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**SHORT COMMUNICATION**

# Inheritance of Grain Filling Duration in Spring Wheat (*Triticum aestivum* L. em Thell)

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**To understand the genetic control of grain filling duration (GFD), i.e., the number of days from anthesis to physiological maturity, we studied the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations of six spring wheat crosses from nine varieties/genotypes. Generation mean analysis for gene effects indicated that one or more types of epistasis were significant in all crosses. In each pairing, the $F_1$ and $F_2$ means were either intermediate or closer to the mean of the parent having the longer GFD. Our narrow-sense heritability estimate was reasonably high, at 47.67 (based on diallel analysis). This demonstrated that progress could be made from the selection in these crosses for either long or short GFD. The two early varieties that had identical maturity durations differed in their GFD values, indicating that maturity dates are not good criteria when choosing parents for modifying GFD. To utilize favorable additive × additive effects during this selection, we suggest that a single seed descent (SSD) or bulk population approach be adopted. In comparison, dominance effects would prove quite useful in hybrid wheat breeding programs.**

*Keywords:* additive × additive gene effects, generation mean analysis, grain filling duration, *Triticum aestivum*, wheat

Grain filling duration (GFD) is a trait with substantial genetic potential to increase wheat yields. It is defined as the period between flowering (anthesis in the middle spike) and physiological maturity (yellowing of the peduncle). After this period passes, there is no significant increase in the amount of grain dry matter produced. Both the rate and duration of grain filling are positively associated with final grain weight (Wardlaw, 1970; Bhatt, 1972; Wiegand and Cuellar, 1981; Gebeyehou et al., 1982; Darroch and Baker, 1990). GFD is important because individual grain weight, a vital yield component, is the product of that rate and period (Nass and Reiser, 1975; Gebeyhou et al., 1982). Temperature and light significantly affect grain filling in this crop (Wardlaw, 1970; Sofield et al., 1977; Weigand and Cuellar, 1981). Furthermore, under semi-arid conditions, plant lines with longer GFD show lower yields if higher temperatures and water deficits occur during grain filling (Przulj and Mladenov, 1999).

Little information is available about the inheritance of GFD and the rate of wheat grain-filling. For barley, however, longer GFD dominant over shorter periods (Aksel and Johnson, 1961). Xie and Zhang (1981) have suggested that the continuous variability for GFD indicates a polygenic inheritance. Beiquan and Kronstad (1994) have observed additive gene action for GFD, although non-additive gene action also plays an important role in certain crosses of wheat. Wong and Baker (1986) have examined the heritability of developmental traits in spring wheat, obtaining GFD estimates that range from low to intermediate. Finally, Przuli and Mladenov (1999) have reported the presence of additive effects and dominance, as well as epistatic interactions, in the expression of wheat GFD, while both additive and dominant gene actions have been associated with GFD under heat stress (Yang et al., 2002).

## MATERIALS AND METHODS

From 320 germplasm lines of wheat (*Triticum aestivum*), we selected nine varieties (Bagula, HD 2285, HP 1633, Veery S, HP 1731, HP 1102, HW 1085, PAVON 76, and PBW 343) for study. These varieties were chosen because they differ in their grain filling duration (GFD) and other important agronomic traits. Among these, PBW 343 is the most commonly grown in India, covering approx. 7 million ha (Joshi et al., 2007a). During the 1980s, HD 2285 was the dominant variety on the Gangetic plains of South Asia. Other varieties, such as HP 1633, HP 1731, and HP 1102, were later released for planting in the eastern part of that region because of their shorter duration and the ability to adapt well to the huge rice-wheat cropping system of India (Joshi et al., 2007b). HW 1084 is a long-duration variety used in the Southern Hill zone of India. Bagula, PAVON 76, and Veery S -- all of which were at one time globally popular -- were developed at the International Maize and Wheat Improvement Center (CIMMYT). These varieties are relatively longer in duration than the others. Detailed characteristics of these varieties are given in Table 1. For this study, we grew the $F_1$, $F_2$, $BC_1$ and $BC_2$ generations of six crosses in a randomized block design with three replications. Each entry was planted in three 3-m-long rows, at a spacing of 25 × 5 cm. Recommended agronomic practices were followed to ensure good crops. Prior to heading, 10 plants each from $P_1$, $P_2$ and $F_1$, as well as 50 plants each from $BC_1$ and $BC_2$ and 100 plants from the $F_2$ plots, were randomly selected and tagged. The dates of anthesis (i.e., the extrusion of the anthers in the middle of the spikes) and of physiological maturity (i.e., a complete loss of green color from the peduncle) were recorded for each selection. GFD was defined as the number of days between anthesis and physiological maturity. For our data conversion, Degree Days for a particular period were computed as Tn = (Tmax+Tmin)/2-Tb, where Tmax and Tmin are the maximum and mini-

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**Table 1.** Pedigrees, sources, and traits associated with grain filling duration (GFD) and growing degree days for spring wheat varieties used in hybridization programs.

| Variety | Pedigree | Source | Sowing-anthesis (days) | Sowing to anthesis (growing degree days) | Anthesis to physiological maturity (days) | Anthesis to physiological maturity (growing degree days) | Sowing to physiological maturity (days) | Sowing to physiological maturity (growing degree days) | Sowing to anthesis (days) |
|---|---|---|---|---|---|---|---|---|---|
| Bagula | Veery selection | CIMMYT | 75 | 849.6 | 41 | 730.3 | 116 | 1579.9 | 75 |
| HD2285 | 249/HD2150 //HD 2186 | India | 76 | 862.6 | 28 | 442.3 | 104 | 1304.4 | 76 |
| HP1633 | RL 6010 / 5* SKA | India | 88 | 1048.0 | 26 | 485.4 | 114 | 1533.4 | 88 |
| Veery S | KAVKAZ / BUHO // KALYANSONA / BLUE BIRD | India | 78 | 897.1 | 32 | 550.0 | 110 | 1447.1 | 78 |
| HP1731 | LIRA //PARULA/TONICHI | India | 90 | 1080.0 | 28 | 542.1 | 118 | 1622.1 | 90 |
| HP1102 | 8156(B) / NAD 63 | India | 78 | 897.1 | 34 | 592.4 | 112 | 1489.5 | 78 |
| HW1084 | UNNATHKALYANSONA*2 // CPAN3057 | India | 77 | 879.9 | 40 | 720.1 | 117 | 1600.0 | 77 |
| PBW343 | ND/VG9144//KAL/BB/3/YCO″S′ /4/VEE##S “S” | India | 70 | 784.3 | 35 | 556.8 | 105 | 1341.1 | 70 |
| PAVON 76 | Vicam 71/7/ /6/Siete Cerros 66/ 8/Kalyansona /6//4/Gabo 55 | CIMMYT | 90 | 1080.0 | 27 | 520.0 | 117 | 1600.0 | 90 |

mum daily temperatures, respectively, and Tb is the base temperature (Tb = 5ºC; Yasuda and Shimoyama, 1965) below which no grain development occurs. Plot means were calculated and an analysis of variance was conducted to determine the significance of differences between family (generations) means. The mean values for each of six generations per cross and their standard errors were used to estimate the mid-parent (*m*), additive (*d*) and dominance (*h*) gene effects (Mather and Jinks, 1982). Adequacy of the additive-dominance model was determined with an ABC scaling test (Mather, 1949; Hayman and Mather, 1955) that used three degrees of freedom (i.e., the number of generations involved in this study minus the number of estimated parameters). When one or more scales were found to be significant, we applied a six-parameter model that incorporated *m*, *d* and *h*, as well as three digenic interactions -- additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) (Mather and Jinks, 1982). The genetic parameters also were tested for significance, using a t-test at 1% and a 5% level of significance, and assuming the fulfillment of assumptions for diallel analysis.

## RESULTS

Although the varietal pairs of HW 1085 and PAVON 76 (117 d) and of HD 2285 and PBW 343 (104, 105 d) had the same maturity durations, they differed in their GFD. This was due to differences in the number of days to anthesis (Table 1). GFD for all varieties ranged from 25.33 d (HP 1633) to 41.67 d (HW 1085). Significant differences were found between parental means in all the crosses (Table 2). In most combinations, the mean values of the back crosses shifted toward the value for the recurrent parent. Some specific features of each cross are described below and also detailed in Tables 1 through 4.

### HP 1633 × Veery S

Our scaling and joint-scaling tests were significant, suggesting the presence of epistasis. Six-parameter models revealed three types of interactions. The means of $F_1$ and $F_2$ showed heterosis for longer GFD, as found in Veery S. This cross also had a significant additive gene effect.

### HP 1731 × Veery S

GFD for these two parents differed by 5 d. The additive dominance model did not fit because both the scaling and the joint-scaling test were significant. However, the six-parameter model suggested the presence of additive, dominance, and two type of interactions -- additive × additive and dominance × dominance. The means of $F_1$ and $F_2$ were intermediate to the parents.

**Table 2.** Means and standard errors for grain filling duration in $P_1$, $P_2$, $F_1$, $F_2$, $BC_1$ and $BC_2$ generations from spring wheat crosses.

| Generation | HP 1633/ Veery S | HP 1731/ Veery S | HP 1102/ HW 1084 | HP 1731/ PBW 343 | HD 2285/ PAVON 76 | HP 1633/ Bagula |
|---|---|---|---|---|---|---|
| $P_1$ | 25.33 ± 0.33 | 27.33 ± 0.67 | 33.00 ± 0.33 | 27.33 ± 0.67 | 27.67 ± 0.33 | 25.67± 0.33 |
| $BC_1$ | 28.67 ± 1.33 | 32.00 ± 0.58 | 30.00 ± 1.00 | 25.67 ± 0.88 | 37.00 ± 0.33 | 27.00 ± 0.23 |
| $F_1$ | 36.00 ± 0.53 | 30.67 ± 0.67 | 38.33 ± 0.33 | 37.00 ± 1.00 | 32.67 ± 0.33 | 40.67 ± 0.33 |
| $F_2$ | 32.67 ± 0.67 | 29.33 ± 0.67 | 38.67 ± 0.33 | 36.00 ± 0.58 | 36.33 ± 0.88 | 39.67 ± 0.33 |
| $BC_2$ | 31.67 ± 0.88 | 33.33 ± 0.33 | 33.00 ± 0.23 | 27.67 ± 0.67 | 36.33 ± 0.88 | 36.33 ± 0.33 |
| $P_2$ | 32.33 ± 0.33 | 32.33 ± 0.33 | 41.67 ± 0.88 | 35.00 ± 0.23 | 25.33 ± 0.88 | 40.67 ± 0.88 |

**Table 3.** ABC scaling and joint-scaling tests with a three-parameter model (m, [d] and [h]) using six generations of six spring wheat crosses for GFD.

| Gene effect | HP 1633/ Veery S | HP 1731/ Veery S | HP 1102/ HW 1084 | HP 1731/ PBW 343 | HD 2285/ PAVON 76 | HP 1633/ Bagula |
|---|---|---|---|---|---|---|
| M | 28.4 ± 0.64 | 30.29 ± 0.64 | 35.94 ± 0.64 | 29.64 ± 0.64 | 28.96 ± 0.64 | 32.25 ± 0.64 |
| D | 2.06 ± 0.63** | 2.26 ± 0.63** | 4.06 ± 0.63** | 3.46 ± 0.63** | -1.06 ± 0.63 | 7.86 ± 0.63** |
| H | 6.47 ± 1.18** | 1.29 ± 1.10 | 0.39 ± 1.18 | 4.31 ± 1.18** | 8.62 ± 1.18** | 6.58 ± 1.18** |
| Scaling test | | | | | | |
| A | 1.66 ± 1.79** | 6.00 ± 1.49** | -11.33 ± 2.02** | -13.00 ± 2.13** | 13.66 ± 0.47** | -12.33 ± 0.47 |
| B | -11.00 ± 2.68** | 3.66 ± 1.00** | -14.00 ± 0.94** | -16.66 ± 1.66** | 14.66 ± 2.00** | -8.66 ± 0.81** |
| C | 0.66 ± 2.70 | -3.66 ± 3.07 | 3.33 ± 1.73 | 7.66 ± 3.12 | 27.00 ± 3.71** | 11.00 ± 1.56** |
| $X^2$ (3d.f.) | 23.38** | 10.35* | 56.91** | 85.58** | 68.80** | 53.43** |

*, **Significant at 5% and 1% level, respectively.

**Table 4.** Estimates of gene effects using a six-parameter model for spring wheat crosses.

| Gene effect | HP1633/ Veery S | HP1731/ Veery S | HP1102/ HW1084 | HP1731/ PBW343 | HD2285/ PAVON 76 | HP1633/ Bagula |
|---|---|---|---|---|---|---|
| M | 32.66 ± 0.66** | 29.33 ± 0.66** | 38.66 ± 0.33** | 36.00 ± 0.57** | 36.33 ± 0.88** | 39.66 ± 0.33** |
| D | 3.00 ± 1.59 | -1.33 ± 0.66** | -3.00 ± 1.00** | -2.00 ± 1.10 | 0.66 ± 0.88 | -9.33 ± 0.33** |
| H | -3.00 ± 4.16 | 14.16 ± 3.07** | -27.66 ± 2.46** | -31.50 ± 3.36** | 7.50 ± 3.98 | -24.50 ± 1.54** |
| I | -10.00 ± 4.16** | 13.33 ± 2.98** | -28.66 ± 2.40** | -37.33 ± 3.19** | 1.33 ± 3.94 | -32.00 ± 1.49** |
| J | 6.33 ± 1.61** | 1.16 ± 0.76 | 1.33 ± 1.09 | 1.83 ± 1.15 | -0.49 ± 1.00 | -18.33 ± 0.40 |
| L | 19.33 ± 6.94** | -22.99 ± 4.06** | 54.00 ± 4.35** | 67.00 ± 5.41 | -29.66 ± 5.12** | 53.00 ± 2.05** |

*, **Significant at 5% and 1% level, respectively.

### HP 1102 × HW 1084

The means of $F_1$ and $F_2$ were intermediate to both parents. Our scaling test detected the presence of epistasis. The six-parameter model indicated additive and dominance gene effects, as well as a dominance × dominance type of epistasis. Furthermore, the three-parameter model revealed a predominant role for the additive gene effect when expressing the GFD in this cross. Here, the dominance × dominance gene effect was positive, thereby prolonging the GFD, whereas the dominance and additive gene effect produced negative values, shortening the GFD.

### HP 1731 × PBW 343

The $F_1$ and $F_2$ means showed heterosis for long GFD. Both the ABC and joint-scaling tests were significant, leading us to apply the six-parameter model. A dominance gene effect and two additive × additive and dominance × dominance gene interactions were found significant. In contrast, the additive gene effect and the additive × dominance interaction were not significant. However, the additive gene effect was significant in this cross when the three-parameter model was used.

### HD 2285 × PAVON 76

The two parents were significantly different for GFD. ABC and joint-scaling tests also were significant, suggesting the presence of epistasis. The dominance × dominance gene interaction was found to be significant. Means for $F_1$ and $F_2$ showed heterosis for longer GFD.

### HP 1633 × Bagula

Means for GFD differed significantly, by 15 d, which was the greatest gap found among the parents of our six examined crosses. The means for $F_1$ and $F_2$ showed heterosis for longer GFD. Our generation means analysis indicated the complex inheritance of GFD in this cross. Both additive and dominance gene effects, as well as three types of interaction, were significant (Table 3). The dominance × dominance effects were positive and prolonged the GFD, whereas the additive and dominance gene effects gave negative values, thereby reducing the GFD.

## DISCUSSION

A generation means analysis approach is useful when explaining the quantitative nature of inheritance for grain filling duration. Here, the six-parameter model was appropriate because epistasis was important in all of our crosses. The estimate of 47.67 for narrow-sense heritability was high (based on diallel analysis) for this trait, which indicated a smaller environmental effect on the expression of GFD. This result agrees with those from earlier reports (Rasyad and van Sanford, 1992; Beiquan and Kronstad, 1994; Przulj and Mladenov, 1999).

The magnitude of additive effects was lower than for dominance × dominance epistasis, which suggests that selection for a shorter GFD might be difficult. Conversely, the positive dominance effects might mean that such selections could be effective (Mather and Jinks, 1982). When the dominance and dominance x dominance estimates have the same sign, the interaction is considered complementary, and is duplicate if both signs are negative (Mather and Jinks, 1982). Applying this criterion here, we found that duplicate gene action was present in all crosses. This may be due to the polyploid nature of wheat. Regardless, our results are consistent with the findings of Przuli and Mladenov (1999).

In the present study, considerable variation in GFD existed among the parents. Those with the same number of days to physiological maturity differed in their GFD because of differences in days to anthesis. Our crosses demonstrated the importance of both additive and dominance gene effects, as well as epistasis. These results suggest that, for spring wheat, there is considerable variability in GFD and days to anthesis, characteristic of a complex nature. However, such variations can be exploited to manipulate GFD for a specific environment by using SSD or a simple bulk population breeding approach that permits the utilization of additive and additive × additive epistatic effects (Przuli and Maladenov, 1999). Furthermore, once an ideal cms system is developed, the dominance gene effects for GFD can be quite valuable to hybrid wheat breeding programs.

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## LITERATURE CITED

**Aksel R, Johnson LPV** (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

**Beiquan M, Kronstad WE** (1994) Duration and rate of grain filling in selected winter wheat populations: I. Inheritance. Crop Sci 34: 833-837

**Bhatt GM** (1972) Inheritance of heading date, plant height and kernel weight in two spring wheat crosses. Crop Sci 12: 95-98

**Darroch BB, Baker RJ** (1990) Grain filling in three spring wheat genotypes: Statistical analysis. Crop Sci 30: 525-529

**Gebeyehou GD, Knott R, Baker RJ** (1982) Rate and duration of grain filling in durum wheat varieties. Crop Sci 22: 337-340

**Hayman BI, Mather K** (1955) The description of genetic interactions in continuous variation. Biometrics 11: 69-82

**Joshi AK, Chand R, Arun B, Singh RP, Ortiz R** (2007b) Breeding crops for reduced-tillage management in the intensive, rice-wheat systems of South Asia. Euphytica 153: 135-151

**Joshi AK, Mishra B, Chatrath R, Ortiz Ferrara G, Singh RP** (2007a) Wheat improvement in India: Present status, emerging challenges and future prospects. Euphytica DOI10.1007/s10681-007-9385-7

**Mather K** (1949) Biometrical Genetics, Ed 1. Methuen, London

**Mather K, Jinks JL** (1982) Biometrical Genetics, Ed 3. Chapman and Hall, London

**Nass HG, Reiser B** (1975) Grain filling and grain yield relationships in spring wheat. Can J Plant Sci 55: 673-678

**Przulj N, Mladenov N** (1999) Inheritance of grain filling duration in spring wheat. Plant Breed 118: 517-521

**Rasyad A, van Sanford DA** (1992) Genetic and maternal variances and covariances of kernel growth traits in winter wheat. Crop Sci 32: 1139-1143

**Sofield I, Evans LT, Cook MG, Wardlaw IF** (1977) Factors influencing the rate and duration of grain filling in wheat. Aust J Plant Physiol 4: 785-797

**Wardlaw IF** (1970) The early stages of grain development response to light and temperature in single variety. Aust J Biol Sci 23: 765-774

**Wiegand CL, Cuellar JA** (1981) Duration of grain filling and kernel weight of wheat as affected by temperature. Crop Sci 21: 95-101

**Wong ISL, Baker RJ** (1986) Selection for time to maturity in spring wheat. Crop Sci 26: 1171-1175

**Xie RS, Zhang ZH** (1981) Investigation of the genetic control of earliness in wheat based upon character correlations and heritability. Sci Agric Sin 3: 16-24

**Yang J, Sears RG, Gill BS, Paulsen GM** (2002) Quantitative and molecular characterization of heat tolerance in hexaploid wheat. Euphytica 126: 275-282

**Yasuda S, Shimoyama H** (1965) Analysis of internal factors influencing heading time of wheat varieties. Ber Ohera Inst 13: 23-38