

Nature of Gene Action for Duration of Grain filling in Crosses of Winter and Spring Wheats (*Triticum aestivum* L. em Thell)

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春·秋 播性 小麦品種間 交雜에서 登熟期間을 지배하는 遺傳子 作用에 關한 研究

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ABSTRACT

Breeders have concerned with the nature of gene action controlling the duration of grain filling period to combine early maturity and acceptable grain yield to fit wheat into multiple cropping systems. The 4 x 4 complete diallel set of F_1 , F_2 and $1/2 (BC_1 + BC_2)$ in crosses of winter and spring wheat cultivars was made to determine the nature of gene action involved for duration of grain filling period. Using the Jinks-Hayman model, no maternal effects were noted nor were any non-allelic interactions observed for total duration of grain filling and lag period. The actual grain filling period was influenced to some degree by such interactions. The spring cultivars Red Bobs and Siete Cerros also appeared to have more dominant genes for longer total duration of grain filling and lag period. In contrast, the winter parents Yamhill and Hyslop had more dominant genes for the longer actual grain filling period. The genes appeared to be independently distributed among the parents.

INTRODUCTION

Grain filling is the result of the translocation of photosynthate from source to sink. The genetic control for assimilate distribution is important for increased rate of grain filling in wheats.

The time and duration of heading, flowering, grain filling and physiological maturity are important latter stages of the life cycle in determining earliness and subsequent grain yield in winter and spring wheats (Bingham¹); Evans⁸); Nass and Reiser¹⁹); Spiertz *et al*²³); Wiegand and Cuellar²⁷); Choi³). Total dura-

tion of grain filling period is defined as the length from inflorescence emergence to physiological maturity and is divided into lag period from heading to flowering and actual grain filling period from flowering and actual grain filling period from flowering to physiological maturity.

Research results indicated that genetic differences between wheat cultivars exist for both duration and rate of grain filling. In most cases, duration of grain filling was more important in contributing to higher grain yield than was rate of grain filling. For example, Evans⁸), working with wheat, suggested that duration was a more powerful determinant of yield than the

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rate of grain filling. In contrast, Nass and Reiser⁹⁾ and Choi³⁾ working with wheat, Czaplowski⁶⁾ with barley, and Fussell and Pearson¹⁰⁾ with pearl millet found that grain yield was more closely related to the rate of grain filling than to the duration of grain filling.

Physiological maturity date is an end point of the life cycle of a wheat plant. The time of physiological maturity can be used to monitor earliness more exactly than other stages of development in life cycle, thereby providing an effective way to maximize grain yield for a specific maturity range³⁾. In a study on the anatomical and physiological development of wheat and barley kernels, Lingle¹⁸⁾ found that in wheat physiological maturity preceded the collapse of the vascular tissue and chalaza by three days, but in barley physiological maturity coincided with the collapse of these tissues. Hanft and Wych¹³⁾ reported that the mean number of days from anthesis to 95% maximum kernel dry weight and to 100% maximum kernel dry weight (physiological maturity) ranged from 22.3 to 33.7 and 27.9 to 40.1, respectively, depending upon planting date and genotype for hard red spring wheats.

The time, duration and rate of grain filling are influenced by environmental factors. Gebeyehou *et al*¹¹⁾ working with durum wheat indicated that longer duration of grain filling was associated with lower temperatures, lower rates of grain filling, and lower grain weights. The higher rate of grain filling was associated with higher air temperatures during the grain filling period. Similarly Sofield *et al*²²⁾ found that rate of grain filling in common wheat was higher at higher temperatures. Grafius¹²⁾ concluded that maximum grain size was determined by the size of the lemma and palea and that actual grain size would be reduced by competitive environmental factors in barley and wheat.

The influence of temperature on the components of grain yield in wheat is known to differ depending on plant growth stage. In studies on yield and development of winter wheat at elevated temperatures, Johnson and Kanemasu¹⁴⁾ reported that increasing temperatures at any of the growth stages

advanced plant development relative to control plants. High temperature treatments at terminal spikelet formation reduced kernels per spike from 19.1 to 15.4, at least partly by reducing grainbearing spikelets per spike. An increase in kernel weight was associated with the reduction in kernels per spike so final yield was not significantly reduced. However, an average reduction of 2.4 kernels per spike by the 101 thermal units $[TU = \sum(\max^{\circ}C + \min^{\circ}C)/2]$ treatment at anthesis significantly reduced grain yield. At the milk stage, average kernel weights were generally reduced by high temperatures.

Thus the pace of crop development increases as temperatures increase, usually resulting in a shorter duration between given growth stages, which can influence yield. For example, when the duration of the grain filling period is shortened by high temperatures, kernel weight is generally reduced Chinoy²⁾, Wiegand and Cuellar²⁷⁾. Fischer and Maurer⁹⁾ postulated that preanthesis temperatures influenced yield components by affecting photosynthate supply, and primarily spike growth duration.

The time, duration and rate of grain filling, which are controlled by genetic and environmental factors, are recognized as important in determining grain yield in cereals as noted from the literature. However, very little information is available concerning the nature of inheritance. An understanding of mode of gene action controlling the duration of grain filling could provide valuable information to be applied in breeding programs.

The objective of this study was to determine the nature of gene action involved for total duration of grain filling from heading to physiological maturity, lag period from heading to flowering and actual grain filling period from anthesis to physiological maturity in crosses of winter and spring wheat cultivars.

MATERIALS AND METHODS

Two winter, 'Hyslop' (HYS) and 'Yamhill' (YMH), and two spring cultivars, 'Siete Cerros' (7C) and 'Red Bobs' (RB), were used as parents in this study. They differ in sources of origin, growth habit, heading and

flowering dates, grain filling and physiological maturity, components of yield and grain yield. Also differences in vernalization requirement, photoperiod and temperature responses can be observed among the cultivars.

A 4 x 4 diallel cross with reciprocals was made to produce the F1 generation. The F2 generations from reciprocal crosses were obtained from selfing the F1 plants. Backcross populations were obtained by crossing the F1's to their respective winter and spring parents. Parents, F1's, F2's, BC1's and BC2's were planted on November 1st, 1979. The experimental design was a randomized complete block with four replications. The experimental material was composed of two rows for each parent (100 plants), two rows per F1 (100 plants), four rows for the backcrosses (200 plants) and eight rows for the F2 populations (400 plants). Rows were planted 30 cm apart and were 2.5 m long. Within the row, plants were spaced 20 cm apart. Ninety kg/ha of N was added as 16-20-10 of the formulation N-P₂O₅-K₂O in a preplant application. This was followed by broadcasting 46 kg/ha of N as urea at jointing stage in the spring. An application of the herbicide Karmex at the rate of 1.68 kg/ha was carried out to control weeds, mainly the grass *Poa annua*. Manual weeding was performed in the early spring. Barley plants were seeded around the border of the experiment to insure equal competition between plants. Barley was also planted in early spring during the growing season to occupy the space where experimental wheat plants were missing. The experimental site was located on the East Farm near Corvallis, Oregon. The soil type is a sandy loam.

The following characters were recorded on an individual plant basis. The per plant values were averaged due to the unequal sample sizes, and the analysis was conducted on the basis of plot means.

Physiological maturity date was recorded when the first spike of the plant lost its green color, and was noted at two-day intervals for all the treatments. Duration of grain filling period was calculated as days from heading to physiological maturity, which was divided into two periods a) lag period from heading

to flowering, and b) actual grain filling period from flowering to physiological maturity.

An analysis of variance of the 4 x 4 complete diallel set of F1, F2 and [(BC1 + BC2) crosses of wheats was conducted to determine if there was a maternal effect for duration of grain filling period. Further analysis of variance of the estimates of variance of the estimates of variance (Vr) and parent-offspring covariance (Wr) for each of the four arrays after averaging over reciprocal crosses of the diallel set was made and graphed using the model proposed by Jinks and Hayman (1953) to determine the nature of gene action involved for duration of grain filling period.

RESULTS AND DISCUSSION

The analysis for variance (Vr) and parent-offspring covariance (Wr) for four arrays of the 4 x 4 diallel crosses was conducted to obtain more detailed information about the nature of gene action controlling duration of grain filling period from heading to physiological maturity.

Table 1. Mean square values of the estimates of maternal effect in a 4 x 4 complete diallel set of F1, F2 and ½(BC1+BC2) crosses for duration of grain filling period in selected wheat populations grown on the East Farm near Corvallis, Oregon, 1979-80.

Source of variation	F1s	F2s	½(BC1+BC2)s
Reciprocal cross differences	.500	28.125	3.125
Block differences	48.333**	25.458	33.375**

**Significant at the .01 probability level.

Estimates of maternal effect

Mean square values of the estimates of maternal effects in the F1's, F2's and ½(BC1 + BC2)'s of the crosses for total duration of grain filling period from heading to physiological maturity are presented in Table 1. No differences in reciprocal crosses were observed, suggesting no maternal effect exerted for

grain filling period. For lag period from heading to flowering there were no differences between the reciprocal crosses nor blocks (Table 2). For duration of actual grain filling period from flowering to physiological maturity, differences in the reciprocal crosses were noted only for F2 populations (Table 3). Thus mean values averaged from the reciprocal crosses were used in Vr - Wr graphic analysis in this study.

Table 2. Mean square values of the estimates of maternal effect in a 4 x 4 complete diallel set of F1, F2 and 1/2(BC1+BC2) crosses for lag period from heading to flowering in selected wheat populations grown on the East Farm near Corvallis, Oregon, 1979-80.

Sources of variation	F1s	F2s	1/2(BC1+BC2)s
Reciprocal cross differences	18.000	2.000	2.531
Block differences	1.333	7.500	1.615

Table 3. Mean square values of the estimates of maternal effect in a 4 x 4 complete diallel set of F1, F2 and 1/2(BC1+BC2) crosses for actual grain filling period from flowering to physiological maturity in selected wheat populations grown on the East Farm near Corvallis, Oregon, 1979-80.

Sources of variation	F1s	F2s	1/2(BC1+BC2)s
Reciprocal cross differences	12.500	45.125*	1.531
Block differences	42.333	27.458*	34.865**

* Significant at the .05 probability level.

** Significant at the .01 probability level.

Vr - Wr graphic analysis

The Vr - Wr graphic analyses for the nature of gene action controlling duration of grain filling period for the three populations are illustrated in Figures 1 through 3. When total duration of grain filling period is considered, as in Figure 1, estimates of regression coefficients indicate that Wr is related to Vr for F1's, F2's and 1/2 (BC1 + BC2)'s. Nonallelic interaction is not involved and the genes controlling the trait are

considered to be independently distributed among the parents. More additive gene action with some partial dominance is involved as the intercept is positive on the Vr axis for all the generations. The relative order of the points along the regression line also indicates the distribution of dominant and recessive genes among the parents for duration of grain filling period. Spring wheats Red bobs and Siete Cerros have more dominant genes than winter wheats, Yamhill and Hyslop. Red Bobs also has more dominant genes than Siete Cerros.

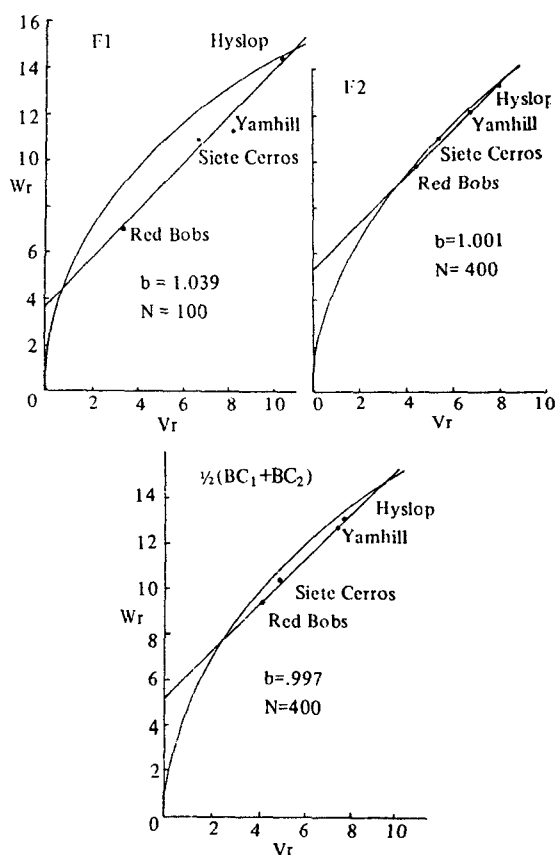


Fig. 1. Vr - Wr graphic analysis of gene action for duration of grain filling period of a 4 x 4 diallel set of F1, F2 and 1/2(BC1+BC2) crosses planted on November 1st, 1979. East Farm near Corvallis, Oregon, 1979-80.

A similar situation is found for the lag period as noted in Figure 2. Estimates of Wr are closely related

to those of V_r for F_1 's, F_2 's and $1/2(BC_1 + BC_2)$'s. Nonallelic interaction is not involved and the genes controlling lag period appear to be independently distributed among the parents. Additive gene action and some partial dominance of a longer lag to shorter lag period are involved as reflected by the positive intercept on the W_r axis for all the generations.

Spring wheats Red Bobs and Siete Cerros appear to have more dominant genes than winter wheats Yamhill and Hyslop. Red Bobs may have more dominant genes than Siete Cerros.

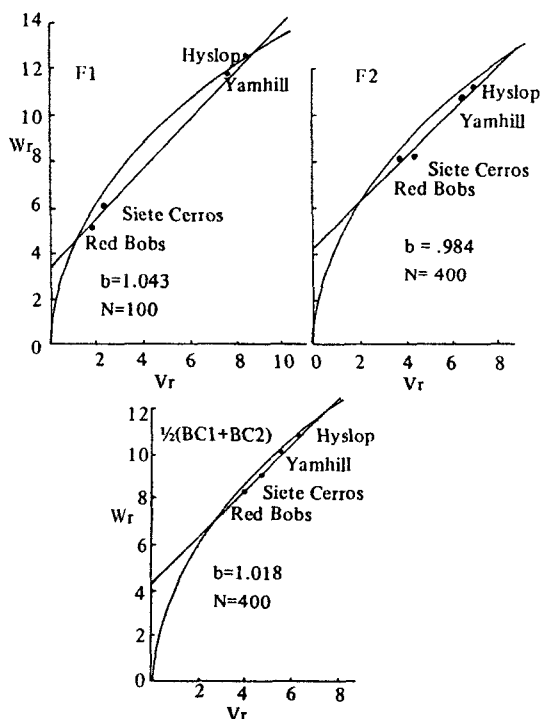


Fig. 2. $V_r - W_r$ graphic analysis of gene action for lag period of a 4×4 diallel set of F_1 , F_2 and $1/2(BC_1+BC_2)$ planted on November 1st, 1979. East Farm near Corvallis, Oregon, 1979-80.

With regard to actual grain filling period from anthesis to physiological maturity, somewhat different results were obtained, as seen in Figure 3. The order of the parents along the regression line indicates that winter wheats Yamhill and Hyslop had more dominant genes than the spring wheats Red Bobs and Siete Cerros. Nonallelic interaction may not be

involved for F_1 's, F_2 's and $1/2(BC_1+BC_2)$'s, as the relationship between W_r and V_r estimates is much closer. More additive gene action is involved together with partial dominance due to the positive intercept on the W_r axis for all the generations.

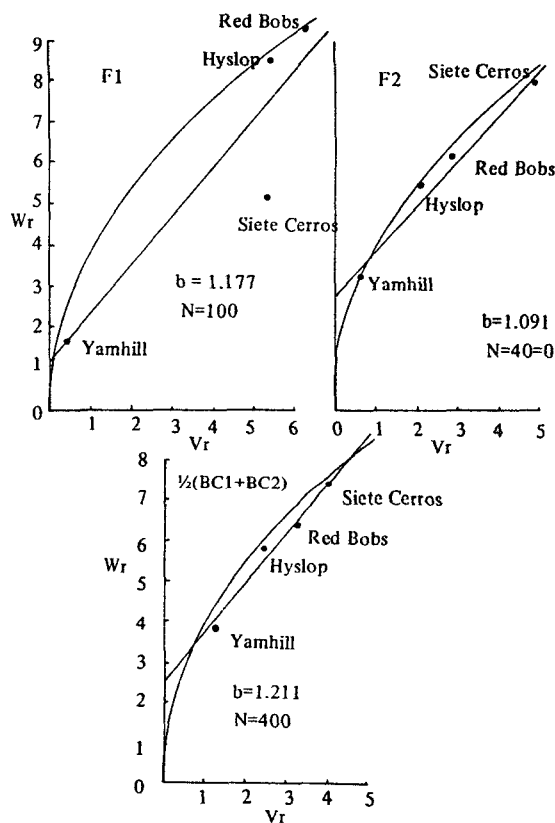


Fig. 3. $V_r - W_r$ graphic analysis of gene action for actual grain filling period of a 4×4 diallel set of F_1 , F_2 and $1/2(BC_1+BC_2)$ crosses planted on November 1st, 1979. East Farm near Corvallis, Oregon.

Further analysis was made to get more information about nonadditive gene action governing duration of grain filling period. Tables 4 through 6 present the mean square values of the estimates of variance (V_r) and parent-offspring covariance (W_r) of four arrays for the 4×4 diallel set of F_1 , F_2 and $1/2(BC_1+BC_2)$ crosses for the traits. For total duration of grain filling period, differences in the magnitude of (W_r+V_r) values over arrays were different at the .05 level for F_1 and $1/2(BC_1+BC_2)$ populations

(Table 4). Hence the arrays had different (Wr+Vr) values. There may be nonadditive genetic variation since (Wr+Vr) values were not different over arrays in the absence of nonadditive genetic variance. The differences in the magnitude of (Wr-Vr) values over arrays, in contrast, were not significant in all generations observed when compared with the differences over replicated blocks. Therefore, more additive gene action with partial dominance is involved for the variation of total duration of grain filling period. The genes are independently distributed among the parental lines.

Table 4. Mean square values of the estimates of Wr and Vr for a 4 x 4 complete diallel set of F1, F2 and ½(BC1+BC2) crosses for duration of grain filling period of wheats. East Farm near Corvallis, Oregon, 1979-80.

Sources of variation	F1s	F2s	½(BC1+BC2)s
(Wr+Vr) Array differences	152.3369*	43.8245	64.6519*
(Wr+Vr) Block differences	158.7181**	115.7041*	149.3926**
(Wr-Vr) Array differences	.8062	.2832	.1074
(Wr-Vr) Block differences	26.7784**	19.0417**	24.2915**

* Significant at the .05 probability level,

** Significant at the .01 probability level.

Table 5. Mean square values of the estimates of Wr and Vr for a 4 x 4 complete diallel set of F1, F2 and ½(BC1+BC2) crosses for lag period from heading to flowering of wheats. East Farm near Corvallis, Oregon, 1979-80.

Sources of variation	F1s	F2s	½(BC1+BC2)s
(Wr+Vr) Array differences	230.8543**	38.7379**	16.7847*
(Wr+Vr) Block differences	35.4815**	10.4092	10.1788
(Wr-Vr) Array differences	.3255	.0429	.0105
(Wr-Vr) Block differences	3.3698**	6.0825**	4.9641**

* Significant at the .05 probability level,

** Significant at the .01 probability level.

Table 6. Mean square values of the estimates of Wr and Vr for a 4 x 4 complete diallel set of F1, F2 and ½(BC1+BC2) crosses for actual grain filling period from flowering to physiological maturity of wheats. East Farm near Corvallis, Oregon, 1979-80.

Sources of variation	F1s	F2s	½(BC1+BC2)s
(Wr+Vr) Array differences	133.4843*	56.0891**	25.0313
(Wr+Vr) Block differences	23.8498	21.3502	28.2692*
(Wr-Vr) Array differences	2.4686	3.0692	.4413
(Wr-Vr) Block differences	11.6267*	4.9209	3.3260**

* Significant at the .05 probability level,

** Significant at the .01 probability level.

For lag period the differences in the magnitude of (Wr + Vr) values over arrays were significant as can be seen in Table 5. Hence the arrays have different (Wr + Vr) values, indicating there is nonadditive genetic variation. The differences in the magnitude of (Wr - Vr) values over arrays, in contrast, were not significant in all the generations observed when compared with the differences over replicated blocks. The additive dominance model is adequate for the variation of lag period. The genes are independently distributed among the parental cultivars.

For actual grain filling period the differences in the magnitude of (Wr + Vr) values over arrays are significant in all the generations except for 1/2(BC1 + BC2)s as shown in Table 6. There are nonadditive genetic variations involved for this trait. The differences in the magnitude of (Wr - Vr) values over arrays are larger than those for total duration of grain filling and lag period even though the values are not significantly different when compared with the differences over replicated blocks. Thus the adequacy of the additive-dominance model with independent gene distribution among the parental cultivars is questionable. The analysis strongly suggests that more non-additive genetic variation must be involved this trait when compared with total duration of grain filling and lag period.

Large differences in the lag period among the

parental cultivars more strongly influenced on total duration of grain filling period when compared to actual grain filling period. Furthermore, the genes governing total duration of grain filling and the lag period acted similarly and in an additive manner as demonstrated in the Vr - Wr graphic analysis. However, the genes governing the actual grain filling period have little influence on total duration of grain filling period. Thus spring type parents Red Bobs and Siete Cerros strongly influenced total duration of grain filling period and lag period when compared to winter type parents Yamhill and Hyslop with a shorter lag period. Considering several loci, the alleles for lag period strongly influence total duration of grain filling, suggesting that large segregating populations are needed in breeding for shorter lag period of early maturing winter wheat cultivars. The overall results suggest that a substantial portion of the total genetic variation is the result of additive type gene action which is encouraging in selecting for early maturity and high grain yield. The spring gene pool provides factors favouring early maturity, while the winter gene pool provides factors governing short lag period and shorter duration of grain filling period leading to higher rate of grain fillings. This then appears to further support the desirability of uses of winter x spring crosses in achieving the desired objective of earliness and acceptable grain yield.

SUMMARY AND CONCLUSIONS

The objective of this study was to investigate the nature of gene action involved for duration of grain filling, lag period, and actual grain filling period in crosses of winter and spring wheat cultivars.

The results from this investigation are summarized as follows:

1. No reciprocal differences were observed involving the grain filling period.
2. The Vr - Wr analysis indicated that nonallelic interaction was not involved for total duration of grain filling or lag period, but might be involved for

actual grain filling period. This model suggested that additive gene action along with some partial dominance was involved for these traits.

3. Spring cultivars Red Bobs and Siete Cerros have more dominant genes than winter wheats Yamhill and Hyslop for duration of grain filling and lag period. In contrast, Yamhill and Hyslop have more dominant genes for actual grain filling period. The genes appeared to be independently distributed among the parents.

摘 要

二毛作栽培에 適合한 極早熟 良質 多收性 小麥品種育成을 爲하여 登熟期間에 關與하는 遺傳子 作用에 對한 研究는 매우 重要하다. 秋播性品種 Yamhill 과 Hyslop, 春播性品種 Red Bobs 와 Siete Cerros 를 使用하여 4 × 4 complete diallel crosses F₁, F₂, BC₁ 및 BC₂ 를 作成, Jinks-Hayman model 를 利用하여 登熟期間에 關與하는 遺傳子 作用을 分析하였다. 本 試驗은 오레곤 주립대학교에서 實施되었다. 그 結果의 概要는 다음과 같다.

全登熟期間인 出穗에서 生理的 成熟期까지의 期間과 出穗에서 開花까지의 期間에서 maternal effect 가 認定되지 않았으며 非對立遺傳子間 相互作用도 發現되지 않았다. 開花에서 生理的 成熟期까지의 期間에서는 非對立遺傳子間에 相互作用이 認定되었다.

春播性 品種인 Red Bobs 와 Siete Cerros 는 全登熟期間과 出穗에서 開花까지의 期間을 지배하는 優性遺傳子들을 가지고 있었으며 짧은 쪽에 比하여 긴쪽이 우성으로 發現되고 있었다.

對照的으로 秋播性 品種인 Yamhill 과 Hyslop 은 開花에서 生理的 成熟期까지의 期間을 지배하는 優性遺傳子들을 가지고 있었으며 긴쪽이 우성으로 作用하고 있었다. 그리고 이 遺傳子들은 文配親들間에 獨立的으로 分布되어 있었다.

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