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Research Article

Combining ability analysis for grain filling duration and yield traits in spring wheat (*Triticum aestivum* L. em. Thell.)

Kamaluddin*, Rishi M. Singh, Lal C. Prasad, Malik Z. Abdin* and Arun K. Joshi

[1]*Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, UP, India.*

Abstract

A diallel analysis of wheat (*Triticum aestivum* L. em. Thell) parents (n = 11) and their F_1 (n = 55) and F_2 (n = 55) offspring was carried out for the following four traits: grain filling duration (GFD), GFD for growing degree days (GDD), 1000 seed weight and seed yield per plant. Analysis of variance for general combining ability (GCA) and specific combining ability (SCA) displayed significant F_1 and F_2 general and specific combining ability effects for the four traits studied. For all the traits the GCA effects were relatively more important than the SCA effects, indicating that additive genetic effects were predominant. Crosses displaying high SCA effects for grain filling duration, seed weight and yield were observed to be derived from parents having various types of GCA effects (high x high, high x low, low x low and medium x low). The single seed descent method can be applied to exploit additive gene effects whereas dominance gene effects could be valuable in hybrid wheat breeding programs. Among the parents, genotypes from the International Maize and Wheat Improvement Center (Centro Internacional de Mejoramiento de Maíz y Trigo, CIMMYT) as well as South Asia were found to be superior general combiners for grain filling duration. Likewise, crosses involving diverse parents from CIMMYT and South Asia showed significant SCA effects for grain filling duration and other traits.

Key words: wheat, combining ability, GCA, SCA, grain filling duration.

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Introduction

The most important yield components of wheat (*Triticum aestivum* L. em. Thell.) are number of kernels per spike and Kernel weight, the latter being the product of the rate and duration of grain filling (Gebeyehou *et. al.*, 1982; Van Sanford and Mackown, 1985; Bruckner and Frohberg, 1987). Grain filling duration (GFD) is the period between flowering and physiological maturity (Przuli and Mladinov, 1999) and, in wheat, has been reported to be significantly affected by temperature and light (Wardlaw, 1970; Sofield *et. al*., 1977; Wiegand and Cuellar, 1981) and hence could be an important trait in terminal heat stress environments (Al-Khatib and Paulsen, 1984). Under semi-arid conditions wheat lines with a longer grain filling duration produced lower yields if high water and temperature deficiency occurred during grain filling (Przulj and Mladenov, 1999). The plant genotype and environment both influence the rate and duration of grain filling (Gallagher *et. al.*, 1974; Metzger *et. al.*, 1984; Bauer *et. al.*, 1985) and significant genotypic differences for this trait have been reported in spring wheat (Mou and Kronstad, 1994; Przulj and Mladenov, 1999; Saadalla *et. al.* 2000; Talbert *et al.* 2001).

The optimum time for sowing wheat on the plains of South Asia is from November the 15th to 25th but in a significantly large area, principally the fourteen-million hectare South Asian rice/wheat cropping system (Hobbs and Morris, 1996; Pandey, 2005; Joshi *et al.*, 2007a), wheat sowing often gets delayed due to the late harvesting of rice (Joshi *et al.*, 1997; Arun *et al.*, 2003). In about four to five million hectares wheat-sowing occurs after December 15th, resulting in high wheat yield losses due to the reduced growth and development period available before harvest (Joshi and Chand, 2002; Arun *et al.*, 2003; Joshi *et al.*, 2007b). Almost the whole of this late sown area is in the eastern Gangetic plains, most of which occurs in the 9.5 million hectare North Eastern Plain Zone (NEPZ) of India where the average wheat yield is only 2.7 tonnes (t) ha^{-1} compared to the 4.7 t ha^{-1} in the Indian state of Punjab (Joshi *et al.*, 2007b). The North Western Plains Zone (NWPZ) of India (extend-

Send correspondence to Arun K. Joshi. Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, 221005 UP, India. E-mail: joshi_vns@yahoo.co.in.

*Present address: Centre for Transgenic Plant Development, Department of Biotechnology, Hamdard University, New Delhi, India.

ing from the state of Punjab to western Uttar Pradesh) has an area almost equal to that of the NEPZ and is the most important wheat-producing zone of Indian, with an average wheat yield of about 4 t ha^{-1}. Resource conservation technologies are spreading rapidly in the North Eastern Plains Zone (NEPZ) region such that zero-till sowing accounted for about 10^5 ha in the 2005/2006 cropping season (Joshi *et al.*, 2007b). However, due to the domination of long duration rice varieties such as MTU 7029, late transplanting, water stagnation and other related factors it is unlikely that, in the near future, the sowing of wheat will be advanced in the NEPZ region by more than two to three weeks. The warm and humid NEPZ region, classified as a Mega Environment 5 by Braun *et al.* (1992), best supports wheat varieties that are heat tolerant or display rapid grain filling. Grain filling duration is an important factor when wheat is grown under conditions of high temperature and water stress and it has been suggested (Wiegand and Cuellar, 1981) that for such environments wheat lines should be developed with a shorter grain filling duration. Better information on the factors involved in the grain filling duration trait, including the gene effects controlling this trait and the combining ability of different wheat lines, could result in the development of heat tolerant or rapid grain filling wheat lines. In barley a long grain filling duration is dominant over a shorter grain filling duration (Aksel and Johnson, 1961) but little information is available on the factors involved in the wheat grain filling duration trait. It has been suggested that the inheritance of the grain filling duration trait is polygenic in wheat because this trait shows continuous variability in wheat (Xie and Zhang, 1981) and some workers have reported that both additive and dominance gene actions are associated with wheat grain filling duration (Saadalla *et. al.*, 2000; Yang *et al.*, 2002).

The study described in this paper was undertaken to determine the gene effects and combining ability of grain filling duration and yield traits in some wheat lines used in India.

Materials and Methods

We investigated wheat (*Triticum aestivum* L. em. Thell.) parent plants (n = 11) and their F_1 (n = 55) and F_2 (n = 55) offspring, the parent plants being selected from the wheat germplasm collection at Banaras Hindu University (WGC-BHU), Varanasi, India based on their grain filling duration. Details of the lines used, including their provenance, are given in Table 1. Some lines came from the International Maize and Wheat Improvement Center, Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), Mexico D.F., Mexico.

Parent plants differing in grain filling duration were crossed in all possible manners during the 1999-2000 cropping season to produce F_1 and F_2 offspring. The parent plants and F_1 and F_2 offspring were then planted in a randomized block design with three replications at the Agriculture Research Farm, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India (25.2° N, 83.0° E) on December 25th 2001-2002. This site is in the eastern Gangetic plains of India and has a loam alluvial soil with a neutral pH of 7.2. Agronomic practices recommended for normal fertility were followed and the soil was fertilized with 60 kg N ha^{-1} of P_2O_5 and 40 kg ha^{-1} K_2O at sowing and 60 kg N ha^{-1} at sowing, 30 kg N ha^{-1} at the first irrigation, 21 days after sowing, and 30 kg N ha^{-1} at the second irrigation, 45 days after sowing.

Each of the line of parents and F_1 offspring were grown in four three-meter long rows with a spacing of 25 cm x 5 cm, the plot size being kept same for the F_2 generation but the number of rows was increased to 12 for each cross. Observations for the different traits were recorded on 20 random plants for the parent plants and F_1 offspring and 250 plants for the F_2 offspring and the plants were tagged

Table 1 - Pedigree of the parent wheat plants and their grain filling duration (GFD) periods in days.

Parent line	Pedigree	Source[1]	GFD
HP 1633	RL6010/6* Sonalika	WGC-BHU, India	26
PBW 343 (Attila)	ND/VG1944//KAL//BB/3/YACO ‘S’/4//VEE?5 ‘S’	CIMMYT	35
Bagula	TTR “S”/JUN “S”	CIMMYT	41
Veery ‘S’	KUZ/BUHO//KAL/B6	CIMMYT	32
PAVON 76	VCM//CNO ‘S’/7C/3/KAL/BB	CIMMYT	27
HP 1731	LIRA ‘S’// PRL ‘S’/TONI	WGC-BHU, India	28
HW 1084	HW1042/NP807	WGC-BHU, India	40
HD 2285	249 / HD2160//HD2186	WGC-BHU, India	28
HP 1102	8156 (B)/Nad63	WGC-BHU, India	34
KRL-1-4	Kharchia/WL711	WGC-BHU, India	36
K 9107	K8101/K68	WGC-BHU, India	29

[1]Key: CIMMYT = Centro Internacional de Mejoramiento de Maíz y Trigo (International Maize and Wheat Improvement Center, Mexico D.F., Mexico); WGC-BHU = Wheat Germplasm Collection, Banaras Hindu University, India.

prior to heading. The three quantitative traits recorded per plant were: grain filling duration (GFD), 1000 seed weight (S_W) and seed yield (S_Y). Grain filling duration was also converted to growing degree days (GDD) by summing the daily degree days (T_n) computed as (T_n) = (T_{max} + T_{min})/2 –T_b, where, T_{max} and T_{min} are the maximum and minimum daily temperatures and T_b is the base temperature (5 °C) below which no development occurs (Yasuda and Shimoyama, 1965). The mean genotype values were subjected to combining ability by diallel analysis, method 2, model I (Griffing, 1956). Analysis of variance (ANOVA) and general and specific combining ability (GCA and SGA) was carried out for all traits, the F test being used to determine significant differences. The statistical tests were carried out using the INDOSTAT program.

Results

Analysis of variance indicated significant differences between parents for all four traits studied (Table 2). The coefficient of variation was highest for seed yield, followed by growing degree days and then grain filling duration (Table 2). For both the F_1 and F_2 generations the general and specific combining ability ANOVA results for all four traits were significant (Table 3), with the general effects being higher than the specific effects. This suggests that the parents used in the study differed significantly for general as well as specific combining ability and that additive genetic effect were predominant. The general combining ability effects of the parents indicated that the CIMMYT lines Veery ‘S’ and Pavon 76 and the WGC-BHU lines HP 1731 and HD 2285 were good general combiners for the grain filling duration trait (Table 4). The CIMMT Veery ‘S’ line was also a good general combiner with regard to the GDD, S_w and S_y traits (Table 4) and the CIMMYT line BW 343 (Attila) displayed good performance with respect to the general combining ability of different traits (Table 4).

The specific combining ability effects of the crosses for grain filling duration and the other traits examined are presented in Table 5. Not all crosses demonstrated significant specific combining ability effects for different traits. Only eight crosses (PBW 343/Bagula, Bagula/Veery ‘S’, HP 1731/KRL-1-4, PBW 343/HP 1102, Bagula/HW 1084, Veery ‘S’/HW 1084, HP 1731/K 9107 and HW 1084/K 9107) of the 55 crosses investigated showed desirable significant grain filling duration specific combining ability effects in both generations, and only two crosses (PBW 343/Bagula and Bagula/Veery ‘S’) exhibited significant and desirable GDD effects. Desirable significant specific combining ability effects were recorded for the HP 1731/KRL-1-4 cross in regard to S_w and for the PBW 343/HP 1102 cross in respect to S_w and S_y.

Discussion

Table 2 - Analysis of variance and coefficient of variation (CV) for grain filling duration (GFD), growing degree days (GDD), 1000 seed weight (SW) and seed yield (SY) per plant for the 11 wheat parents involved in the diallel cross.

		Mean squares			
Source of variation	DF	GFD	GDD	SW	SY
Replication	2	0.082	4.88	2.27	0.14
Treatment	120	57.75**	18922.46**	260.07**	55.27**
Error	240	0.79	1845.72	3.48	0.32
CV%		28.00	29.00	17.00	33.00

**Significant at p = 0.01 by the F test.

Table 3 - Analysis of variance for combining ability for the grain filling duration (GFD), GFD for growing degree days (GDD), 1000 seed weight (SW) and seed yield (SY) per plant for the F_1 and F_2 offspring of the 11 wheat parents involved in the diallel cross.

		Mean squares				
Source of variation	Generation	DF	GFD	GDD	SW	SY
GCA	F_1	10	22.34**	6818.43**	39.83**	34.22**
	F_2	10	13.43**	5747.67**	44.31**	17.21**
SCA	F_1	55	17.79**	5440.63**	11.38**	16.52**
	F_2	55	22.85**	6955.50**	14.95**	26.63**
Error	F_1	130	0.29	961.77	0.17	0.100
	F_2	130	0.22	888.27	0.032	0.070

**Significant at p = 0.01 by the F test.

Table 4 - Estimates of general combining ability (GCA) effects for the F_1 and F_2 offspring of 11 wheat parents and their mean performance (MP) for grain filling duration (GFD), GFD for growing degree days (GDD), 1000 seed weight (SW) and seed yield (SY) per plant.

	GFD			GDD			SW			SY		
	GCA effects		MP	GCA effect		MP	GCA effect		MP	GCA effect		MP
Parents	F_1	F_2		F_1	F_2		F_1	F_2		F_1	F_2	
HP 1633	0.13	-0.24	25.67	4.47	-0.25	463.77	0.09	-0.38**	40.10	0.24	-0.08	21.37
Bagula	1.16**	0.58**	40.67	-12.21	-23.27**	503.31	-0.35**	-0.16**	32.53	-0.14	-0.36**	20.47
PBW 343	1.18**	0.91**	35.00	13.20	2.29	559.43	2.32**	1.31**	39.03	2.84**	2.79**	27.23
Veery 'S'	-1.51**	-1.91**	32.33	-27.64**	-35.15**	559.63	0.50**	0.49**	39.17	2.07**	0.47**	28.27
PAVON 76	-1.02**	-0.06	25.33	-12.72	12.12	487.27	-1.06**	-0.38**	33.53	-1.94**	-0.47**	22.30
HP 1731	-1.82**	-0.99**	27.33	-22.63	3.28	529.13	1.65**	1.43**	40.10	-0.47**	1.07**	28.33
HW 1084	1.26**	1.76**	41.67	34.84**	46.89**	771.37	-2.43**	-1.90**	33.10	-0.90**	-0.58**	21.20
HD 2285	-1.02**	0.91**	27.67	-28.19**	11.67	442.63	-2.66**	-3.05**	37.47	-1.81**	-0.60**	19.43
HP 1102	2.00**	0.09	33.00	33.71**	-2.49	567.33	-0.74**	-1.19**	35.37	-0.86**	-0.61**	20.20
KRL-1-4	0.57**	-0.45**	36.00	17.80	-11.17	634.70	-0.06	-0.10	40.03	-1.03**	-1.63**	28.43
K 9107	-0.92**	-0.60**	29.00	-0.63	-3.92	530.27	2.75**	3.93**	44.13	2.01**	-0.02	33.43
Xp	34.02	32.65		610.43	570.77		36.65	34.93		20.59	18.78	
SE (gi)±	0.14	0.12		8.20	7.88		0.10	0.04		0.08	0.07	
SE (gi-gj)	0.20	0.18		12.16	11.68		0.16	0.07		0.12	0.10	

**Significant at p = 0.01 by the F test.
Key: Xp = grand mean of Parents, F_1 and F_2; SE = Standard error; gi = General combining ability effects for line i; gj = General combining ability effects for line j.

Table 5 - Estimates of desirable specific combining ability (SCA) effects for the F_1 and F_2 offspring of 11 wheat parents for grain filling duration (GFD), GFD for growing degree days (GDD), 1000 seed weight (SW) and seed yield (SY) per plant.

Cross combinations	SCA effects															
	GFD				GDD				SW				SY			
	F_1	Mean	F_2	Mean	F_1	Mean	F_2	Mean	F_1	Mean	F_2	Mean	F_1	Mean	F_2	Mean
PBW 343/Bagula	-10.36**	26.00	-11.14**	23.00	-135.36**	476.07	-162.55**	387.23								
Bagula/Veery 'S'	-7.00**	26.67	6.32**	25.00	-100.32**	470.27	-93.27**	418.63								
HP 1731/KRL-1-4	-5.44**	27.33	-3.88**	27.33					4.96**	43.20	2.94**	39.20				
PBW 343/HP 1102	-4.54**	32.67	-2.65**	31.00					3.00**	41.23	2.18**	37.23	5.63**	28.20	4.63**	25.60
Bagula/HW 1084	-3.44**	33.00	-3.32**	31.67												
Veery 'S'/HW 1084	-3.11**	30.67	-5.50**	27.00												
HP 1731/K 9107	-3.29**	28.00	-3.06**	27.00												
HW 1084/K 9107	-2.03**	32.33	-4.47**	29.33												
Xp	34.03	32.65			610.44	570.77			36.66	34.93			20.56	18.78		
SE Sij	0.48	0.43			28.74	27.62			0.37	0.16			0.28	0.24		
SE (Sij-Sik)	0.73	0.65			42.13	40.49			0.56	0.25			0.43	0.36		

** Significant at p = 0.01 by the F test.
Key: Xp = grand mean of Parents, F_1 and F_2; SE = Standard error; Sij = Specific combining ability effects between ith and jth lines; Sik = Specific combining ability effects between ith and kth lines.

Analysis of variance indicated significant differences between parent plants for all the four traits studied (Table 2). Parent plants with the same number of days to physiological maturity differed in grain filling duration due to difference in the number of days to anthesis. The combining ability analyses showed that both general and specific combining ability effects played an important role in the control of the grain filling duration of the genotypes studied, with the general effects being greater than the specific effects. This suggests a prominent role for additive genetic effects, although the significance of specific combining ability effects indicates that dominance and epistasis were also involved in the expression of the traits studied. Similar results have also been reported in wheat by other workers (Ahmed *et. al.*, 1991; Mou and Kronstad, 1994; Sharma *et. al.*, 1996; Sharma and Pawar, 2000). Przuli and Mladenov (1999) observed the presence of additive and dominance as well as epistatic interactions in the expression of grain filling duration in wheat, while Yang *et al.*, (2002) reported that both additive and dominance gene effects were associated with grain filling duration in wheat plants subjected to heat stress. In our study, the greater magnitude of additive effects compared to non-additive effects suggests that selection for shorter grain filling duration might be effective in the early segregating generations.

The magnitude and direction of combining ability effects are known to be useful in selecting parent plants in crop improvement programs (Mather and Jinks, 1971). In our study, crosses displaying high specific combining ability effects for grain filling duration, seed weight and yield were derived from parents with various types of general combining ability effects (high x high, high x low, low x low and medium x low). The occurrence of crosses with high specific combining ability effects involving low x low general combining ability parents indicates that although the parents in such crosses lacked additive gene effects compared to high general combining ability parents, heterozygotes were highly responsive to the environment due to non additive effects such as dominance and epistasis (Jinks and Jones, 1958). It has been suggested (Joshi and Sharma, 1984; Singh *et. al.*, 1986) that intermating between crosses followed by selection may be a useful strategy for obtaining desirable segregants in crosses from high x low and low x low general combining ability parents. The superior performance of crosses between parents from diverse origins (CIMMYT, Mexico and South Asia) also demonstrated the role of a wider genetic base in the crossing program (Kronstad, 1996).

Our results show the importance of both additive and non-additive gene effects in the expression of grain filling duration and yield related traits in wheat. It appears, therefore, that single seed decent or the bulk method of handling segregating generations can also be used to utilize additive or additive x additive gene effects to manipulate grain filling duration for developing better yielding cultivars suited to different environmental conditions (Przulj and Maladenov, 1999), especially terminal heat stress. Dominance genetic effects will be valuable in wheat breeding programs when hybrid seed production is made economically feasible through an efficient cytoplasmic male sterility system (Pickett, 1993). It also seems that parent plants with better general and specific combining ability for grain filling duration need to be given greater consideration when developing varieties for warmer areas such as eastern and central South Asia where wheat generally is allowed less time to complete its life cycle.

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