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Genetic and time series analysis for grain growth rate and grain filling duration under conservation agriculture in wheat (*Triticum aestivum* L.)

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Abstract

Grain filling rate (GFR) and grain filling duration (GFD) are most important growth traits. Therefore, the present investigation was carried out to analyze the trend for these traits in the mega varieties released at the different time and to identify the type of gene action governing these traits. The study showed continuous improvement in grain filling rate over time and there is no indication of its saturation and therefore, can be further explored to achieve yield gains. Grain filling duration indicates no change in mega varieties over time for normal sown condition largely because of the trade-off between time and heat stress, however, conservation agriculture condition can provide an opportunity for its exploitation. Under late sown linear regression showed a strong declining trend over the years. The analysis of variance revealed the presence of significant genetic variability, not only among the elite breeding material specifically developed for conservation agriculture (CA) condition but also among released varieties, indicating sufficient scope for their exploitation. Diallel analysis of 21 F_1s generated from 7 parents for GFD and GFR indicated the preponderance of additive gene action in the material validating the effectiveness of progeny based selection for both traits under study. Elite breeding material CSW02 displayed high GCA for both the traits and therefore, can be effectively involved in the crossing program to make further gain. Cross CSW77 × CSW57 having a high value of SCA effect for both GFR and GFD provide scope for its exploitation through hybrid development.

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

Introduction

Physiologically, grain yield of wheat is a complex trait dependent upon several components including the number of grains per unit area and grain weight (Calderini and Reynolds, 2000). Yield component i.e., seed weight is decided by the rate of grain growth after fertilization and its duration. Indian sub-continent experiences fluctuation in temperature throughout the wheat growing season, however, the most frequent and significant fluctuation happens during terminal stage of grain/crop growth. Heat stress during the grain filling (Wardlaw and Moncur, 1995) is the most conspicuous environmental factor affecting grain weight (Calderini et al. 2001). At the physiological level, grain weight is decided by grain growth rate and grain filling duration, however, both of these factors are reported to be inversely related (Housley et al. 1982) putting a challenge to the breeders to increase yield by exploiting variation in grain weight. Faster accumulation of growing degree days generally reduces grain filling duration and increases grain filling rate (Johnson and Kanemasu, 1983). To increase and stabilize the yield at higher levels, grain growth rate and grain filling duration are the parameters which need to be optimized. Among semi-dwarf wheat genotypes, total crop duration along with GFD has been most extensively exploited phenological traits in wheat for yield improvement. Increased duration has, however, added uncertainty in wheat production (Gupta and Yadav, 2014) and therefore, to stabilize the yield at a higher level, grain growth rate has to be increased without further altering grain fill duration.

Beside the ability of the plant to store assimilates in the stem, its efficiency to mobilize and translocate the reserved materials to the grains decide the final grain yield. Translocation of assimilates depends upon the sink strength which in turn is decided by a number

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of grains per spike and mean grain weight (Ehdaie and Waines, 1996). Though both GFD and GFR are important in potential grain weight realization, GFD seems to be more affected by environmental factors than GFR (Wiegand and Cuellar 1981; Royoet al. 2000). Grain filling process is a crucial and dynamic process of wheat growth. Its main components are duration and rate that determine the individual grain size, grain weight and ultimately the economics of the crop (Li and Pan, 2005). The logistic curve based on biological principles of growth was found more suitable to determine rate and duration of grain filling (Loss et al. 1989; Darroch and Baker, 1990). However, before exploitation of such traits under Indian condition, characterization of genetic variability in the elite germplasm along with knowledge about its genetic control is essential. Thus the objective of the present study was to do time series analysis of the released cultivars for grain filling rate and duration and genetic analysis of grain filling rate and duration under conservation agriculture (CA).

Materials and methods

Plant Material for time series analysis

Fourteen genotypes comprising of mega varieties, three recently released varieties for normal sown and seven for late sown condition were evaluated for genetic gain trend analysis (Table 1). The material was grown on a permanent bed of CA condition in a randomized block design (RBD) during *rabi* 2014-15 at the experimental farm of Indian Agricultural Research Institute, New Delhi. CA condition is maintained at IARI farm since 2007 by non-tilling and retaining full residue on the surface in the maize-wheat cropping system. At the time of heading, 25 plants from each genotype were tagged randomly in each plot for collecting the data for the gain filling rate. Five random spikes were harvested at every 10 days interval, starting from two days before anthesis to 40 days after anthesis. Harvested spikes were oven dried at 65^{o}C for 3 days to completely remove the moisture from the spikes and seed, and then average weight of the five spikes was taken. This generated the data for spike weight at 0, 10, 20, 30 and 40 days after anthesis.

Plant material for genetic study on GFR and GFD

Seven genotypes with distinctly variable grain weight and grain filling duration *viz*., CSW02, CSW16, HDCSW18, CSW57, CSW77, CSW78, and HD 3117 were selected for genetic study. These were crossed in half diallel fashion during the *rabi* 2013-14 to generate 21 F$_1$s for genetic study. The F$_1$s along with their parents were raised in *rabi* 2014-15 in RBD with two replications. The data on GFD and GFR were recorded for the F$_1$s and parents as described for the first experiment.

Table 1. Time series analysis for normal sown and late sown varieties

S.No.	Variety	Year of release	Production condition
1	Kalynsona	1967	Normal Sown
2	WL 711	1977	Normal Sown
3	UP 262	1978	Normal Sown
4	HD 2329	1985	Normal Sown
5	WH542	1992	Normal Sown
6	UP2338	1995	Normal Sown
7	PBW 343	1996	Normal Sown
8	PBW550	2007	Normal Sown
9	DBW 17	2006	Normal Sown
10	PBW621-50	2011	Normal Sown
11	HD 2967	2011	Normal Sown
12	WH1105	2012	Normal Sown
13	HD 3086	2014	Normal Sown
14	HDCSW18	2014	Normal Sown
15	Sonalika	1965	Late Sown
16	HD 2285	1983	Late Sown
17	PBW 373	1997	Late Sown
18	Raj 3765	1996	Late Sown
19	UP2425	1999	Late Sown
20	PBW 590	2009	Late Sown
21	HD 3059	2014	Late Sown

Statistical analysis

The mean rate of grain growth per spike was estimated from slopes of linear relationships between grain dry weight per spike and time from 50% anthesis until physiological maturity for each spike. The fitted functions were in the form of equation

$$Y = \beta_0 + \beta_1 X$$

where β_1 indicates the slope of the equation and β_0 is Y intercept.

GFD was calculated as the difference between the date of physiological maturity (identified as the date at which seed stopped growing) and date of anthesis.

The combining ability analysis for GFD and GFR was worked out according to Method 2, Model 1 of Griffing (1956). The diallel crossing system gives P (P-1)/2 F_1 hybrids excluding reciprocals, where P is the number of parental lines.

Results

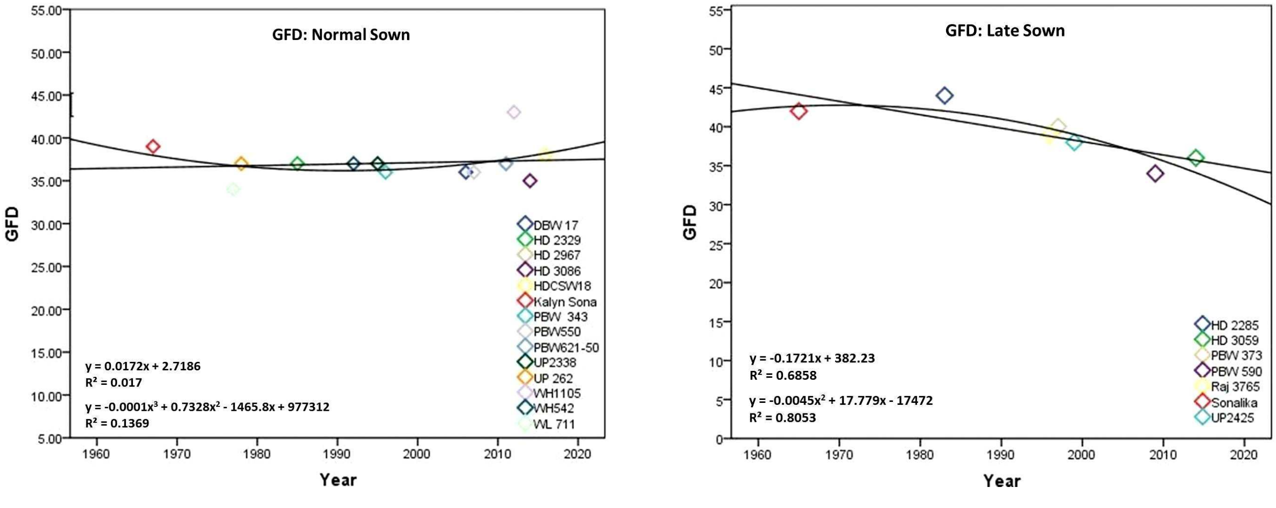
Grain filling duration (GFD)

Analysis of variance revealed no significant differences in the grain filling duration among the fourteen genotypes studied under normal sown condition. GFD ranged from 35 days in HD 3086 to 43 days in WH 1105. WH 1105 has the longest GFD than rest of the varieties. Some of the varieties like HDCSW 18 and HD 2967 despite longer crop duration were constrained due to late heading and high temperature toward their terminal stage. Linear regression analysis showed that there is no trend in grain filling duration across the time period from 1966 to 2014 under normal sown condition (Fig. 1a). A mega variety Kalyansona which was released in 1967 is having GFD of 39 days, whereas a recently developed wheat variety HDCSW18 showed GFD of 38 days. Another popular variety HD 2329, released in 1985 showed a higher value for GFD of 37 days. Looking at the GFD values of mega wheat varieties released from the period of the green revolution to till date, GFD has not changed over the period. But in the case of late sown varieties, there is a continuous drop in GFD (Fig. 1b). A 1965 released variety Sonalika showed GFD of 42 days, whereas a 2014 released variety HD 3059 showed little reduction in GFD (36 days). HD 2285 recorded highest value (44 days) for this trait.

Grain filling rate (GFR)

Analysis of variance revealed a significant difference in grain filling rate even among the selected varieties picked up for the trend analysis. The value for GFR ranged from 0.257 g/spike/day in WL 711 to 0.566 g/spike/day in WH 1105 under normal sown condition. The trend showed linear progression in GFR over the time period from 1967 to 2014 (Fig. 2a). Before the introduction of 1B/1R translocation carrying varieties, GFR was comparatively lower in all the varieties. Most of the varieties with 1B/1R have comparatively good GFR except WH 542. Two groups of varieties are clearly distinguishable in the present era varieties. The group represented by HD 3086 and HD 2967, which are non 1B/1R and has comparatively moderate grain filling rate, whereas another non 1B/1R variety like WH 1105 and DPW 621-50 has quite high grain filling rate.

Under late sown condition, linear regression indicates no significant trend among the varieties released between 1965 to 2014; however, polynomial regression shows a definite trend with significant R^2 value. It shows that varieties like Raj 3765, PBW 373, released in 1996 and 1997, respectively showed lower GFR than the first product of green revolution. These varieties possess 1B/1R translocation. GFR varied between 0.225 g/spike/day in PBW 373 to 0.527 g/spike/day in the recently released variety HD 3059 (Fig. 2b). After strong decline initially, GFR showed a continuous increasing trend.


(a)

(b)

Fig. 1: Genetic trend analysis for grain fill duration under normal sown condition (a) and late sown condition (b)

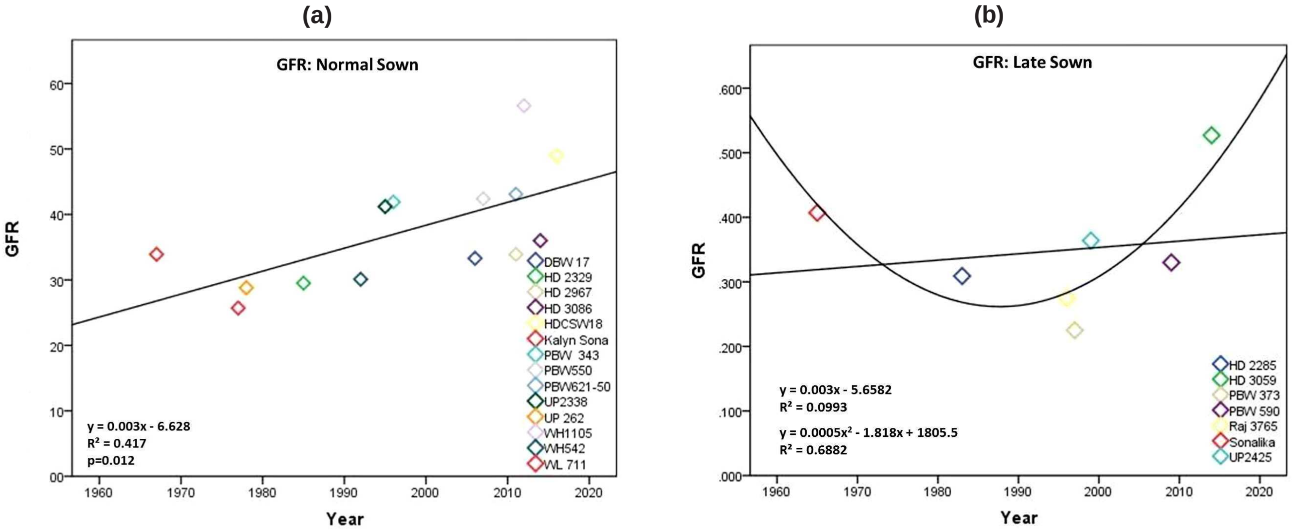


Fig. 2. Genetic Trend analysis for GFR in varieties released for normal sown(a) and late sown condition (b)

Genetic study for GFD and GFR

Analysis of variance for combining ability in a set of 21 crosses from 7 parents shows that both *GCA* and *SCA* were highly significant for both the traits. As shown in Table 2 for GFR, the value of GCA variance is 32.533** which is a reflection of very high additive gene action to the value of SCA variance 7.96** which is a reflection of non-additive gene action. In the case of GFD, the situation is the same *i.e.* value of GCA variance is very high than that of SCA variance. The ratio of mean square due to *GCA* and *SCA* shows the preponderance of additive gene action than non-additive gene action for both traits. The ratio is more significantly distorted toward *GCA* for GFD and therefore indicating the validity of progeny testing for GFD in the breeding program.

Table 2. Analysis of variance for combining ability for grain filling rate (GFR) and grain filling duration (GFD)

Source of variation	DF	MSS GFR	MSS GFD
Genotype	27	13.421**	5.737**
GCA	6	32.533**	19**.00
SCA	21	7.96**	1.94**
Error	27	1.313	0.682

The value for GCA effect is presented in Table 3. Only two parents were having positive and significant GCA effect value for each trait *viz*., CSW02 and CSW77 for GFD and CSW02 and HD3117 for GFR, respectively. Therefore, the parents CSW02, CSW77 are good combiner for GFD and CSW02, HD3117 are good combiner for GFR. CSW02 was in general good combiner for both the traits under study.

Table 3. *GCA* effects for GFD and GFR among seven parents

Parent	GFD		GFR	
	Mean	*GCA* effects	Mean	*GCA* effects
CSW02	43.00	**1.22****	27.00	**1.729****
CSW78	41.00	0.415	21.55	-0.921
CSW77	42.42	**0.913****	23.75	-0.316
HD 3117	40.50	0.137	27.55	**2.04****
CSW16	40.00	-0.069	18.75	-0.527
HDCSW 18	39.50	-0.863	20.70	-0.521
CSW57	35.00	-1.752	20.00	-1.483
CD @ 5%	1.704		2.363	

Effects for specific combining ability (SCA)

There was very significant variation found for GFR & GFD among diallel crosses. For GFR (CSW02 × CSW57, CSW78 × HDCSW18, CSW77 × CSW57, and CSW16 × HDCSW18) crosses showed very significant *SCA* effects, whereas for GFD the crosses CSW78 × CSW57, CSW77 × CSW57 and CSW16 × CSW57 showed significant *SCA* variance (Table 4). The cross CSW77 × CSW57 showed significant effects for both GFR and GFD traits and therefore has a direct bearing

Table 4. SCA effects among crosses for GFD and GFR in wheat

Cross	GFD		GFR	
	Mean	*SCA* effects	Mean	*SCA* effects
CSW02 × CSW78	42.00	-0.075	19.50	**-3.15**
CSW02 × CSW77	43.00	0.427	20.60	**-2.656**
CSW02 × HD 3117	42.00	0.203	26.30	0.689
CSW02 × CSW16	41.00	-0.591	23.50	0.456
CSW02 × CSW18	41.00	0.203	22.65	-0.40
CSW02 × CSW57	39.50	-0.408	23.75	**1.661***
CSW78 × CSW77	41.00	-0.767	18.70	**-1.906**
CSW78 × HD 3117	40.75	-0.241	23.55	0.589
CSW78 × CSW16	41.00	0.215	20.10	-0.294
CSW78 × CSW18	39.50	-0.491	22.65	**2.25****
CSW78 × CSW57	41.00	**1.898****	18.85	-0.589
CSW77 × HD 3117	41.00	-0.49	22.25	-1.317
CSW77 × CSW16	39.90	**-1.388**	22.55	1.55
CSW77 × CSW18	41.00	0.51	18.60	**-2.406**
CSW77 × CSW57	41.00	**1.399***	21.70	**1.656***
HD 3117 × CSW16	41.00	0.493	24.70	1.344
HD 3117 × CSW18	40.00	0.287	22.50	-0.861
HD 3117 × CSW57	39.00	0.175	18.70	-3.70
CSW16 × HDCSW18	39.75	0.243	22.75	**1.956***
CSW16 × CSW57	40.25	**1.632****	18.90	-0.933
CSW18 × CSW57	35.50	**-2.325**	19.50	-0.339
CD @ 5%	1.70		2.34	

The figure in bold face indicate the crosses with significant sca effect in desirable direction

on exploitation as a hybrid, combining both traits. For GFD crosses CSW77 × CSW16, HDCSW18 × CSW57 and for GFR CSW02 × CSW78, CSW02 × CSW77, CSW78 × CSW77, CSW77 × HDCSW18 showed negative effects.The crosses with high *SCA* effects were derived from the parents with high x low mean as well as medium × low mean value for GFD, indicating thereby the importance of additive x dominance gene interaction.

Mean performance of parents and crosses for GFR: some parents, as well as many crosses, showed the high value of GFR e.g., parents like CSW02, HD3117 and four crosses like CSW02 × HD3117, CSW02 × CSW57, CSW78 × HD3117, HD3117 × CSW16. CSW16 showed the lowest mean value (18.6) of grain filling rate, whereas HD3117 showed highest mean value (27.55) of this trait.

Discussion

The number of grains/m^2 is decided quite early in the plant life and has been reported to be the main trait contributing to yield gain under a wide range of environmental conditions (Perry and D’Antuono 1989; Donmez et al. 2001; Royo et al. 2007). The increase in grain number has been exploited to a large extent and further increase seems to be difficult. On the other hand, grain weight has not been exploited to a very large extent largely because of poor understanding of its genetic control and physiology. Grain weight is dependent upon GFD and grain growth. Grain growth comprises of three main phases *viz*., small increase in grain dry weight occurs immediately after anthesis (initial lag phase). Grain dry weight then increases rapidly during the grain-filling period. The end of the grain-filling period has been termed mass maturity. Grain dry weight increases as a linear function of time during the grain-filling phase (Biscoe and Gallagher 1977; Brocklehurst 1977; Jenner 1991). Analysis of variance clearly shows the presence of enough genetic variability at least under conservation agriculture condition for both the traits under study in the released varieties and these can be used as donors/base material for future improvement. Although, GDF is highly influenced by environment (Knot and Gebeyhou 1987), GFR is environmentally more stable and has high heritability (Van Sanford 1985). Indian wheat breeders, like many others throughout the world, have exploited many traits including total crop duration. Despite the increase in total duration, GFD has more or less remained unchanged. Linear regression analysis of the old mega varieties and newly developed strains shows no change in GFD among the varieties released for normal sown conditions between 1968 to 2014. Starting from Sonalika, the first variety released through selection among introductions from Mexico to the latest release for late sown condition i.e., HD 3059, trend analysis through linear equation reveals a clear drop in GFD over the years. It is clear from the analysis that, GFD hardly played any role in yield improvement under normal sown condition, however under late sown, it has been under selection, however differently in a different phase.

Grain growth is a consequence of supply of carbon from three sources: current assimilates produced by photosynthesis in leaves and stems, mobilization of the stored carbohydrates and transport of nitrogen containing compounds from these organs to the spike and growing kernels, and assimilates produced by the spike (Bradford and Hasio 1982). Transportation of stored assimilates is further dependent upon the capacity to store assimilates in the stem and efficiency to mobilize and translocate the reserved materials to the grains. The second component being a function of sink strength in a genotype depends on the number of grains per spike and mean grain weight (Ehdaie and Waines 1996). For GFR, the linear regression analysis shows continuous improvement over the year, however, the value of slope indicates that the trend is not so strong. The equation explained less than 50 percent of variation. It is clear from the analysis that GFR has been continuously improved by the breeders though inadvertently as it was never easy to select for the trait. Under late sown, linear regression equation indicate no trend over time for GFR, however, polynomial regression show clear cut dip in grain filling rate during the phase of IB/IR varieties *viz*., Raj 3765 and PBW 373 followed by a strong gain in recent years.

The present results indicate a poor correlation between GFD and GFR in contrast to previous reports (Gebeyehouet al. 1982; Roy et al. 2006). Changes in phenology and sink size may have affected the rate and duration of grain filling without altering final grain weight. As evidence are accumulating that wheat is not source limited and it is possible to increase the yield by greater partitioning of assimilates to spikes during their development without even improving photosynthetic conversion of intercepted radiation to spike dry matter (Parry et al. 2011). Despite of no trend over a period of time among the released varieties for normal sown condition, it is very clear that breeders had already realised that GFD is very important for yield realization and therefore, this trait was not compromised in breeding programmes. Foulkes et al. (2011) in his review on increasing yield potential identified increasing grain number by prolonging spike development without increasing crop duration and better partitioning of dry matter to spikes without sacrificing capacity for resource capture by roots. Our results show that under normal sown condition, there has been hardly any change in GFD since the release of Kalyansona, despite increase in crop duration. Breeders in India has probably exploited more grain number per unit area through delayed heading and increased tillering. However, this has increased the risk of losses may be due to terminal heat leading to a significant dip in productivity in Haryana and Western UP in 2012-13 and 2015-16. Elite breeding lines like CSW 02 has increased GFD without a parallel increase in the overall crop cycle, similar to what Reynolds et al. (2010) has suggested in Wheat Yield Consortium for increasing wheat yield potential. Time series analysis, therefore, clearly suggests that under normal sown conditions, selection should be directed toward increased GFR without further increase in overall duration. Increased GFD has been exploited to a large extent up to 1995 and further increase seems to be difficult under conventional condition. However, conservation agriculture condition because of lesser increase in temperature toward terminal stage offers an opportunity for a simultaneous increase in duration and GFD. The present study clearly indicates that GFR has been increased linearly over the years in the varieties released for normal sown conditions and there is no indication of its saturation and further improvement is feasible through the integration of trait related to better partitioning and potential grain weight.

Future yield progress will depend on the synergy between increased photosynthetic capacity and grain sink capacity without any tradeoff between traits and this will require trait based breeding. We have moved a step ahead in this direction by phenotyping the two important traits deciding grain growth under the condition of conservation agriculture which to the large extent minimize the terminal stress due to heat by modulating the temperature and better retention of moisture in the soil profile. Analysis of variance for combining ability for GFR and GFD indicates significant differences among parents and crosses for the trait under study. The variance due to *GCA* for both the traits under study was at least four times more than the variance for *SCA* indicating a preponderance of additive variance over non-additive variance, indicating thereby that the performance of the progeny can be predicted. However, as both non-additive and additive components are important for the expression of GFD and GFR, simple pedigree method of selection would not be able to exploit non-additive genetic component. Reciprocal recurrent selection allowing the fixing of favorable alleles with adequate maintenance of heterozygosity through crossing seems appropriate to exploit non-fixable gene effects (Joshi 1979). However, keeping in view self-pollinated nature of the crops mating design like Diallel selective mating (Jensen 1970) or biparental mating in F_2 can be highly rewarding. CSW 02 could be used in making large scale crosses because of high general combining ability for both GFD and GFR. Other parents like CSW 77 and HD 3117 can also be used in crossing because of their better *GCA* effect for GFD, GFR, respectively.

The hybrids which have shown significant *SCA* for GFD and GFR are CSW78 × CSW57, CSW77 × CSW57 and CSW78 × HDCSW18, CSW77 × CSW57 CSW16 × CSW18, CSW02 × CSW57, respectively. Most of these hybrids have been derived from the parental combination of medium × medium and high × low and low × low, suggesting thereby importance of additive × additive and/or additive x dominance genetic interactions in their inheritance. The superiority of these crosses may be due to complementary and duplicate type gene interactions. Therefore, these crosses are expected to produce desirable segregants and could be exploited successfully in varietal improvement program. The hybrid development program is also in advanced stage with almost exemplary seed production techniques of cytoplasmic male sterility (CMS) sources; the crosses could be effective for yield enhancement by exploiting both GFR and GFD. Breeding wheat cultivars specifically for conservation agriculture to realize higher yield require information about yield enhancing or limiting traits, the status of genetic diversity available and gene action determining these traits. Because of the tradeoff between duration and higher yield under conventional tillage conditions, conservation agriculture provides an opportunity for yield enhancement by exploiting both GFD and GFR or at least GFR.

Authors' contribution

Conceptualization of research (RY and AK); Designing of the experiments (RY and AK); Contribution of experimental materials (RY, AK and KG); Execution of field/lab experiments and data collection (AK and RY); Analysis of data and interpretation(RY, AK, KG, VS and NJ); Preparation of the manuscript (AK, RY, KG, VS and NJ).

Declaration

The authors declare no conflict of interest.

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