Indian J. Genet. Plant Breed., (2024); 84(4): 602-609
https://doi.org/10.31742/ISGPB.84.4.10
ISSN: 0975-6906
www.isgpb.org

RESEARCH ARTICLE

Understanding the genetics of physiological traits to achieve next breakthrough in bread wheat (*Triticum aestivum* L.)

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Abstract

Optimization of different physiological processes to meet the requirement of various agronomic traits consolidation now appears to be necessary to break the fast-approaching yield ceiling. Source-sink relationship in the new high-yielding genetic base, along with better partitioning of assimilates toward developing grain, requires synergy between various developing traits at the physiological level. In the current study, eight lines with improved genetic base for the grain yield with diverse physiological traits were crossed in a diallel fashion to generate 64 crosses. The F_1s were grown along with their parents to study their physiological behavior vis-a-vis combining ability. All the physiological traits are controlled by both additive and non-additive gene action with strong maternal effects. HDCSW18(P8) and HD 3226(P6) were found be good general combiners for grain yield. HDCSW18 was found to be the best general combiner for a majority of physiological traits like crop growth rate (CGR), leaf area index (LAI) and NDVI, along with grain yield. DBW 187 was found to be a good combiner for photosynthetic efficiency and may complement well with HDCSW18 for developing a highly physiologically efficient genotype. Strong deviation in expression from normal expected value in F_1 combinations for grain yield was realised in cross combinations 35th ESWYT-147 (P2) X HDCSW18 (P8) for CGR, NIAW34/PHW12//43IBWSN-1187(P3) X HDCSW18(P8) for canopy temperature depression, NDVI, NIAW34/PHW12//43IBWSN-1187(P3) X HD 3226(P6) for LAI, DBW187 (P5) X HD3086(P7) for chlorophyll content, and in 35th ESWYT-147(P2), XHDCSW18 (P8) and NIAW34/PHW12//43IBWSN-1187(P3) XDBW187 (P5) for grain yield, respectively. More than 10% standard heterosis in DBW187(P5) X HDCSW18(P8), NIAW34/PHW12//43IBWSN-1187(P3) XDBW187 (P5) and HD3117 (P1) X HD2967//HD2887/HD2946//HD2733 (P4) for grain yield seems to be mainly because of highly improved leaf area index and grain weight. The high proportion of non-additive components in the genetic control of yield and harvest index offers us an opportunity either for exploitation of heterosis by developing hybrids or improvement in these traits by following a population improvement program. The presence of significant and positive standard heterosis for each of the physiological traits in at least one of the crosses offers an opportunity to develop physiologically improved fixed lines with a higher probability of higher grain yield.

Keywords: Leaf area index, Crop growth rate, Wheat, Combining ability, heterosis

Introduction

Wheat, as a major food grain crop in the world, meets around 20% of the total energy and protein requirement in the human diet (FAO 2016). Being grown in diverse ecologies, wheat occupies a maximum acreage of around 220.75 million hectares with an annual production of around 770.87 million tonnes (FAOSTAT 2022). Wheat grain is consumed in the form of a large number of products and its demand is continuously expanding at a rate of approximately 2% per year (Rosegrant et al. 1995), while genetic gains in yield potential of irrigated wheat in the major wheat growing ecologies stand at less than 1% (Yadav et al. 2021). Grain yield realization in wheat is decided by optimizing physiological functioning (Ding et al. 2020; Liu et al. 2015; Yadav et al. 2018). Empirical selection has played a significant role in wheat improvement since the beginning of systematic wheat breeding. However, further gain on the basis of component traits alone is becoming increasingly difficult. Increased

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How to cite this article: Singh S.K., Yadav R., Kumar M., Bainsala N., Gaikwad K., Babu P., Kumar S., Yadav R.N., Ansari R., Saifi N. and Das T.R. 2024. Optimizing the physiology to achieve next break-through in wheat through better understanding the genetics of physiological traits in bread wheat (*Triticum aestivum* L.). Indian J. Genet. Plant Breed., **84**(4): 602-609.

Source of support: Nil

Conflict of interest: None.

Received: Feb. 2024 **Revised:** Sept. 2024 **Accepted:** Oct. 2024

wheat production can be achieved through physiological breeding emphasizing effective nutrition and radiation use efficiency under improved agronomy. Empirical selection, as well as selection based on agronomic traits because of conflict introduced in a source-sink relationship, is not delivering the desired dividend in the absence of focus on efficient physiological functioning. There is a need for physiological-based breeding by combining favorable alleles dispersed in improved genotypes to accelerate further grain yield improvement in wheat (Reynolds et al. 2017; Gupta et al. 2017). In the past, improvement of self-pollinated crops was achieved through random selection of parents from the naturally occurring variability, without emphasis on their genetic effects. However, the success of any crop improvement program depends on the selection based on the actual performance of the parents as well as their combining ability for traits of agronomic importance (Bertan et al. 2007). In this context, knowledge of the genetic control of these traits related to wheat grain yield is essential in a breeding program to draw a selection strategy and manage the offspring. Knowledge of the type of gene action, the magnitude of genetic variance, and combining ability estimates are needed to develop improved cultivars (Singh et al. 2016).

Agronomic traits are the reflection of physiological processes. Their further improvement can not be realized unless we understand the genetic basis for the variation of these traits and integrate these traits in selection in early generations (Gami et al. 2020). Combining ability provides information about inheritance patterns of gene action to breeders for developing effective breeding strategy of (Hayman 1954; Jinks 1954). How the favorable alleles for various physiological processes are dispersed among the recently developed high-yielding varieties and improved breeding lines and how they combine in character consolidation can be best predicted by combining ability analysis. It also plays a vital role in obtaining genetic information on a particular trait of interest via fixed and random selection of parental lines in the shortest possible time (Griffing, 1956). Besides combining ability, measurement of heterosis for various traits, including physiological traits, gives a tentative idea about a particular set of germplasm and provides scope for improvement by fixing the new combination of various genes in pure line or development of hybrids. Most of the wheat breeders, due to a lack of suitable genetic information about the physiological traits, have not integrated these into their selection programme. The present study was therefore, planned to understand the genetic architecture of physiological traits in the improved spring wheat germplasm being used in India.

Materials and methods

Two hundred and sixty genotypes were evaluated for physiological and agronomic traits during 2020-21. On the basis of data collected during the season, eight genotypes were selected on the basis of their contrasting behavior for crop growth rate, leaf area index, chlorophyll content and harvest index. Tvhe details of the genotypes are presented in Table 1. These genotypes were crossed in full diallel fashion and, thus, generated 64 F_1s. All the F_1s, along with their parents, were grown to assess the general combining ability (GCA) and specific combining ability (SCA) and heterosis was sown at ICAR- Indian Institute of Wheat and Barley Research, off-season center, Dalanag Maidan, Lahaul and Spiti valley, Himachal Pradesh in randomized block design (RBD) with three replications.

Table 1. Details of the genotype and their behavior for physiological traits to generate the full diallel

Parents	Parentage	Parameters
P1	HD3117	Low crop growth rate
P2	35th ESWYT-147	Low leaf area index
P3	NIAW34/ PHW12//43IBWSN-1187	High harvest index
P4	HD2967//HD2887/ HD2946//HD2733	High leaf area index
P5	DBW187	Low chlorophyll content
P6	HD 3226	Low harvest index
P7	HD3086	High crop growth rate
P8	HDCSW18	High chlorophyll content

Each plot consisted of four rows and each row was 3m long and 20 cm apart. The seeds within the row were spaced 10 cm apart. All recommended cultural practices were followed to have healthy growth. The studied traits were crop growth rate ($mg^{-1}cm^{-1}$day-1), canopy temperature (℃), canopy temperature depression (℃), days to 50% heading, days to 50% flowering, days to maturity, grain yield (q/ha), harvest index, leaf area (cm^2), leaf area index, normalized difference vegetation index (NDVI), number of tillers per 10 cm row, plant height (cm), leaves chlorophyll content (SPAD_L), flag leaf chlorophyll content (SPAD_FL) and thousand-grain weight (g).

Observations were recorded on the basis of the whole plot for days to 50% heading, days to flowering, days to maturity, NDVI, grain yield and harvest index, whereas the characters such as canopy temperature, SPAD_L, SPAD_FL, etc., were taken over five competitive plants selected randomly from each plot. The average values for five plants were calculated and used for statistical analysis.

Statistical analysis

The data after compilation were subjected to a simple analysis of variance technique (Steel and Torrie, 1980) to see whether significant differences existed among the wheat genotypes for further analysis. For features where significant differences were identified, the combining ability analysis was performed in Method 1, Model 1 as proposed by Griffing (1956) using computer software 'AGD-R (2015) Version 2.0' developed by Rodriguez et al. (2015). General combining ability is used to indicate the average performance of a genotype in a hybrid combination, while SCA is used to identify situations where certain combinations perform relatively better or worse than expected based on the average performance of the genotype concerned (Sprague and Tatum, 1942). The percent increase or decrease of F1 hybrids popular check variety was calculated to estimate possible heterotic effects for the characters by using the formula of Fonseca and Patterson (1968):

$$\text{Standerd heterosis} = \frac{\overline{F_1} - \overline{CV}}{\overline{CV}} X100$$

Where,
$\overline{F_1}$ = $Mean$ value of F1 hybrid
$\overline{CV}$ = value of check variety
The significance of heterosis was worked out following 't' test as given below:
Standard heterosis, $t = (\frac{\overline{F_1}-\overline{CV}}{\sqrt{3M_e/2r}})$

M_e = Error mean square from ANOVA table
R = number of replication

Results and discussion

The next breakthrough in wheat yield can be realized by a simultaneous increase of source supply and sink capacity (Murchie et al. 2023), along with optimization of various physiological processes and traits. In India, biomass, along with crop duration (Yadav et al. 2021) and LAI (Gupta et al. 2017), have been important components of genetic gain enhancement over the years. Therefore, to understand the role of physiological traits in furthering the genetic gain and the kind of genetic variance available in the advance material to refine the breeding approach, the present investigation was carried out in wheat. The results of analysis of variance (ANOVA) for GCA and SCA (Table 2) revealed that all the parents and their cross combinations (F_1) are significantly differed for all the agro physiological traits, namely crop growth rate ($mg^{-1}\ cm^{-1}\ day^{-1}$), canopy temperature ($^0C$), canopy temperature depression (^0C), days to heading, days to flowering, days to maturity, grain yield (q/ha), harvest index leaf area (cm^2), leaf area index (cm/cm^2), normalized difference vegetation index (NDVI), number of tillers per 10 cm row, plant height (cm), leaves chlorophyll content (SPAD_L), flag leaf chlorophyll content (SPAD_FL) and thousand-grain weight (g). It was expected as the parents were selected through a preliminary exploration of all these traits in advance of the high-yielding lines of a breeding program. The mean square for GCA was higher than sca for most of the traits except CGR, grain yield and harvest index, indicating the preponderance of additive gene effect for most of the physiological traits and thus providing enough scope for improvement through selection for these traits. However, many of these traits seem to be in conflict with each other, indicating both by a preponderance of non-additive gene effect for grain yield and harvest index. The preponderance of the non-additive gene effect for grain yield and harvest index indicates that favorable alleles for different physiological traits might be linked in the repulsion phase and introduce conflict for better yield realization in homozygous lines. Interestingly, the reciprocal effect is present for almost all physiological traits, which indicates the presence of maternal effect for all the traits, including yield and warrants for a carefully planned crossing program. Similar reports have been documented previously by several researchers (Kumar et al. 2015; Abas et al. 2018; Mohamed 2019; Shamsabadi et al. 2019; Sharma and Kamaluddin 2020; Kamara et al. 2021; Mohamed et al. 2021).

Knowledge about gene action such as additive, dominance, epistatic, or overdominance effects for physiological traits like crop growth rate and leaf area index can help in designing the ideotype for the future (Fasoula and Fasoula 2003). Simultaneously, the magnitude and their direction combining ability effect and level of heterosis for individual traits helps in designing breeding and selection strategies (Ma-Teresa et al. 1994). The general combining ability of the parents is reflected as the average performance of its hybrid combination and can be a measure of additive gene action. SCA is a deviation in the performance of hybrid from the expected value based on the GCA effect of parents involved and can be regarded as a measure of non-additive gene action. The estimation of general combining ability revealed that HDCSW-18 (P8), a variety released for conservation agriculture conditions, showed very good combining ability for CGR, leaf area index, CTD and grain yield and crossing of this variety with Parent2 (an international advanced material 35th ESWYT-147) and Parent 5 (DBW187), an Indian variety released through direct introduction of CIMMYT material with high gca for some of the complementary traits like high chlorophyll content in flag and other leaves variety can help in optimizing physiological process for further yield consolidation. The majority of hybrids of HDCSW18 had higher source as well as sink, resulting in improved HI. The hybrids of 35th ESWYT-147, on the other hand, achieve the same through faster and higher crop growth and highly efficient flag leaf. The other interesting genotype that achieves a similar result is DBW187 (Parent 5), a CIMMYT-introduced material but with reduced HI, probably because of some conflict in source and sink. The parents with highest positive and significant GCA effect were DBW187(0.11) and HDCSW18 (0.07) for crop growth rate, canopy temperature depression, leaf area index and grain yield, 35th ESWYT147 for grain yield (2.67), HD2967//HD2887/HD2946//HD2733 (1.10) for NDVI, HD 3226 (1.52) for SPAD _FL and SPAD_L. These parents can be utilized in the crossing program for the development of high-yielding and climate resilient progenies in bread wheat. Similar results for the GCA effects have been reported earlier by many researchers (Fillahi et al. 2017; Mohamed et al. 2019; Shamsabadi et al. 2019; Kamra et al. 2021; Mohamed et al. 2021; Biligin et al. 2022; Fouad et al. 2022).

The pure line varieties being the most popular mode of action, higher general combining ability of genotypes provide scope for yield consolidation through selection and fine-tuning the phenology and growth physiology in the segregating material and early generation bulks. The breeding value of parents being regularly estimated in various molecular breeding tools is an indirect reflection of general combining ability and can be a good way of selecting the parent for the crossing program. With the availability of robust cms-based seed production feasible in wheat, the development and deployment of hybrids in the farmer's field is not far away. SCA effect is a good measurement of specific nicking of parental lines as it results from over dominance or dominance effect of favorable allele linked in the repulsion phase and dispersed among the different parents (Falconer and Mackay 1996). The effects of SCA on direct crosses and their reciprocals are presented in Table 4. The highest SCA effect was realized in the cross 35th ESWYT-147 x HDCSW18 (Parent 2 X Parent 8) along with very high SCA effect for crop growth rate (0.050), harvest index (1.749), leaf area (70.188), leaf area index (0.357), NDVI (2.640), SPAD flag leaf (0.754), SPAD leaves (0.506), grain yield (13.555) and TGW (4.025). It is largely because of the accumulation of favorable alleles dispersed in the two for different physiological traits in F1 and their linkage.

Ten cross combinations were found to have very good SCA effects for most of the studied agro-physiological traits. Some of the cross combination worth mentioning is NIAW34/PHW12//43IBWSN-1187 (P3) X HD 3226 (P6) found the best combiner among them as estimated positive significant SCA effects for the traits crop growth rate (0.18), grain yield (3.64), harvest index (1.09), leaf area index (0.93), NDVI (2.07), number of tillers (0.83), SPAD_L (0.90). Interestingly there were many crosses like HD3117 (P1) XHD2967//HD2887/HD2946//HD2733 (P4),35th ESWYT-147 (P2) XHDCSW18 (P8), DBW187(P5) XHD3086 (P7), DBW187 (P5) X HDCSW18 (P8) and HDCSW18 (P8)X 35th ESWYT-147 (P2) with positive and significant sca effect as well as commercial/ standard heterosis for grain yield and highly optimized physiology either for CGR, leaf area index, grain weight and or SPAD value, however, in the absence of large amount of F1 seed needed to raise a commercial crop and comparatively

Table 2. Analysis of variance due to combining ability and reciprocal effects for important physiological trait and grain yield in wheat

Source of variance	d.f.	CGR	CT	CTD	LA	LAI	NDVI	SPAD_FL	SPAD_L	HI	GY
GCA	7	0.08***	2.85***	1.8***	14766.12***	0.35***	12.70***	25.62***	20.44***	1.62***	44.76***
SCA	28	0.37***	0.88***	1.1***	8513.57***	0.21***	19.60***	11.62***	12.07***	10.60***	95.28***
Reciprocal	28	0.06***	1.44***	1.20***	2361.58***	0.06***	9.17***	14.61***	8.52***	24.32***	112.23***

**p <= 0.05; ***p <= 0.01; CGR = Crop growthrate (mg^{-1}cm^{-1}day-1); CT = Canopy temperature (^{0}C); CTD = Canopy temperature depression (^{0}C); LA = Leaf area (cm^2); LAI = Leaf area index; NDVI = Normalized difference vegetation index; SPAD_L = Leaves chlorophyll content; SPAD_FL = Flag leaf chlorophyll content; HI = Harvest index and GY = Grain yield (q/ha)

Table 3. General combining ability effects for important physiological traits in wheat

Parent	CGR	CT	CTD	LA	LAI	NDVI	SPAD_FL	SPAD_L	HI	GY
HD3117 (P1)	-0.07**	0.21*	0.30**	-33.69**	-0.16**	-0.18ns	-1.25 **	-0.77**	0.01 ns	0.44**
35th ESWYT-147 (P2)	0.04**	0.57**	-0.23**	-8.66**	-0.04**	-1.80**	0.84**	-0.55**	0.34 **	2.67**
NIAW34/PHW12// 43IBWSN-1187 (P3)	-0.07**	0.64**	0.04ns	13.17**	0.06**	0.27*	-0.63**	-0.75**	-0.22**	-1.06**
HD2967//HD2887// HD2946//HD2733 (P4)	-0.03**	-0.17ns	-0.41**	14.62**	0.07**	1.10**	-1.51**	-1.79**	-0.23**	-0.87**
DBW187 (P5)	0.11**	-0.17ns	-0.27**	-25.23**	-0.11**	-0.32*	1.11**	1.76**	-0.43 **	0.93**
HD 3226 (P6)	-0.01**	-0.31**	-0.22**	31.30**	0.14**	-0.14ns	1.52**	1.62**	-0.15*	-2.50**
HD3086 (P7)	-0.03**	-0.33**	0.28**	-35.81**	-0.17**	0.19ns	0.41**	-0.31**	0.23**	-1.05**
HDCSW18 (P8)	0.07**	-0.42**	0.52**	44.30**	0.21**	0.88**	-0.49**	0.81**	0.46**	1.44**
(GCA σ^2/SCA σ^2)	0.13	0.23	0.1	0.1	0.1	0.04	0.1	0.13	0.009	0.02

*: Least significant difference test at $p < 0.05$ level; **: Least significant difference test at $p < 0.01$ level; ns = non-significant

Table 4. Specific combining ability effects for the crosses highly significant for yield and key physiological traits

Cross	CGR	CT	CTD	LA	LAI	NDVI	SPAD_FL	SPAD_L	HI	GY
HD3117 (P1) X35th ESWYT-147 (P2)	-0.017**	0.148ns	0.256ns	-13.855**	-0.071**	1.369**	-0.628*	-1.875**	1.269**	0.632*
HD3117 (P1) XNIAW34/PHW12//43IBWSN-1187 (P3)	-0.137**	-0.080ns	0.688**	-16.430**	-0.063**	-0.046ns	2.396**	1.841**	1.264**	6.270**
HD3117 (P1)X HD2967//HD2887/HD2946//HD2733 (P4)	0.088**	0.073ns	-0.547*	57.121**	0.280**	0.953**	-1.689**	-2.302**	0.552**	7.532**
HD3117 (P1) XDBW187 (P5)	0.117**	0.106ns	-0.103ns	41.823**	0.207**	2.390**	-0.232ns	1.325**	2.438**	4.331**
35th ESWYT-147 (P2)X HD2967//HD2887/HD2946//HD2733 (P4)	0.020**	0.360ns	-0.424ns	-4.265**	0.001ns	-0.421ns	-3.724**	1.345**	2.034**	5.251**
35th ESWYT-147 (P2)XHD3086 (P7)	0.225**	0.217ns	0.173ns	8.876**	0.053**	1.161**	2.694**	-1.168**	1.253**	5.340**
35th ESWYT-147 (P2) XHDCSW18 (P8)	0.050**	-0.030ns	-0.082ns	70.188**	0.357**	2.640**	0.754**	0.506*	1.749**	13.555**
NIAW34/PHW12//43IBWSN-1187 (P3) XHD2967//HD2887/HD2946//HD2733 (P4)	-0.120**	0.531*	-0.609**	-70.037**	-0.357**	-0.171ns	-0.132ns	0.962**	1.370**	0.653*
NIAW34/PHW12//43IBWSN-1187 (P3)XDBW187 (P5)	-0.153**	0.215ns	-0.299ns	-100.728**	-0.513**	1.432**	-2.043**	-2.610**	-2.582**	7.495**
NIAW34/PHW12//43IBWSN-1187 (P3)X HD 3226 (P6)	0.187**	0.438ns	-0.268ns	184.802**	0.934**	2.078**	-1.599**	0.906**	1.095**	3.646**
NIAW34/PHW12//43IBWSN-1187 (P3)XHD3086 (P7)	0.367**	0.171ns	-0.845**	2.689*	0.028**	-1.588**	2.352**	0.864**	2.303**	6.672**
NIAW34/PHW12//43IBWSN-1187 (P3)XHDCSW18 (P8)	0.106**	-0.159ns	1.581**	79.006**	0.382**	3.557**	-1.237**	-0.627*	-0.018ns	3.481**
DBW187 (P5)XHD 3226 (P6)	0.080**	0.158ns	-0.609**	35.490**	0.188**	1.682**	3.038**	0.672**	-2.974**	1.566**
DBW187 (P5)XHD3086 (P7)	-0.056**	-0.057ns	0.046ns	25.451**	0.132**	-1.317**	-1.609**	1.797**	1.116**	0.798*
DBW187 (P5)XHDCSW18 (P8)	0.006ns	-0.105ns	-0.259ns	2.880*	0.019ns	2.328**	-1.699**	-2.577**	4.592**	5.290**
gca(j)	0.003	0.148	0.129	0.692	0.005	0.195	0.150	0.143	0.105	0.177
sca(ii)	0.011	0.513	0.449	2.400	0.020	0.676	0.522	0.495	0.363	0.613
sca(ij)	0.010	0.491	0.430	2.298	0.019	0.647	0.500	0.474	0.348	0.587
reci(ij)	0.009	0.418	0.366	1.959	0.016	0.552	0.426	0.404	0.297	0.501

*: Least significant difference test at $p < 0.05$ level; **: Least significant difference test at $p < 0.01$ level; ns: non-significant

longer breeding period for the development of hybrids, exploitation of these crosses by developing commercial hybrids is less likely to feasible. Only limited literature is available who have reported genetics of physiological traits, and some of the important ones are Kumar et al. (2015), Fillahi et al. (2017), Abas et al. (2018), Mohamed et al. (2019), Shamsabadi et al. (2019) Kamra et al. (2021), Mohamed et al. (2021), Biligin et al. (2022) and Fouad et al. (2022) who has estimated gca and sca for number of morpho-physiological traits, however, systematic interpretation keeping in view the physiological base is missing.

The magnitude of heterosis and a number of cross combinations showing heterosis over check variety HDCSW18 (P8) for grain yield per plant and its related agro-physiological traits are presented in Table 5. Out of 56 hybrids, some exhibited significant and desirable direction of standard heterosis for various agro-physiological traits such as crop growth rate (52.11) for cross combination HDCSW18 (P8) X 35th ESWYT-147 (P2), canopy temperature depression (51.28) for NIAW34/PHW12//43IBWSN-1187 (P3) X HDCSW18 (P8), grain yield (14.91) for cross combination DBW187 (P5) X HDCSW18 (P8), leaf area index (142.42) for hybrid NIAW34/PHW12//43IBWSN-1187 (P3) X HD 3226 (P6), normalized difference vegetation index (24.76) for cross combination NIAW34/PHW12//43IBWSN-1187 (P3) X HDCSW18 (P8), chlorophyll content for leaf (18.14) for HD 3226 (P6), X 35th ESWYT-147 (P2) and chlorophyll content for flag leaf (10.64) for the cross combination 35th ESWYT-147 (P2) X HD 3226 (P6).

The majority of hybrids flowered earlier than parents likely because of the dominant Vrn allele being accumulated in F_1s. The highest yielding parent was HDCSW18(P8) and 11 combinations displayed standard heterosis, which was maximum in DBW187 (P5) X HDCSW18 (P8) (14.91), a cross combination involving HDCSW18 as one of the parents and it was followed by 35th ESWYT-147 (P2) X HDCSW18 (P8) (12.39), HDCSW18 (P8) X 35th ESWYT-147 (P2) (12.11) and HD3117 (P1) X HD2967//HD2887/HD2946//HD2733 (P4) (11.83). Interestingly, most of these cross also shows standard heterosis for leaf area and LAI, a slight increase in harvest index and bolder grain. Gimenez et al. (2021) obtained similar findings for the different physiological traits. A similar level of heterosis was also realized by Sharma and Kamaluddin (2020) in their study on total protein content, chlorophyll content, proline content, chlorophyll stability index and grain yield per plant. Similar findings with respect to standard heterosis have been reported by Biligin et al. (2022), Found et al. (2022) and Kumawat et al. (2023). It is thus clear from the present study that there is the existence of sufficient genetic variability for various physiological traits, which can be used as a selection criterion at least to choose the parents for the crossing program and if feasible, can also be integrated into the selection strategy for yield consolidation. 35th ESWYT-147

Table 5. F_1 combinations with highly significant standard heterosis for yield and key physiological traits

Cross	CGR	CT	CTD	LA	LAI	NDVI	SPAD_L	SPAD_FL	HI	GY
HD3117 (P1) X NIAW34/PHW12//43IBWSN-1187 (P3)	-18.17 **	7.25 **	24.79 ns	-3.30 **	0.00	11.88 **	2.26 **	-1.97 ns	-2.29 **	1.75 **
HD3117 (P1) X HD2967//HD2887/HD2946//HD2733 (P4)	-20.01 **	5.15 *	-21.37 **	19.93 **	18.18 **	11.39 **	-15.81 **	-18.53 **	1.14 **	11.83 **
HD3117 (P1) X DBW187 (P5)	19.24 **	8.05 *	-11.97 *	-13.04 *	-12.12 ns	13.86 **	-8.75 **	-9.66 ns	2.31 ns	5.65 **
35th ESWYT-147 (P2) X HD3086 (P7)	3.99 **	12.08 **	-31.62 ns	-1.27 **	0.00	13.86 **	-5.22 **	4.93 **	-1.08 ns	11.06 **
35th ESWYT-147 (P2) X HDCSW18 (P8)	-7.54 **	12.40 *	-41.03 ns	37.53 **	36.36 **	15.84 **	7.76 **	4.53 **	3.74 ns	12.39 **
NIAW34/PHW12//43IBWSN-1187 (P3) XDBW187 (P5)	-12.33 *	13.53 **	-29.91 **	-41.97 **	-45.45 **	12.87 **	-9.46 **	-9.59 **	-29.33 **	3.04 **
NIAW34/PHW12//43IBWSN-1187 (P3) X HD3086 (P7)	44.10 **	14.17 **	-67.52 **	23.24 ns	24.24 ns	12.38 **	0.00 ns	-2.43 *	-1.44 ns	1.74 **
DBW187 (P5) X HD3086 (P7)	20.69 **	3.06 ns	-44.44 ns	-1.88 **	0.00 *	9.41 **	6.56 **	1.18 ns	3.77 **	2.46 **
DBW187 (P5) X HDCSW18 (P8)	4.92 **	4.19 ns	-51.28 *	26.28 **	27.27 **	17.33 **	4.45 ns	-0.33 **	6.42 **	14.91 **
HD 3226 (P6) X HD2967//HD2887/HD2946//HD2733 (P4)	32.99 ns	3.54 ns	-47.01 **	-0.59 **	0.00 **	8.42 **	1.20 *	-0.20 ns	5.45 **	-14.68 **
HD 3226 (P6) XDBW187(P5)	-1.27 **	3.38 ns	-54.70 **	-3.23 **	-3.03 **	10.40 **	5.86 **	15.37 **	6.39 **	-9.78 **
HDCSW18 (P8) X35th ESWYT-147 (P2)	52.11 **	-0.32 *	-2.56 ns	79.90 **	81.82 **	13.86 **	-6.07 ns	-3.09 ns	-2.90 ns	12.11 **
SE	0.59	0.012	0.51	2.77	0.02	0.78	0.6	0.57	0.42	0.7

*: Least significant difference test at $p < 0.05$ level; **: Least significant difference test at $p < 0.01$ level; ns: non-significant

and HDCSW 18 have been identified as very good combiners for the majority of physiological traits and grain yield and, therefore, are strongly recommended to be part of the wheat improvement breeding strategy. Presence of strong sca effect along with the exploitable level of heterosis for grain yield, largely because of improved LAI and harvest index in some of the crosses like DBW187(P5) X HDCSW18 (P8), NIAW34/PHW12//43IBWSN-1187 (P3) XDBW187 (P5) and HD3117 (P1)X HD2967//HD2887/HD2946//HD2733 (P4) open an opportunity for using the identified parent for diversification of cms and restorer gene in this background. The large effect may also be due to the linkage of favorable alleles in the repulsion phase and dispersed among the parents and, therefore, requires strong population improvement activities to break the undesirable linkages to provide new opportunities for accumulating favorable genes in a single genotype. Photosynthetic improvement, along with improved canopies for better light capturing and optimal formation and filling of the sink (Murchie et al. (2023) under an optimum environment (Sagar et al. 2014), is necessary for furthering the gain in grain yield. Indication of sufficient genetic variability, clearly worked out genetics and exploitable level of standard heterosis for all of these traits and processes in the breeding material through the present study demonstrate the feasibility of further yield enhancement through directed crosses and selection involving important physiological traits and processes.

Authors' contribution

Conceptualization of research (SKS, RY); Designing of the experiments (SKS, RY); Contribution of experimental materials (RY, KG, MK, NB, PB, TR); Execution of field/lab experiments and data collection (SKS, NS, RA, RN, SK); Analysis of data and interpretation (SK, RY, MK); Preparation of manuscript (SKS, RY, KG, MK, NP, PB, TR, NS, RA, BN, SK).

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