rice. Steps are being taken to alleviate this problem by expanding the wheat area and increasing yield potential per unit area. A double cropping system with rice in paddy fields is one of the ways to expand cultivated wheat area; however, this is not feasible for most of the rice growing paddy fields because of the conflicting stage of grain filling period of wheat with transplanting time of rice. Therefore, it is necessary to reduce the total growth period of wheat to fit the double cropping system with rice. Reducing total growth period can be done by selection lines having early heading dates and/or developing lines with relatively short grain filling period. If this cannot be done in the near future, the alternative method is to increase yield potential per unit area.

The objectives of this wheat study were: (1) to determine the relationships of grain filling duration with grain yield and yield components, (2) to evaluate the interrelationships among yield and yield components, and (3) to define the relationships between yield and other important agronomic characters such as heading date, plant height, and harvest index.

LITERATURE REVIEW

The objective of most plant breeding programs is to increase grain yield, however, progress is very slow due to the complexity of many genetic and environmental factors.

In some parts of the world, multiple cropping is practiced and two or three crops per year are harvested from the same land. In order to fit crops into such a growing cycle, early maturing cultivars are required. Normally higher yields are expected from longer duration cultivars and early maturity reduces total yield capacity. An important factors to consider, however, is total yield per unit area per year rather than total yield per crop.

Cereal consumption has continued to increase dramatically in Korea and total production is relatively low. The primary objective for the Cereal Research Institute is to increase total grain yield yet maintain early maturity to coincide with cropping rotation in the multiple crop system. The grain filling duration in the cereal growth cycle is of special interest and will be addressed in this study. Also of interest were relationships between yield with yield components and other agronomic traits. The literature will be discussed in terms of yield as affected by a) maturity duration, b) yield components, and c) other agronomic traits.

Maturity Duration

The term, maturity duration, also referred to as grain filling duration, is interpreted differently by scientists. It may be the total growth period from heading to maturity (Spiertz et al., 1971), or from anthesis to maturity (Nass and Reiser, 1975).

Archbold (1942) evaluated various organs of barley plants using a series of defoliation and shading experiments. His data showed that assimilated by-products were translocated directly to the developing grain. The total assimilates available in samples collected 19 weeks after sowing, were 15 percent in the leaves, 15 percent in the flag leaf sheath, 40 percent in the stem and leaf sheaths, and 30 percent in the spikes. He confirmed that the current assimilation during the grain filling period, from the various parts of green organs, was more important to the development of the ear than transportation of stored sugar in the stem.

In a growth analysis study including winter and spring, and old and new wheat cultivars, Watson et al. (1963) indicated that extension of the period between ear emergence and ripening in spring cultivars results in decreasing the difference in grain yield between winter and spring cultivars. The new cultivars of both winter and spring wheat produced higher yields partly because their spikes emerged sooner and this lengthened the grain filling period.

Fischer and Kohn (1966) conducted wheat experiments having treatments of seeding date, seeding rate, and fertilizer levels, and obtained a highly correlated value (r=0.969) of grain filling duration with grain yield over the wide range of grain filling duration values recorded (21-99 days). They reported that the earliest seeding dates had the longest grain filling duration. The increased rate of leaf senescence was usually associated with reduced post-flowering plant water-status under conditions of limited soil moisture. Similar results reported by Welbank et al. (1966) indicated that anthesis was expected to correspond more closely with the beginning of grain growth than ear emergence, however, no significant difference was detected between them.

Spiertz et al. (1971) observed high positive correlation values in spring wheat cultivars between grain yield from heading to ripening and from flowering to ripening. The period from heading to ripening was more closely correlated to grain yield than the period from flowering to ripening, causing the scientists to wonder whether the period between heading and flowering affected the ultimate grain yield.

Daynard et al. (1971) reported that a significant portion of the yield differences among corn genotypes might be attributable to differences in the length of grain filling period. They concluded that significant potential exists for higher corn yields through the genetic extension of the effective grain filling period. Daynard and Kannenberg (1976) confirmed the positive relationships between the grain filling period and grain yield in corn.

While many experiments in cereal crops have shown positive relationships between maturity duration and grain yield, other experiments failed to support this relationship. Askel and Johnson (1961) reported that cultivars with longer sowing-to-heading period have higher kernel numbers per spike and produce higher yields in barley. They indicated that a long vegetative period tends to be controlled by recessive genes, thus, short sowing-to-heading period was dominant over long and long heading-to-ripening period was dominant over short. They also reported that kernel weight is positively related with both periods, however, it is more closely related to heading-to-ripening period. In a greenhouse experiment involving 120 wheat cultivars, Simpson (1968) reported that correlation coefficients were very low between days from anthesis to grain maturity and the other variables including grain yield per plant and grain weight per spike. He concluded that persistence of chlorophyll in the spike over 41 days might be a poor indicator of duration of assimilation into spikes. Nass and Reiser (1975) indicated that days from planting to anthesis, from anthesis to maturity, and from planting to maturity were not significantly correlated with grain yield in the ten cultivars fo spring wheat studied, while the rate of grain filling was more important in maximizing grain yield.

From a study designed to identify the variation existing in the vegetative and grain filling period of barley, Rasmusson et al. (1979) reported that the highly heritable character, duration of the vegetative period, could be easily modified by selection. However, duration of the grain filling period is not easily modified. They also stated that selection to lengthen or reduce the grain filling period was possible when replicated plots were used, but they did not indicate whether a few days difference in grain filling could affect the final yield. They suggested that more imformation was needed concerning the relationship between effective grain filling and duration of the growth period before proceeding with substantial breeding work.

Environmental factors also have a large influence on the grain filling duration. Chinoy (1947) showed negative correlation between grain yield and mean maximum temperature during the ripening period of wheat in dryland conditions. Shortening the ripening period by increasing temperature resulted in reduced 1000 kernel weight and grain yield. He indicated that high temperature during the ripening period accelerated the rate of cell division in the developing grain.

Marcellos and Single (1972) concluded that air temperature was the principal factor influencing the rate of post-anthesis development in eight spring wheat cultivars and the factors of cultivar and photoperiod had no measurable effect. They found that raising the mean daily temperature of the post flowering period from 17.5 to 22.5 C reduced the number of days available for photosynthesis by approximately 30 percent.

In an irrigated wheat study in Sudan, Khalifa (1973) found that early nitrogen application benefited leaf growth and increased leaf area index. This advantage persisted during most of the period following ear emergence. As a result, leaf area duration after ear emergence was was higher with early than late nitrogen application. He concluded that the variation in grain yield was mainly a reflection of the effect of the nitrogen treatments on the leaf area duration after ear emergence.

Spiertz (1974) reported that within the range of 15 to 25 C, a rise in temperature increased the growth rate of the grain but greatly reduced the duration of the post-floral development of the plant. Finally, Spiertz concluded that higher temperatures caused lower grain yields. He also showed that seed yield and growth rate of the grain increased with an increase in light intensity. However, the advantage of higher light intensity for grain growth was partially off-set by more rapid leaf senescence.

Yield Components

Wheat yield can be divided into the following components: number of spikes per plant, number of spikelets per spike, number of kernels per spikelet, and weight per kernel.

Kronstad and Foote (1964) indicated that where little progress could be made selecting directly for grain yield, amore realistic approach would be to select for specific components followed by a combination of all components as a final step.

Yield components have been studied by many scientists as potential factors for increasing yield capacity. It is widely known that negative correlationships exist between yield components, and these findings were the most logical reason for the lack of using components as selection criterion. However, in recent years, as cereal crops reached yield plateaus, emphasis has been directed to increasing the expression of specific characters for long-range yield improvement.

In a study of yield components in oats, Grafius (1956) introduced the idea that yield might be represented geometrically as the volume of a rectangular parallelepiped with the edges represented as the number of panicles per unit area (X), the average number of kernels per panicle (Y), and average kernel weight (Z). He suggested that it might be easiest to improve yield by increasing the short edge among three edges (X, Y, and Z) for an otherwise good variety. He concluded that recurrent selection for yield would be futile without strong positive correlations between the yield components. Based on the former study of the geometry of yield, Grafius and Wiebe (1959) questioned whether the greatest gain in yield might result from an increase in one edge alone, two edges, of three edges. They concluded that it would be better to select for three yield components in oats, if they have high heritable values; however, if yield components are independent, it would be advisable to concentrate on one or two traits having the highest heritable values. If they are not independent, it may be better to select for one trait when correlation coefficients are positive between the yield components but for both traits when they are negative.

McNeal (1960) reported that in wheat crosses, kernel number per plant had the highest association with yield among the various characters of both F_2 plants and F_3 progenies. He also indicated that spikes per plant and kernels per spike were more highly correlated with plant yield than was kernel weight. In a comparative study of winter wheat cultivars varying in height, Johnson et al. (1966) reported significantly higher yield for the semi dwarf cultivar, C.I.13678 than for the taller cultivar, Pawnee, as a result of higher kernel number per spike. They stated that the major advantage of C.I.13678 was the stability and magnitude of expression of kernel number per spike which more than compensated for deficiencies in the other two components, kernel weight and number of spikes. They concluded that the components approach for yield would provide a better basis for selection of parents and for evaluation of their progenies than yield itself.

In 1967, Adams compiled an extensive literature review supporting the occurrence of negative correlations among morphological components of yield in crop plants as a widespread phenomenon. These negative correlations must arisen in response to competitional forces operating on developmentally flexible components rather than genetic interrelationship among components. His study of the navy bean showed low positive correlations among the components in the non competitive plants spaced at 45 cm but negative correlations occuring in those at 7.5 cm. He stated that negative correlations among components could not prevent the selection for high yield in the navy bean. Fonseca and Patterson (1968) reported that in winter wheat, the three components of yield, kernel weight, number of spikes, and number of kernels per spike had high positive correlations with yield. However, negative correlations were observed between yield components. They concluded that progress in breeding by selection for components of yield rather than yield itself may be limited by the negative correlation among yield components.

In two barley populations, Rasmusson and Cannell (1970) found that genetic as well as environmental factors were responsible for the phenotypic correlations between the components of yield. Thus, selection for yield through yield components was very effective in certain situations, but could not be recommended as a routine procedure. They reported that the environment has a strong influence on the genotypic expression of kernels per spike and number of spikes but small effect on kernel weight. They concluded that selection for kernel wight would be advantageous in all environments, and recommended maximum utilization of the environment during the grain filling period. In an experiment to study seed weight and its effects on yield, other yield components and quality in wheat, Knott and Talukdar (1971) reported negative correlations between the yield components. An increase in seed weight, for example, caused a reduction in kernel number due to fewer kernels per spike and spikes per unit area. However, seed weight showed a highly significant positive correlation with yield. They concluded that though compensating effects occur, a genetic increase in one component may result in increased yield. Seed weight in wheat is more highly heritable than the other components of yield and should be a useful character for improving wheat yield.

In a study conducted at three locations in one year with five wheat generations from F_4 to F_8, McNeal et al (1978) reported that direct selection for yield per plant showed lack of response, however, kernel weight and kernel number per spike were good characters for indirect selection for yield. They also found in some cases yield components were genetically independent. For example, there were no correlated responses between kernel weight and spike number when selection was done for kernel weight and likewise for kernels per spike when kernel number was the character selected. They concluded that selection for a single character can result in improved yield, as shown for kernel weight, however, long range yield improvement probably results from concomitant improvement in all yield components.

In comparative studies between yield components and other measurable traits, positive relationships were reported between kernel weight and grain filling duration (Askel and Johnson, 1960; Welbank et al., 1966). Relationships between kernel number and grain filling duration were reported both positively (Watson et al., 1963) and negatively (Mohiuddin and Croy, 1980). Spiertz et al (1971) stressed the importance of the correlation between green leaf area (maturity) duration and grain yield. When the total green leaf area is limited or duration is short, lack of adequate carbohydrate reduces potential production of the ear. When sufficient carbohydrates are provided and the grain filling period is extended, the sink strength of the ear increases potential grain yield, for example, in kernel number. Tiller number did not show any relationship with grain filling duration (Askel and Johnson, 1961;

Mohuddin and Croy, 1980).

Other Agronomic Characters

Several scientists have reported positive relationship between harvest index (grain-straw ratio) and yield. Both Sims (1963) and Rosielle and Frey (1975) reported positive effects of harvest index on yield in oats. Singh and Stoskopf (1971) reported similar results in barley and wheat. In ten spring wheat cultivars, Nass and Reiser (1975) showed that the highest yielding cultivars had a higher harvest index, whereas those with lower grain yield had a lower harvest index. Donald and Hamblin (1976) recommended that the wider use of harvest index in agronomic research and plant breeding would make a notable contribution to the understanding and advancement of crop performance.

Many cereal breeding programs are trying to reduce plant height while increasing grain yield. This is mainly due to the advantage of short, stiff straw for reducing lodging. Donald (1967) stressed the important of short stature in designing a wheat ideotype. Johnson and Mekasha et al.(1966) showed that the two short statured cultivars were more productive than the two taller wheat cultivars in a competitive study. In another correlation study, Johnson and Biever et al. (1966) observed high positive correlations between plant height and kernel weight, grain yield and spike length. They indicated that short plant height was associated with low kernel weight, short spike length, early maturity, lower number of spikes per plant and low yield for dwarf cultivar, Seu Seun 27. In contrast, Simpson (1969) found that tall selections were lower than short plants in grain yield per plant and kernel numbers per spike, but higher in grainweight per tiller.

In the case of earliness, Fonseca and Patterson (1968) reported that the total correlation between earliness and yield was relatively low, and early geneotypes tended to have fewer tillers and higher kernel weight but fewer kernels per spike. Askel and Johnson (1961) reported negative relationship between sowing-to-heading period and heading-to-ripening period.

MATERIALS AND METHODS

Two winter wheat cultivars (Roussalka and Yamhill) and two advanced lines (Tesopaco 76 and Aspen) were selected to evaluate the influence of grain filling period (maturity duration) on yield response. The cultivar, Roussalka developed in Bulgaria is known for its earliness whereas Yamhill, released by Oregon State University (OSU), is a late flowering variety. Tesopaco 76 is a mid-early flowering spring wheat line from the International Maize and Wheat Improvement Center in Mexico. Aspen is a late maturing advanced day length insensitivity line selected and named from the International Winter X Spring Wheat program at OSU. These parents are detailed in Appendix Table 1.

Two wheat populations were obtained by crossing the cultivars, Tesopaco 76 X Roussalka (cross I) and Aspen X Yamhill (cross II). The F_1 populations from cross I and cross II were then backcrossed only to the winter cultivars, Roussalka and Yamhill, respectively. At the same time, the F_1 populations were being multiplied to produce F_2 seed. Thus, the genetic material for this study was composed of the four parental cultivars, backcrosses to the winter parents, and F_2 geenrations. The parents, backcrosses, and F_2 generation populations were space planted 30 cm apart within and between rows. Each row contained 10 plants with a border plant of barley to reduce competition effects. Individual parents were planted in three rows, backcrosses in ten rows, and the F_2 generations in fifty rows. Missing hills due either to poor germination, mechanical damage or birds were replanted by barley.

The experimental site was the East Farm, approximately one mile east of Corvallis, Oregon. The soil type is a Chehalis silt loam.

Total precipitation for the growing season from October 1979 to July 1980, was 997 mm. The average maximum and minimum temperatures at this experimental site during the growing period were 15.2 C and 4.8 C, respectively and the highest and lowest single day temperature being 36.7 C and -10.6 C, respectively.

The field experiment was performed in the 1979-1980 growing season using a split plot design with five replications. The main plots were crosses (I and II) and subplots were generations (P_1, P_2, BC, and F_2). 33 kg of nitrogen was applied prior to planting. This was followed by side dressing at tillering stage with 51 kg and at heading time with 66 kg for a total of 150 kg actual N/hectare.

Data were collected on an individual plant basis. Poorly developed and damaged plants due to birds or small animals were eliminated during the data collection process. The following methods were used for measuring nine agronomic traits:

Heading date: number of days from january 1 to the date when spike of the primary tiller was fully emerged from the flag leaf sheath.

Maturity date: number of days from january 1 to the date when the flag leaf surface of the primary tiller completely changed from green to yellow color.

Maturity duration: number of days from the heading date to maturity date.

Plant height: height in centimeters from the soil surface to the tip of the spike of the tallest culm (excluding awn).

Tiller number: number of culms bearing spikes per mature plant.

Mean kernel number per spike: kernel numbers were calculated by dividing grain yield (g) by tiller number and 100 kernel weight (g) and multiply the total by 100.

Kernel weight: total weight in grams of 100 randomly selected kernels.

Grain yield: total weight in grams of the clean dry seed.

Harvest index: the ratio in percent of grain yield divided by total plant weight.

Though data were collected on an individual plant basis, it was impossible to conduct the analysis of variance on individual plants due to the differences in number of harvested plants in each generation of the two crosses. Therefore, mean values for each generation were calculated and used in the analysis of variance. All nine agronomic traits were included in the analysis of variance to detect the differences among crosses, and generations. Comparisons were made only for the traits whose values for each generation showed signigicant F values in the analysis of variance. Duncan's New Multiple Test was used to determine significant levels of difference between means. Simple phenotypic correlations were computed among nine traits on a per plant basis for the parents, backcrosses, and F_2 generations in both crosses. In addition, simple correlations were derived for cross I and cross II including all generations. Finally, path coefficient analysis was utilized on a per plant basis to investigate the direct and indirect effects of specific characters including maturity duration on yield. Five agronomic traits, maturity duration, tiller number, kernel number, and kernel weight as causal factors and grain yield as a resultant factor for computation of the path coefficient.

EXPERIMENTAL RESULTS

The results of this experiment will begin with analysis of variance for nine agronomic traits between cross I and cross II population and among generations within crosses. Comparisons of nine agronomic traits between crosses will be emphasized more than comparisons among generation within crosses because differences between crosses were larger than among generations within crosses. Simple phenotypic correlations among nine agronomic traits were computed separately on an individual plant basis for the F_2 populations of cross I and cross II. The correlations among maturity duration, yield components, and grain yield will be further analyzed using path coefficient analysis for measuring direct and indirect effects.

Analysis of Variance

Analysis of variance tables were obtained for observing differences of measured traits between crosses, and among generations within the cross I and cross II populations. Observed mean squares showed significant differences for all measured traits except plant height between the two crosses (Appendix Table 2). Coefficient of variations were low for most traits in Appendix Table 2 ranging from 1.2 to 8.4 percent; the exceptions being tiller number and grain yield which were higher at 17.0 and 16.9 percent, respectively. Since each of the crosses included two parents, a backcross, and F_2 generation, separate comparisons were conducted among generations for cross I and cross II populations. Differences among generations in cross I (Appendix Table 3) were noted for heading date, maturity date, 100 kernel weight, kernel number and grain yield. No differences were found for maturity duration, tiller number, and harvest index. The generations in cross I also had low coefficient of variations for most of the traits except tiller number and grain yield. Observed mean squares for nine agronomic traits of the cross II population are represented in Appendix Table 4. Difference were observed for heading date, maturity duration, plant height, tiller number and harvest index. No differences were noted for maturity date, kernel number, 100 kernel weight, and grain yield. There were marked differences in the observed mean squares for most agronomic traits between cross I and cross II in Appendix Table 2; however, there were not the same levels of significance among generations within cross I and II (Appendix Tables 3 and 4). Therefore, more stress will be placed on comparative agronomic traits between cross I and cross II than differences among generations within the two crosses.

Observed mean values for nine agronomic traits of crosses are given in Table 1. The cross I population, derived from early genotypes, had an earlier mean heading date, maturity date, and longer maturity duration than cross II by 26, 16, and 10 days, respectively. No striking difference was found in plant height between the two crosses, and harvest index was higher in cross I. In the case of yield components, tiller numbers and kernel numbers were higher in cross II as was total yield, while cross I had heavier kernel weight. As mentioned above, observed mean values for nine agronomic traits of the cross I population had earlier maturity date, longer maturity duration, higher harvest index and heavier kernel weight than cross II, but fewer tiller numbers, kernel numbers, and lower grain yield.

Table 1. Observed mean values for nine agronomic traits for the parents, backcrosses, and F_2 generations between the cross I and cross II populations.

	Agronomic traits								
Population	Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	Kernel weight (g)	Grain yield (g)	Plant height (cm)	Harvest index
Cross I	127.8	185.85	57.60	6.15	55.50	5.828	20.95	85.10	41.74
Cross II	154.8	201.70	47.45	7.55	69.85	5.084	28.65	86.55	35.72

Observed mean values for agronomic traits among generations within cross I and cross II populations (Table 2 and 3) did not express the same range in differences as those shown between crosses. The major differences in mean values among generations of cross I (Table 2) were found between parent 1 and parent 2, with backcross and F_2 generations being intermediate between the two parents for all traits except kernel weight. Interestingly, the interrelationships between the agronomic traits of parent 1 and 2 in cross I (Table 2) were very similar to the same interrelationships between crosses I and II in Table 1. That is to say that parent 2 (Tesopaco 76) was consistently higher than parent 1 (Roussalka) for the major agronomic traits as was cross II over cross I. The lower yielding parent 1 (Roussalka) had earlier heading date, earlier maturity date, higher harvest index, and heavier kernel weight than parent 2, but fewer tiller numbers and kernel numbers. The only exception, maturity duration, was two days later for the high yielding parent 2 than the lower yielding parent 1, however the high yielding cross II was 10 days earlier than the lower yielding cross I population. Differences based on the Duncan's New Multiple Range Test were not found between backcross and F_2 generations for any of the traits measured except plant height (Table 2).

Observed mean values for agronomic traits among generations of the cross II population are presented in Table 3. In contrast to the observed mean values for traits among generations of cross I, there were four traits out of nine where the mean values of backcross and F_2 generations exceeded their parental mean values. Plant height and kernel weight of the backcross and F_2 generations exceeded the mean values of the highest

Table 2. Observed mean values for nine agronomic traits among the parents, backcross, and F_2 generations of the cross I population.

	Agronomic traits								
Generations	Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	Kernel weight (g)	Grain yield (g)	Plant height (cm)	Harvest index
P_1	126.8^{b}	184.2^{b}	57.4	6.0	52.4^{b}	5.66^{b}	18.2^{b}	73.4^{d}	42.86
P_2	129.4^{a}	188.2^{a}	58.8	6.8	60.6^{a}	5.62^{b}	25.0^{a}	97.2^{a}	41.02
BC	127.6^{b}	185.2^{b}	57.6	5.6	51.4^{b}	6.11^{a}	22.4^{ab}	81.2^{c}	41.44
F_2	127.4^{b}	185.8^{b}	58.4	6.2	57.6^{ab}	5.92^{a}	20.95^{ab}	88.6^{b}	41.62

Based on Duncan's New Multiple Range Test at .05 level of difference within columns.

P_1 = Roussalka, P_2 = Tesopaco 76

Table 3. Observed mean values for nine agronomic traits among the parents, backcross, and F_2 generations of the cross II population.

	Agronomic traits								
Generations	Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	Kernel weight (g)	Grain yield (g)	Plant height (cm)	Harvest index
P_1	156.0^{a}	202.0	45.4^{c}	7.8^{ab}	70.0	5.034	29.0	84.2^{b}	36.66^{a}
P_2	153.0^{c}	201.4	47.6^{a}	8.8^{a}	66.6	5.008	31.0	81.4^{c}	35.00^{b}
BC	155.4^{ab}	201.6	46.0^{c}	6.8^{b}	73.2	5.156	28.2	90.6^{a}	36.56^{a}
F_2	154.8^{b}	201.8	46.8^{b}	6.8^{b}	69.6	5.138	26.4	90.0^{a}	34.66^{b}

Based on Duncan's New Multiple Range Test at .05 level of difference within columns.

P_1 = Yamhill, P_2 = Aspen

parent, whereas tiller number and grain yield of these generations had lower mean values than the lowest parent. Mean values of the remaining traits of backcross and F_2 fenerations were located between the values of the two parents. The observed mean values for all traits of the two parents were so close that comparison between them would be meaningless.

Simple Phenotypic Correlations among Agronomic Traits

Simple correlation studies were completed on an individual plant basis for the agronomic traits of the F_2 populations of cross I and cross II. The correlation coefficients for the F_2 population of cross I were comprised of 1240 individual plants and are presented in Table 4. Maturity duration showed a high positive relationships with maturity date, kernel weight, plant height, harvest index, grain yield and a high negative relationship with heading date. Minimal relationships were found between maturity duration and tiller number and kernel number. Heading date also showed a high negative relationship with tiller number, grain yield, plant height and kernel weight, and positive relationships with maturity date and harvest index. Grain yield showed high positive relationships for all traits except heading date. Among traits which expressed positive relationships with yield, tiller number had the strongest relationship (r=.826), followed by kernel number (r=.429) and kernel weight (r=.192). Although maturity duration showed a positive relationship with yield, the correlation coefficient was very low (r=.075). Interrelationships among yield components were not detected between tiller number, kernel number and kernel weight, except for a negative relationship between kernel number and weight, however, the correlation

Table 4. Correlation coefficients of nine agronomic traits for the F_2 population of cross I.

Traits	Maturity date	Maturity duration	Tiller number	Kernel number	Kernel weight	Grain yield	Plant height	Harvest index
Heading date	.335	-.256	-.098	.011	-.066	-.082	-.340	.187
Maturity date		.748	-.025	-.041	.208	.166	-.057	.252
Maturity duration			.034	-.040	.273	.075	.166	.156
Tiller number				-.045	.015	.826	.168	.161
Kernel number					-.095	.429	.062	.278
Kernel weight						.192	.118	.255
Grain yield							.193	.364
Plant height								-.359

The correlation coefficients over .062 and .082 are significant at the .05 and .01 levels, respectively.

n=1230, D.F.=1238

was low (r=-.095). The other important agronomic traits, plant height and harvest index showed positive relationships with yield and yield components, but interrelationship between these two traits was negative (r=-.359).

There were 1383 F_2 individual plants included in the simple phenotypic correlations among agronomic traits of the cross II population. Many of the correlation coefficients for this cross (Table 5) showed similar tendencies as reported for the simple correlations in the F_2 population of cross I. However, several exceptions were observed. Heading date expressed a negative relationship with kernel number, while there was essentially no relationship between these traits in cross I. Heading date also showed a negative relationship with harvest index in contrast to a positive response in cross I. Maturity date had highly negative relationships with kernel weight and grain yield in cross II which was the exact opposite of the highly positive relationship with kernel weight and grain yield in cross I. The relationship between maturity duration and kernel number was positive in cross II (r=.129), but negative in cross I (r=-.040). Kernel number had a positive relationship with kernel weight (r=.068) in cross II. while they showed a negative relationship in cross I (r=-.095).

In summerizing the simple phenotypic correlation studies presented in Tables 4 and 5, the results of both crosses I and II showed that heading date had negative relationships with maturity duration, tiller number, and grain yield. Maturity duration had no significant relation with tiller number, but significant positive relationships with kernel weight and grain yield in both crosses. Maturity duration showed a

Table 5. Correlation coefficients of nine agronomic traits for the F_2 population of cross II.

Traits	Maturity date	Maturity duration	Tiller number	Kernel number	Kernel weight	Grain yield	Plant height	Harvest index
Heading date	.485	-.789	-.087	-.113	-.222	-.202	-.812	-.144
Maturity date		.113	-.116	.007	-.086	-.120	-.065	-.062
Maturity duration			.015	.129	.208	.142	.172	.113
Tiller number				-.049	-.022	.815	.225	-.046
Kernel number					.068	.443	.065	.250
Kernel weight						.221	.114	.250
Grain yield							.255	.302
Plant height								-.142

The correlation coefficient over .062 and .082 are significant at the .05 and .01 levels, respectively.

n=1383, D.F.=1381

positive relationship with kernel number in cross II, but none in cross I. The correlation coefficients between maturity duration and grain yield were very low in both crosses I and II being r=.075 and r=.142, respectively. The three yield components showed generally high positive relationships with grain yield; tiller number expressing the strongest coefficients in both cross I (r=.826) and cross II (r=.815). Correlation coefficients between kernel number and grain yield were .429 in cross I and .443 in cross II. Relatively low correlation coefficients were recorded between kernel weight and grain yield in cross I (r=.192) and cross II (r=.221). Interrelationships among yield components were not observed between tiller number, kernel number, and kernel weight in either of the crosses. Significant relationships were found between kernel number and kernel weight in both crosses, however, they were negative (r=-.095) in cross I and positive (r=.068) in the cross II population.

Path Coefficient Analysis

Among nine agronomic traits, five traits were selected for path coefficient analysis which permitted the separation of the correlation coefficient into components of direct and indirect effects (Dewey and Lu, 1959). Grain yield was selected as the resultant trait, and maturity duration, tiller number, kernel number, and kernel weight were the traits chosen to study their association with yield. Following the same procedure as for the simple correlation study, path coefficients were determined separately for the F_2 populations of cross I and cross II. The path coefficient analysis of cross I is presented in Table 6. The

Table 6. Path coefficient analysis for four agronomic traits with grain yield in the F_2 population of cross I.

Traits	Association with yield (r)	Direct effect (b')	Indirect effects by way of: Maturity duration	Tiller number	Kernel number	Kernel weight
Maturity duration	.075	.005		.029	-.020	.061
Tiller number	.826	.845	.000		-.022	.003
Kernel number	.429	.489	.000	-.038		-.021
Kernel weight	.192	.225	.001	.031	-.046	

R^2 = .952

association of maturity duration with grain yield was very low (r=.075) compared to the yield components with grain yield. The direct effect of maturity duration on grain yield (b'=.005) was smaller than the simple correlation coefficient (r=.075) for these two traits. The indirect effects of maturity duration on tiller number, kernel number, and kernel weight were .029, -.020, and .061, respectively. The direct effect of tiller number on grain yield was higher (b'=.845) than the simple correlation coefficient (r=.826); however, indirect effects for maturity duration, kernel number, and kernel weight were extremely low being .000, -.022, and .003, respectively. Kernel number also expressed a higher direct effect (b'=.489) with grain yield than the simple correlation coefficient (r=.429). Indirect effects of kernel number on tiller number and kernel weight were -.038 and -.021, respectively, and as was shown for tiller number, there was no indirect effect of kernel number with maturity duration. The direct effect of kernel weight to grain yield was .225, a higher value than the simple correlation (r=.192), and indirect effects of kernel weight with maturity duration, tiller number, and kernel number were .001, .013, and -.046, respectively.

The path coefficient analysis for the F_2 population of cross II is presented in Table 7. Similar results were observed for several of the comparisons in the cross II population with the cross I data reported above; however, there were some differences. The direct effect of kernel weight on grain yield (b'=.203) was lower than the simple correlation (r=.221) and the indirect effects of kernel weight on tiller number and kernel number were -.019, and .032, respectively. In addition to these differences, the indirect effect of maturity duration on kernel number

Table 7. Path coefficient analysis for four agronomic traits with grain yield in the F_2 population of cross II.

Traits	Association with yield (r)	Direct effect (b')	Indirect effects by way of Maturity duration	Tiller number	Kernel number	Kernel weight
Maturity duration	.142	.027		.013	.060	.042
Tiller number	.815	.842	.000		-.023	-.004
Kernel number	.443	.467	.003	-.041		.014
Kernel weight	.221	.203	.006	-.019	.032	

$R^2 = .942$

in cross I was a negative value (-.020), but was posirive in cross II (.060). The indirect effect of tiller number on kernel weight was positive in cross I while negative in cross II. Kernel number also expressed differences in indirect effect on kernel weight between the two crosses. Differences between the two populations, in the path coefficient analysis, were so small that it is hard to distinguish real differences between them, especially, the indirect effects, even though positive and negative values were observed.

DISCUSSION

Many scientists have emphasized grain filling duration as a selection criterion in increasing yield potential for cereal crops. Some researchers obtained positive relationships of grain filling duration with yield (Watson et al., 1963; Fischer and Kohn, 1966), while others did not find relationships between these two traits (Askel and Johnson, 1961; Nass and Keiser, 1975). Environmental effects, especially, air temperature have a marked influence on the variation of grain filling duration (Marcellos and Single, 1972). Rasmusson et al. (1979) attempted to quantify the variation of grain filling duration with the hope of increasing grain yield in barley, but they were unable to satisfactorily meet their objectives.

The other important aspect for breeding cereal crops is to use the yield components as selection tools for yield improvement. The negative interrelationships among yield components have discouraged scientists from using these traits in their breeding programs, however, long range yield improvement should include the close evaluation of yield components as they influence yield (Kronstad and Foote, 1964; McNeal et al., 1978).

As described above, several studies were conducted to determine the effects of grain filling duration on yield, and the feasibility of using a components approach for crop improvement. If grain filling duration has a positive relationship with grain yield, it might also have relationships with at least one of the yield components and possibly other agronomic traits such as plant height and harvest index.

Two populations were created for this study, one an early population from the cross Roussalka/Tesopaco 76, and the other a later population from the cross Yamhill/Aspen. Comparative studies were conducted for nine selected agronomic traits between the two populations (Tables 1). Significant differences between the two populations were found for all traits except plant height. The early population, cross I, showed relatively longer grain filling duration, heavier kernel weight, and higher harvest index than the late population, cross II; however, cross I had an earlier maturity date, lower tiller and kernel numbers and less grain yield than cross II. Similar results were observed in the Fonseca and Patterson (1968) study of winter wheat when considering heading date and yield components. Askel and Johnson (1961) reported that in barley a longer sowing-to-heading period which is negatively associated with heading-to-ripening period, had more kernel numbers per spike and higher yields. Grain filling duration has a definite influence on increased kernel weight (Tables 4 and 5). This supports the theory that longer grain filling duration allows more assimilates to be transferred from the green plant organelles into the kernel. However, grain filling duration did not show any effect on the formation of tiller number and kernel number in this comparative study of cross I and II. Heavier kernel weight does not seem to be a major contributor to grain yield when combined with fewer tiller and kernel numbers as noted in the early maturing, lower yielding cross I. Tiller and kernel numbers, however, seem to be the main factors for increased grain yield in cross II although this population has a short grain filling duration and lower kernel weight compared to cross I.

Growth stages of crop plants are commonly divided into three stages, vegetative, reproductive, and grain filling period (Evans and Wardlaw, 1976). Tiller number is mainly determined in the vegetative period, potential kernel size is largely determined in the reproductive period, and final yield is realized in the grain filling period. Evans and Wardlaw (1976) stated that all three stages must be balanced to obtain stable high yield. From the results of comparative studies between the two populations, earlier heading in the cross I population reduced vegetative and reproductive periods which might have reduced production of tillers and kernels and, therefore, potential yield in this space planted condition. In considering agronomic traits, the longer maturity date of cross II increased grain yield. Although differences in plant height between the two populations were not large, the taller population in this comparison did have higher yield. The higher observation for harvest index of the cross I population was associated with a lower yield than for cross II.

Generally, there were few differences noted among parents and generations for traits within cross I and cross II (Tables 2 and 3). This facts is partly a consequence of the parents within a population having similar heading dates. This was surprising from fall seeding of spring, spring X winter, and winter parents. We would have expected much wider heading dates between the parental cultivars due to their origin and growth habit.

Phenotypic correlation coefficients among traits of F_2 populations in cross I and II were summarized in Tables 4 and 5, respectively. There were a number of interesting relationships among the traits in these comparisons. Negative relationships were found between heading date and maturity duration in cross I (r=-.256) and cross II (r=-.789). Certainly, early heading date was associated with longer maturity duration. Interestingly, heading date shows negative relationships with grain yield in both cross I (r=-.082) and cross II (r=-.202). Negative relationships are also found between heading date and tiller number in cross I (r=-.098) and cross II (r=-.087). Since tiller numbers have strong positive relationships with yield in cross I and II of r=.826 and r=.815, respectively, the negative relationships between heading date and grain yield are assumed to be largely affected by tiller number. These contradictory results, which show negative effects of heading date on tiller number within populations, seem to be due to a genetic limitation in these particular environmental conditions to express tiller number within crosses I and II.

Maturity duration related positively with grain yield, however, correlation coefficients were quite small in both crosses I and II (r= .075 and r=.142), respectively. These positive relationships indicate that limitations exist in utilizing maturity duration as a factor for improving grain yield in early generation selection, at least based on the populations in this study. Actually, the cross I population expressing long grain filling duration had lower grain yield than the cross II population with relatively short grain filling duration. No relationship was noted between maturity duration and tiller number, as expected, since grain filling duration occurs after tillering stage. Consistent results were obtained for the relationships between maturity duration and kernel weight within the cross I and cross II populations. These positive relationships indicate that longer maturity duration contributes more assimilates into the grain, thus an increase in kernel weight. However, maturity duration had no association with kernel number in cross I, while being a positive relationship in cross II. It was felt that lack of a significant relationship between maturity duration and kernel number in cross I accounted for its lower yield although this population had a higher relationship between maturity duration and kernel weight (r=.273) than cross II (r=.208). These association between maturity duration and kernel number, kernel weight, and grain yield in the F_2 populations of both crosses are shown in Appendix Figure 1. It can be clearly seen that kernel weight increases consistently as maturity duration increases, however the limiting factor to grain yield is kernel number which remained constant during the entire maturity duration in cross I. In cross II, the limiting factor to grain yield appears to be maturity duration; as it increases, kernel weight and kernel number also increase continuously, together with yield. Although the period of maturity duration of cross II is very short compared to that of cross I, there was a strong positive relationship with yield and both kernel weight and kernel number contributed significantly; however, kernel number had a strong influence overall than kernel weight. One point worthy of discussion is the consistency of the kernel number curve with the grain yield curve throughout the period of maturity duration in the cross I population. The cross I population had a longer grain filling duration and heavier kernel weight but lower grain yield, partly at least, because of fewer kernel numbers. The reduced kernel number might be attributed to an earlier heading date which may restrict the potential number of productive flowers in the reproductive period which extends from floral induction and the initiation of inflorescence to anthesis and fertilization. Evans and Wardlaw (1976) stated that conditions during this stage determine the rate and extent of floral differentiation, and therefore the potential storage capacity of the crop. Consistent interrelationships among yield components were not detected between tiller number, kernel number, and kernel weight in either of the populations. The relationships between kernel number and kernel weight were small and expected negatively in cross I (r=-.095) and positively in cross II (r=.068). In correlation studies, negative relationships among yield components restrict their use as selection tools for increasing yield potential in crop breeding (Fonseca and Patterson, 1968). However, Adams (1967) has demonstrated, in space planting studies of navy beans, that the negative correlation among yield components is caused by competitional forces in the course of developmental processes rather than genetic interrelationships. In the present study, negative relationships among yield components were of low magnitude. These results are strongly supported by the research of Adams (1967). Further, reference will be made to this subject in the path coefficient analysis. All agronomic traits were positively associated with grain yield with the exception of heading date in both populations and maturity date in cross II. The most important component for grain yield was tiller number in both populations of the cross I (r=.826) and cross II (r=.815), which corresponds to the observation of Fonseca and Patterson (1968), and Hsu and Walton (1971). It was interesting to note the highly positive relationship between harvest index and grain yield within each population although this relationship was not observed in comparisons of cross I and cross II. It may be possible to use harvest index as a criterion for selecting higher potential within segregating populations. Johnson and Biever (1966) indicated that the taller wheat plants generally produced higher grain yield if lodging was not a problem. The present study also showed a positive relationship of plant height with grain yield in both populations. In considering the relationships of grain yield and other important agronomic traits for both populations, tiller number had the highest correlation value with grain yield, followed by kernel number, and kernel weight. Maturity duration expressed the least correlation with yield of any measured character in this experiment. These results indicate that although there was a positive relationship between maturity duration and grain yield within populations, the contribution of maturity duration was small compared to other agronomic traits.

Path coefficient analysis separates simple correlations of selected traits into direct and indirect effects on grain yield. The direct effects of yield components on yield were consistently higher than the simple correlations for all traits in both populations with the exception of kernel weight in cross II. Maturity duration, however, expressed a lower direct effect than simple correlation for yield (Tables 6 and 7) indicating that it has no influence on grain yield, while the yield components expressed a contribution. Path coefficients show that in cross I, maturity duration contributed most of its effects to grain yield by way of kernel weight (Table 6), while kernel number was more important in cross II (Table 7). Therefore, the following conclusions can be drawn for the relationships of maturity duration with yield and yield components: First, maturity duration has a positive relationship with grain yield within populations, however, the effects are generally small. Second, maturity duration influences yield indirectly by way of kernel weight and kernel number in the late population (cross II). Third, Maturity duration influences yield only by way of kernel weight in the early population (cross I). Fourth, there was no indirect effect of maturity duration for yield components in either population.

The other indirect effects among yield components were shown both positively and negatively, however, they were very small and insignificant compared to the direct effects. Interpretation of the results from this experiment would lead to the conclusion that there were neither interactions among yield components arising from phenotypic competition nor any genotypic interaction between them. Results of the present space planted study strongly supports the conclusion of Adams (1967) in terms of yield component interactions.

Environmenatal conditions, especially air temperature, during the crop season of this experiment, caused variation in maturity date which, in turn, affected maturity duration. The range of maturity date of cross I, from June 23rd to July 14th, was 22 days. During this period, the average maximum and minimum air temperature were 22.7, 9.8 C, respectively, while the range of maturity date of cross II from July 17th to 26th was only 10 days. The average maximum and minimum air temperature during these 10 days were 28.9,12.6 C, respectively. Furthermore, ninety percent of the maturity dates were distributed within only 4 days from July 19th to 22nd, 1980.

SUMMARY AND CONCLUSION

The objective of this study was to study the relationships of grain filling duration with grain yield and yield components with the hope that cereal breeders could optimize the duration of grain filling period for increased yield potential. A secondary objective was to determine the interrelationships among yield, yield components and other important agronomic traits such as heading date, plant height and harvest index. Establishment of relationships of agronomic traits with yield would be useful for making phenotypic selection, a common practise by most cereal breeding programs.

To obtain this information, two winter wheat cultivars (Roussalka and Yamhill) and two advanced lines (Tesopaco 76 and Aspen) were used to create the two base populations. The early population (cross I) was obtained from the cross Roussalka/Tesopaco 76 and the late population (cross II) from the cross Yamhill/Aspen. Parents, backcrosses, and F_2 generations of each population were space planted in a split plot design at East Farm adjacent to the Horticulture Farm located one mile east of Corvallis, Oregon. Crosses (I and II) were used as main plot treatments and generations (parents, backcross, and F_2) as subplot treatments. Nine agronomic traits, heading date, maturity date, maturity duration, tiller number, kernel number, kernel weight, grain yield, plant height, and harvest index were measured on an individual plant basis.

Analysis of variance was computed to determine the differences between crosses and among generations within cross I and cross II. Total mean values of agronomic traits of cross I and cross II were calculate to evaluate the differences between crosses. Generation mean values of agronomic traits within cross I and cross II were also obtained to observe differences among generations. Duncan's New Multiple Range Test was used to determine significant levels of differences among means. Simple phenotypic correlations were computed among nine traits on an individual plant basis. Path coefficient analysis was performed to determine direct and indirect effects of selected agronomic traits on yield. Maturity duration, tiller number, kernel number, and kernel weight were selected for this path coefficient study. From the experimental results in this study, conclusion were drawn as follows:

1. Extension of grain filling period had positive relationships with grain yield within cross I and cross II populations. The late population, cross II, had a higher positive relationship than cross I, however generally low correlation coefficients were recorded for grain filling period with yield compared to other agronomic traits in both cross I and cross II populations.
2. Grain filling duration had most of its influence on increased grain yield indirectly by way of kernel weight in both populations (crosses I and II), and also indirectly to a marked degree by way of kernel number in the cross II population.
3. Grain filling duration showed a high negative relationship with heading date. Generally, the earlier heading plants had a long grain filling duration while late heading plants had a short grain filling period.
4. Grain filling duration were greatly influenced by environmental factors, especially air temperature. Maturity dates in the later cross II population were greatly accelerated from exposure to

higher temperature compared to cross I.

5. Yield components generally showed high positive relationships with grain yield. Among these traits, tiller number was the most important component for grain yield, followed by kernel number, and kernel weight.
6. Negative interrelationships among yield components were noted but insignificant in this study, with the exception of the negative relationship between kernel number and kernel weight in the cross I population.
7. Tiller number and kernel number were the most important factors in determining grain yield in this study. The cross I population was earlier heading, had longer grain filling duration, heavier kernel weight, and higher harvest index, but lower tiller numbers, lower kernel numbers, and lower total grain yield.
8. Plant height and harvest index showed high positive relationships with grain yield.

LITERATURE CITED

Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, Phaseolus vulgaris Crop Sci. 7:505-510.

Archbold, H. K. 1942. Physiological studies in plant nutrition XIII. Experiments with barley on defoliation and shading of the ear in relation to sugar metabolism. Ann. Bot. 6:487-531.

_____________. 1945. Some factors concerned in the process of starch storage in the barley grain. Nature (London) 156:70-73.

Askel, R., and L. P. V. Johnson. 1961. Genetic studies in sowing-to-heading and heading-to-ripening periods in barley and their relation to yield and yield components. Can. J. Genet. Cytol. 3:242-259.

Chinoy, J. J. 1947. Correlation between yield of wheat and temperature during ripening of grain. Nature 159:442-444.

Daynard, T. B., J. W. Tanner, and W. G. Duncan. 1971. Duration of the grain filling period and its relation to grain yield in corn, Zey mays L. Crop Sci. 11:45-48.

_____________ and L. W. Kannenberg. 1976. Relationships between length of the actual and effective grain filling periods and grain yield of corn. Can. J. Plant Sci. 56:237-242.

Dewey, D. R. and K. H. Lu. 1959. A correlation and path coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

____________ and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Ads. in Agronomy 28:361-405.

Evans, L. T. and I.F. Wardlaw. 1976. Aspects of the comparative physiology of grain yield in cereals. Ads in Agronomy 28:301-359.

Fisher, R. A. and G. D. Kohn. 1966. The relationships of grain yield to vegetative growth and post flowering leaf area in the wheat crop under conditions of limited soil moisture. Aust. J. Agric. Res. 17:281-295.

Fonseca, s. and F. L. Patterson. 1968. Yield component heritabilities and interrelationships in winter wheat (Triticum aestivum L.) Crop Sci. 8:614-617.

Grafius, J. E. 1956. Components of yield in oats: A geometrical interpretation. Agron. J. 48:419-423.

____________ and G. A. Wiebe. 1959. Expected genetic gain in yield in small grain: A geometrical interpretation. Agron. J. 48:419-423.

Hanway, J. J. and W. A. Russell. 1969. Dry matter accumulation in corn (Zea mays L.) plants: Comparison among single cross hybrids. Agron. J. 61:947-951.

Hsu, P. and P. D. Walton. 1971. Relationships between yield and its components and structure above the flag leaf in spring wheat. Crop Sci. 11:190-193.

Johnson, V. A., J. W. Schmidt, and W. Mekasha. 1966. Comparison of yield components and agronomic characteristics of four winter varieties differing in plant height. Agron. J. 58:438-441.

____________, K. J. Biever, A. Haunold, and J. W. Schmidt. 1966. Inheritance of plant height, yield of grain, and other plant and seed characteristics in a cross of hard red winter wheat, Triticum aestivum L. Crop Sci. 6:336-338.

Khalifa, M. A. 1973. Effects of N on leaf area index, leaf area duration, net assimilation rate, and yield of wheat. Agron. J. 65:253-256.

Knott, D. R. and B. Talukdar. 1961. Increasing seed weight in wheat and its effect on yield, yield components, and quality. Crop Sci. 11:280-283.

Kronstad, W. E. and W. H. Foote. 1964. General and specific combining ability estimates in winter wheat (Triticum aestivum Vill., Host). Crop Sci. 4:616-619.

Marcellos, H. and W. V. Single. 1971. Quantitative responses of wheat to photoperiod and temperature in the field. Aust. J. Agric. Res. 22:343-357.

____________ 1972. The influence of cultivar, temperature, and photoperiod on post-flowering development of wheat. Aust. J. Agric. Res. 23:533-540.

McNeal, F. H. 1960. Yield components in a Lemni X Thatcher wheat cross. Agron. J. 52:348-349.

____________, C. O. Qualset, D.E. Baldridge, and V. R. Stewart. 1978. Selection for yield and yield components in wheat. Crop Sci. 18: 795-799.

Mohiuddin, and L. I. Croy. 1980. Flag leaf and peduncle area duration in relation to winter wheat grain yield. Agron. J. 72:299-301.

Nass, H. G. and B. Reiser. 1975. Grain filling period and grain yield relationships in spring wheat. Can. J. Plant Sci. 55:673-678.

Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Regression, analysis of variance, and experimental designs. Richard D. Irwin, Inc. Homewood, Illinois.

Rasmusson, D. C. and R. Q. Cannell. 1970. Selection for grain yield and components of yield in barley. Crop Sci. 10:51-54.

______________, I. McLean, and T. L. Tew. 1979. Vegetative and grain filling periods of growth in barley. Crop Sci. 19:5-9.

Rosielle, A. A. and K. J. Frey. 1975. Application of restricted selection indices for grain yield improvement in oats. Crop Sci. 15:544-547.

Steel, R. G. D. and J. H. Torrie. 1960. Principle and procedures of statistics. McGraw-Hill, Inc. New York, N. Y.

Simpson, G. M. 1968. Association between grain yield per plant and photosynthetic area above the flag leaf node in wheat. Can. J. Plant Sci. 48:253-260.

Sims, H. J. 1963. Changes in the hay production and the harvest index of Australian oat varieties. Aust. J. Exp. Agr. Anim. Husb. 3:198-202.

Singh, I. O. and N. C. Stoskopf. 1971. Harvest index in cereals. Agron. J. 63:224-226.

Spiertz, J. H. J., B. A. Tenhag, and L. J. P. Kupers. 1971. Relation between green area duration and grain yield in some varieties of spring wheat. Neth. J. Agric. Sci. 19:211-222.

______________. 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. Neth. J. Agric. Sci. 22:207-220.

Watson, D. J., G. N. Thorne, and S. A. W. French. 1958. Physiological causes of differences in grain yield between varieties of barley. Ann. Bot. (N.S.) 22:321-352.

__________, __________, and __________. 1963. Analysis of growth and yield of winter and spring wheats. Ann. Bot. (N.S) 27:1-22.

Welbank, P. J., S. A. W. French, and K. J. WITTS. 1966. Dependence of yields of wheat varieties on their leaf area duration. Ann. Bot. (N.S.) 30:291-299.

Yap, J. C. and B. L. Harvey. 1971. Relation between grain yield and photosynthetic parts above the flag leaf node in barley. Can. J. Plant Sci. 52:241-246.

APPENDICES

APPENDIX TABLE 1. Pedigrees and descriptions of lines and cultivars.

Roussalka(S-13/Ban 54). An early, semi-dwarf, and awned winter wheat with red grain color. Developed in Bulgaria.

Yamhill(Heines VII/Redmond(Alba)). A late, medium height, and soft white awnless winter wheat. Released by Oregon State University.

Tesopaco 76(INIA "S"/SOTY//CZHO). A mid-early flowering, semi-dwarf, awned spike, hard red spring wheat. Developed and named by the International Maize and Wheat Improvement Center in Mexico.

Aspen(HN4/4/KT54A/N10B//KT54B/3/NAR). A mid-late, semi-dwarf. awned spike, soft red winter advanced line. Named by Oregon State University from the International Spring X Winter Wheat Program.

Appendix Table 2. Observed mean square values for nine agronomic traits involving parents, backcrosses, and F_2 generations for two spring X winter wheat crosses.

Source of Variation	D.F.	Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	100 kernel weight	Grain yield	Plant height	Harvest index
		Mean Squares								
Replication	4	.29	6.71	6.23	2.40	205.16	.12	2.96	6.91	33.59
Crosses	1	7290.00**	2512.23**	1243.23**	19.60*	2059.22**	5.54**	592.90**	21.03	361.80**
Error	4	.31	4.54	7.41	1.35	27.79	.01	17.53	6.84	2.84
C.V. (%)		3.1	1.2	5.2	17.0	8.4	1.8	16.9	3.0	4.4

*Significant at the five percent probability level.

**Significant at the one percent probability level.

Appendix Table 3. Observed mean square values for nine agronomic traits among the parents, backcross, and F_2 generations of cross I.

Source of Variation	D.F.	Mean Squares								
		Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	100 kernel weight	Grain yield	Plant height	Harvest index
Replication	4	.18	10.32	13.20	2.33	98.75	.05	6.18	.58	16.54
Generations	3	6.26**	14.45**	4.13	1.25	94.73*	.27*	56.05*	517.93**	3.13
Error	12	.31	2.33	2.80	.46	25.15	.01	10.68	4.48	1.79
C.V. (%)		.4	.8	2.9	11.0	9.0	1.9	15.6	2.5	3.2

*Significant at the five percent probability level.

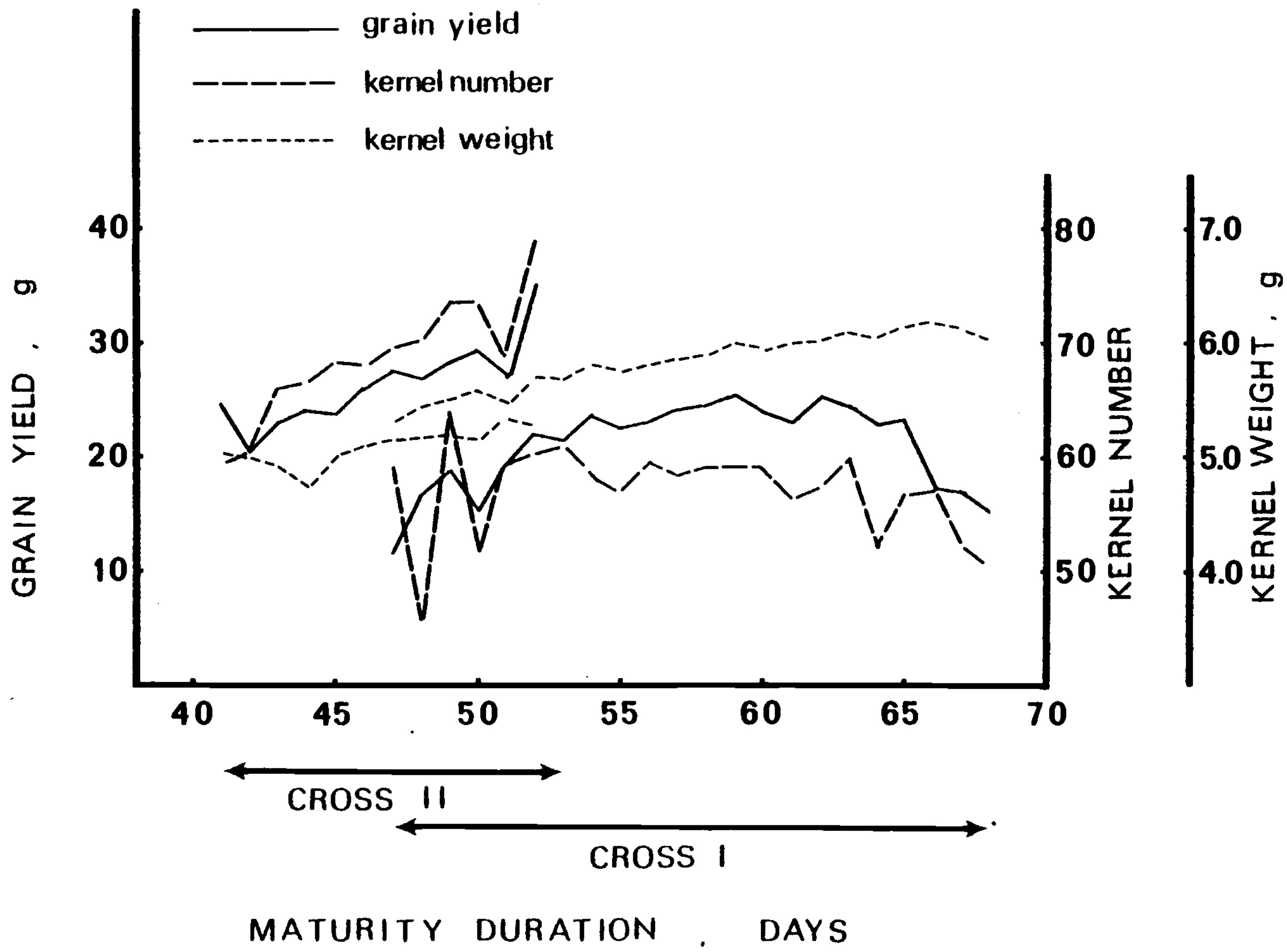
**Significant at the one percent probability level.

Appendix Table 4. Observed mean square values for nine agronomic traits among the parents, backcross, and F_2 generations of cross II.

Source of Variation	D.F.	Heading date	Maturity date	Maturity duration	Tiller number	Kernel number	100 kernel weight	Grain yield	Plant height	Harvest index
		Mean Squares								
Replication	4	.43	.93	.43	1.43	134.20	.09	14.33	13.17	19.90
Generations	3	8.40**	.33	4.58**	4.58*	36.45	.02	18.18	100.58**	5.39*
Error	12	.36	.13	.29	.79	20.20	.04	14.56	1.54	.99
C.V. (%)		.5	.2	1.2	11.8	6.4	3.7	15.4	1.4	2.7

*Significant at the five percent probability level.

**Significant at the one percent probability level.



Appendix Figure 1. Association of grain yield, kernel weight, and kernel number with maturity duration for the F_2 populations in cross I and cross II.