



## Original article

Deciphering the environmental impact on spike architectural traits for grain yield consolidation in bread wheat (*T. aestivum* L.)

Manjeet Kumar<sup>a,\*</sup>, Rajbir Yadav<sup>a,\*</sup>, Kiran B. Gaikwad<sup>a</sup>, Prasanth Babu<sup>a</sup>, Naresh Kumar Bainsla<sup>a</sup>, Palaparathi Dharmateja<sup>a</sup>, Anis Ahmad Chaudhary<sup>b</sup>, Riham Ansari<sup>a</sup>

<sup>a</sup> Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

<sup>b</sup> Department of Biology, College of Science, Imam Mohammad Ibn Saud Islamic University (IMSIU), Riyadh 11623, Saudi Arabia

## ARTICLE INFO

## Article history:

Received 19 June 2021

Revised 30 December 2021

Accepted 2 January 2022

Available online 15 January 2022

## Keywords:

Grain Yield

Spike architectural traits (SATs)

Early sown

Timely sown

## ABSTRACT

The realization of grain yield in wheat is decided by source-sink balance under prevailing environmental conditions. Management conditions like changing the sowing time influence the source-sink capacity through modification in agronomic traits. Therefore, this experiment was conducted to decipher the influence of spike architectural traits (SATs) on grain yield and to open avenues for further grain yield enhancement. Comparatively early sowing over timely sowing gives the advantage of realizing higher grain yield with a positive relationship with SATs namely spike length, spikelets per spike, individual spike weight, individual grain weight, number of grains per spikelet, grain length, and grain width of upper and lower spike portion. Confirmatory factorial analysis revealed that spike length, spikelets per spike, individual spike weight, grains per spikelet were having a significant effect in deciding grain yield in early sown. The presence of a significant effect of genotype by environment interaction over grain yield and SATs allows the exploitation of available genotypic and environmental variability for further yield enhancement. GGE analysis on transformed and standardized grain yield-trait (GY-trait) combinations was used in the selection of genotypes having high GY-trait combinations for both sowing times. In early sowing, WG 11 was the best for high GY with high individual spike weight; grain length and grain width at lower and upper parts of the spike; and shorter days to 50% flowering. Genotypes exclusively having the high GY-trait combination along with low values of remaining GY-trait combinations were also selected with genotype focused GGE approach.

© 2022 The Authors. Published by Elsevier B.V. on behalf of King Saud University. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

Wheat is one of the oldest cereal crops of the world's food crops, and a major source of one-fourth of total dietary protein and one-fifth of calories across the globe (Cao et al. 2020; <http://www.fao.org/faostat/en/#data/CC>). Globally the current growth rate of wheat ~0.9% per year (Ray et al., 2013) would fall very short of the required 60% yield enhancement with ~1.7% gain per year (<https://www.wheatinitiative.org/vision-paper>, n.d.). Wheat

being most suffered cereal crop from global warming; unpredictable fluctuation of temperature at the time of flowering and grain filling hampers in sustaining and enhancing the wheat productivity (Yadav et al., 2017b, 2018), and again grain yield is bound to be negatively affected under changing climatic scenario (Cao et al., 2020). Since the green revolution across the globe was the direct result of the integration of better agronomy management like high fertilizer dose and responsive genotypes in which high yielding responsive genotypes were very efficient in conversion of agronomic inputs like fertilizer into grain yield. Again, integration of genotype by environment interactions along with agronomic management and responsive genotypes could help to achieve the target for food security for the everlasting growing population. Early sowing (ES) along with responsive genotypes under conducive weather conditions may be one of the best-integrated practices, which would provide longer crop duration leading to higher yield, and chances of escape from terminal heat (Yadav et al., 2017b). In response to the targeted efforts of the

\* Corresponding authors.

E-mail addresses: [manjeetbhu615@gmail.com](mailto:manjeetbhu615@gmail.com), [manjeet@iari.res.in](mailto:manjeet@iari.res.in) (M. Kumar), [rajbiriyadav@yahoo.com](mailto:rajbiriyadav@yahoo.com) (R. Yadav).

Peer review under responsibility of King Saud University.



Production and hosting by Elsevier

<https://doi.org/10.1016/j.sjbs.2022.01.007>

1319-562X/© 2022 The Authors. Published by Elsevier B.V. on behalf of King Saud University.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

research community and policymakers, the area under ES is being continuously increased in the North-Western Plain Zone of India. However, systematic breeding efforts for developing responsive genotypes for ES are at the naïve stage. In this direction, the world's first very high-yielding bread wheat variety for ES adapted to conservation agriculture was developed and released for commercial cultivation by ICAR-IARI, Delhi, India (Yadav et al., 2017a). Since then focused approach for ES of wheat is gaining attention among the wheat community including researchers and farmers in respect of changing climatic conditions for different wheat growing zones.

The targeted exploitation of genetic variation for yield component traits is required for continuous yield enhancement (Würschum et al., 2018). Therefore, an in-depth understanding of component traits would be a key step for making fine-tuning among traits and prevailing environmental conditions for further yield enhancement. Grain yield in wheat is generally more related to grain number than to the average grain weight (Fischer, 2008) due to the high plasticity of the number of grains than grain size (Sadras and Slafer, 2012). Likewise, the grain yield of mega varieties over the decades has been improved with a linear increase in the number of grains per meter square (Ferrante et al., 2017; Serrago et al., 2013) without significant change in grain weight. Our recent study over genetic gain based on historical mega varieties released from 1900 to 2016 for NWPZ, India, indicated that yield gain has come through the linear increase in days to heading, biomass, tiller number, grains per spike and TGW (Yadav et al., 2021). The number of grains per unit area is highly influenced by spike fertility (Foulkes et al., 2011; Reynolds et al., 2012) and the number of spikelets per spike (Wolde et al., 2019). Wheat spike consists of a varying number of spikelets attached to each rachis node with a terminal spikelet at its apex. Each spikelet generates several numbers of florets up to twelve attached to the rachilla (Sakuma et al., 2019). The number and arrangement of each spikelet are under strong genetic, hormonal, and environmental control (Boden et al., 2015; Dixon et al., 2018; McSteen, 2009; Poursarebani et al., 2015), and spike fertility over the spike architecture is also under the strong genetic and environmental influence.

The yield of crop plants is defined by the acquisition and allocation of photosynthates in sink organs (Wolde et al., 2019). Grain growth in modern wheat cultivars is not strongly limited by the source (Borrás et al., 2004; Pedro et al., 2011) but is sink limited (Borrás et al., 2004; Miralles and Slafer, 2007; Serrago et al., 2013; Zhang et al., 2010). The major determinants of sink size are the number of spikelets per spike, floret/grain number per spikelet, and dry matter accumulation (Wolde et al., 2019). The number of grains per spikelet depends on floret primordia survival at anthesis than the number of initiated floret primordia per spikelet at the early stage (González-Navarro et al., 2015). Moreover, generation and degeneration of floret primordia are variable along with spikes, and chances of the fertility of more distal florets are less in the apical or basal spikelets (González-Navarro et al., 2015; Prieto et al., 2018). The grain yield along with spike architecture is very complex and polygenic (Foulkes et al., 2011; Parry et al., 2011; Reynolds et al., 2009). The variability in inflorescence/spike architecture is decided by the integrative network of developmental pathways and environmental signals (Gao et al., 2019).

Grain yield being the quantitative trait and decided by the number of component traits is highly influenced by genotype by environment interaction (GEI). The GEI reduces the heritability of grain yield and its component traits resulting reduction in response to selection, accuracy and predictability of statistically superior genotypes under contrasting environments (Gerard et al., 2020). Therefore, it is very plausible that elucidation of genotype by environment interaction (GEI) over grain yield and spike architectural traits being an integral component in deciding final

grain yield is of utmost importance to open avenues for further grain yield enhancement.

## 2. Material and methods

The forty-three advance wheat lines were tested for grain yield (GY), days to 50% flowering (DF), and spike architectural traits (SATs) in early sowing (ES) and timely sowing (TS) conditions over two consecutive years, i.e. 2018–19 and 2019–20, respectively in the experimental farm of ICAR-Indian Agricultural Research Institute, Delhi, India. The composition of environments was ES 2018–19; TS 2018–19 for the year 2018–19; and ES 2019–20 and TS 2019–20 for the year 2019–20, likewise, forty-three genotypes were named as WG1 to WG43 (Table 1; Supplementary Table 1). The experiment was conducted with two replications of  $5 \times 1.2$  m<sup>2</sup> plot size in randomized block design, and ES 2018–19 and ES 2019–20 sowing were conducted on 25th Oct in both years, while TS 2018–19 sowing was conducted on 10<sup>th</sup> Nov 2018, and TS 2019–20 was conducted on 11th Nov 2019. For the SATs study uniform looking ten spikes from the main tiller (tagged at the time of spike emergence) were harvested from each replication at the time of maturity over the environments. To understand the G × E interaction (GEI) over GY, DF, and SATs, data were recorded for respective traits (Table 1). The data on SATs were recorded for individual spike weight (ISW), spikelets per spike (SPS), and for an in-depth understanding of GEI at different positions of spike focusing on the side and central florets, each spike was cut into lower and upper half to take data separately. The notations of the SATs, based on floret attachment position on rachis i.e. side and central florets of each spikelet, were designated as given in Table 1. The data on individual grain weight (IGW), grain length (GL), and grain width (GW) of side and central florets having in consideration of the differential effect of environments were taken. The GL and GW were calculated with the help of smart grain software with scale settings (<https://www.quantitative-plant.org/software/smartgrain>).

**Table 1**  
Notations for grain yield and spike architectural traits (SAT) and environments.

Category	Notation	Description
A. Yield	GY	Grain yield (q/ha)
B. Flowering	DF	Days to 50% flowering
C. Spike architecture traits (SAT)		
i. Spikelets	SPS	Spikelets per spike
ii. Spike Weight	ISW	Individual Spike Weight
iii. Spike length	SL	Spike length (cm)
Lower half of spike (iv.-viii)	LGPS	Grains per spikelet of lower half of spike
	LSIGW	Individual grain weight (IGW) of <i>SIDE</i> florets of lower half of spike (mg)
	LCIGW	Individual grain weight (IGW) of <i>CENTRAL</i> florets of lower half of spike (mg)
	LCGL	Grain length of <i>CENTRAL</i> florets of lower half of spike (mm)
	LCGW	Grain width of <i>CENTRAL</i> florets of lower half of spike (mm)
Upper half of spike (ix.-xiii)	UGPS	Grains per spikelet of upper half of spike
	USIGW	Individual grain weight (IGW) of <i>SIDE</i> florets of upper half of spike (mg)
	UCIGW	Individual grain weight (IGW) of <i>CENTRAL</i> florets of upper half of spike (mg)
	UCGL	Grain length of <i>CENTRAL</i> florets of upper half of spike (mm)
	UCGW	Grain width of <i>CENTRAL</i> florets of upper half of spike (mm)
D. Environments		
ES 2019–20		ES 2019–20
ES 2018–19		ES 2018–19
TS 2019–20		TS 2019–20
TS 2018–19		TS 2018–19
Sowing Time		ST

The boxplots of all traits under study were generated to describe the center values and spread of variation of data to minimize the outliers' effect of small sample size with ggplot2 package v3.3.5 (Wickham H., 2016). The analysis of variance for each environment and combined environment for all the traits were carried with R-based STAR software and RGxE (STAR, version 2.0.1; Dia, M., et al., 2017; R Core Team, 2020). Analysis of variance was performed considering all variable random effects, while, combined analysis of variance was performed considering the sowing time (ST) as the fixed effect and remaining variables as random effects, and replications were nested within the environment (ST and Year) with following model (Eq. (1) and Eq. (2)).

$$Y_{ir} = m + G_i + R_r + E_{ir} \quad (1)$$

$$Y_{ijk} = m + G_i + S_j + Y_k + R_r(S_jY_k) + GS_{ij} + GY_{ik} + SY_{ik} + GSY_{ijk} + E_{ijk} \quad (2)$$

To draw information about the influence of DF and SATs over GY, and their interrelationship with each other, genetic correlation, regression and heatmap analysis with BLUE (Best Linear Unbiased Estimate) values were carried out. The BLUE (Best Linear Unbiased Estimate) analysis was carried out with R-based META-R software (CIMMYT) separately for ES and TS over years due to positive correlation in respective sowing time to get the best estimated value having minimum residual variance. The exploratory and confirmatory factor analysis (Brown T.A., 2015) were performed to estimate the latent component traits affecting significantly GY.

GEI was performed with Additive Main effects and Multiplicative Interaction model (AMMI) (Gauch and Zobel, 1988; Zobel et al., 1988) and Genotype main effects and Genotype Interaction model (GGE) analysis (Yan et al., 2000) having into consideration the main and interaction effects are equally important. In both models, singular value decomposition (SVD) is subjected to original two-way data ("G" genotypes tested in "E" environments) to produce the two-component matrix i.e. G matrix and E matrix, which is graphically displayed with genotype and environment scores based on PCs/singular/eigenvalue as biplot (Gabriel, 1971; Gauch and Zobel, 1988; Gauch 2006; Yan et al., 2000; Yan, 2001, Yan and Tinker, 2006; Zobel et al., 1988).

Eq. (3) general linear model of AMMI was applied for finding the different effects and graphical displays.

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_{n=1}^N \lambda_n \gamma_{gn} \delta_{en} + \theta_{ge} \quad (3)$$

In GGE, SVD with column centric scaling was subjected to data minus environment means (environment centered data) to get G and E scores i.e.  $\sum_{n=1}^N \lambda_n \gamma_{gn} \delta_{en}$  of Eq. (4), for the graphical display of mixed effects of G and GE interaction (Gauch, 2006; Yan, 2002; Yan et al., 2000).

$$Y_{ge} - \mu - \beta_e = \sum_{n=1}^N \lambda_n \gamma_{gn} \delta_{en} + \theta_{ge} \quad (4)$$

Yan and Reid (2018) proposed the novel approach to incorporate the multiple component traits in genotype selection by genotype by yield  $\times$  trait (GYT) biplot. In this approach, the GYT table was generated by multiplying the grain yield with SATs and inverse of DF i.e. DF<sup>-M</sup> as such without giving due weightage to anyone (Supplementary Table 3). Since, DF was negatively correlated in early as well as in timely sowing, but to have the positive impact of DF, it was inverted by uniformly subtracted the DF of each genotype from two times of average of DF in respective sowing time as a common factor. The GYT table was initially standardized with standard-scaler as the same method used by Yan and Reid (2018). In this approach, GGE analysis was performed with

GY-trait centered (as tester) G + GE and GY-trait/column metric preserving SVD to focus on cluster formation of GY-trait combinations as mega-environment analysis (Yan and Frégeau-Reid 2018). To select genotypes having an exclusively high value of specific GY-trait combination along with the low value of remaining GY-trait combination for studying the impact of that trait on GY, a genotype-centered (as tester) G + GE and genotype/column metric preserving SVD. All these analysis were performed using ggplot2 package v3.3.5 in R (Wickham H., 2016; R Core Team, 2020).

### 3. Results

The boxplots of grain yield (GY), days to 50% flowering (DF), and spike architectural traits (SATs) over the environments have been demonstrated in Fig. 1 and Supplementary Fig. 1, with mean values as "\*". The average values for GY, DF, and SATs of ES over both years were higher than the average values of TS having higher value ranges from 0.67% for LCGW to 8.18% for SPS followed by 7.98% for UCIGW; and 7.57% for UGPS (Table 2). The average of GY in ES had gain of 5.83% over TS, whereas, SATs in ES had superiority with an average of 4.80%. The spread of variability between the first quartile and third quartile for most of the traits was higher in ES than TS. Analysis of variance indicated the presence of significant variations among the genotypes for grain yield, DF and SATs in each environment. The broad-sense heritability for each trait was also quite high ranges from 0.74 (UCGW in ES 2018–19) to 0.99 (DF; LCGL; UCGL in ES 2018–19; and DF in ES 2019–20) in each environment (Supplementary Table 4).

### 4. Associations among the variables and factor analysis over the early (ES) and timely sown (TS)

The differential regression relationships of GY with DF and SATs over ES and TS were observed (Fig. 2 and Supplementary Fig. 2). The DF had a negative relationship with GY over both sowing conditions, however, the magnitude of the negative relationship was higher in TS (R = -0.38; R<sup>2</sup> = 0.144) than ES (R = -0.16; R<sup>2</sup> = 0.026) (Fig. 2). In ES, GY comparatively had low to moderate significant positive relationship with SATs viz., with SL (R = 0.33; R<sup>2</sup> = 0.109); LCGL (R = 0.34; R<sup>2</sup> = 0.12); UCGL (R = 0.31; R<sup>2</sup> = 0.096); LGPS (R = 0.26; R<sup>2</sup> = 0.068); UGPS (R = 0.28; R<sup>2</sup> = 0.078); however, in TS, no such relationship except the weak relationships (p value =>0.2) of GY with LCGL, LGPS and UGPS were observed (Fig. 2). The remaining SATs except for SPS also had positive relationships but with a high p-value with GY in ES, while, SPS had a negative relationship with GY in TS (R = -0.29; R<sup>2</sup> = 0.078) (Supplementary Fig. 2). This regression relationship indicates that the expression of the spike length, number of grains per spikelet in upper and lower half of spike (LGPS and UGPS) and grain length of central floret of upper and lower half of spike (LCGL and UCGL) were having a larger influence in deciding the GY only in ES. The predictability of UGPS, LCGL and UCGL for the next generations and different environment is also high due to their high heritability observed in combined analysis of GEI. However, SL and LGPS were having the quite low heritability (0.41 each) in combined analysis of variance. Therefore, SL and LGPS (having high heritability in ES) exclusively would be highly effective in exploitation for yield maximization in ES. While, UGPS, LCGL and UCGL can be exploited for yield maximization in ES, however, these traits would also perform quite well in TS due to their high heritability. In TS, very little to no relationship of SATs with GY indicates that their major influence on deciding the GY comes in combinations with each other and other un-accounted traits under this study. Fig. 3a & Fig. 3b represent the genetic correlation matrix of traits under study, DF had negative correlations for most of SATs except positive correlation with SPS

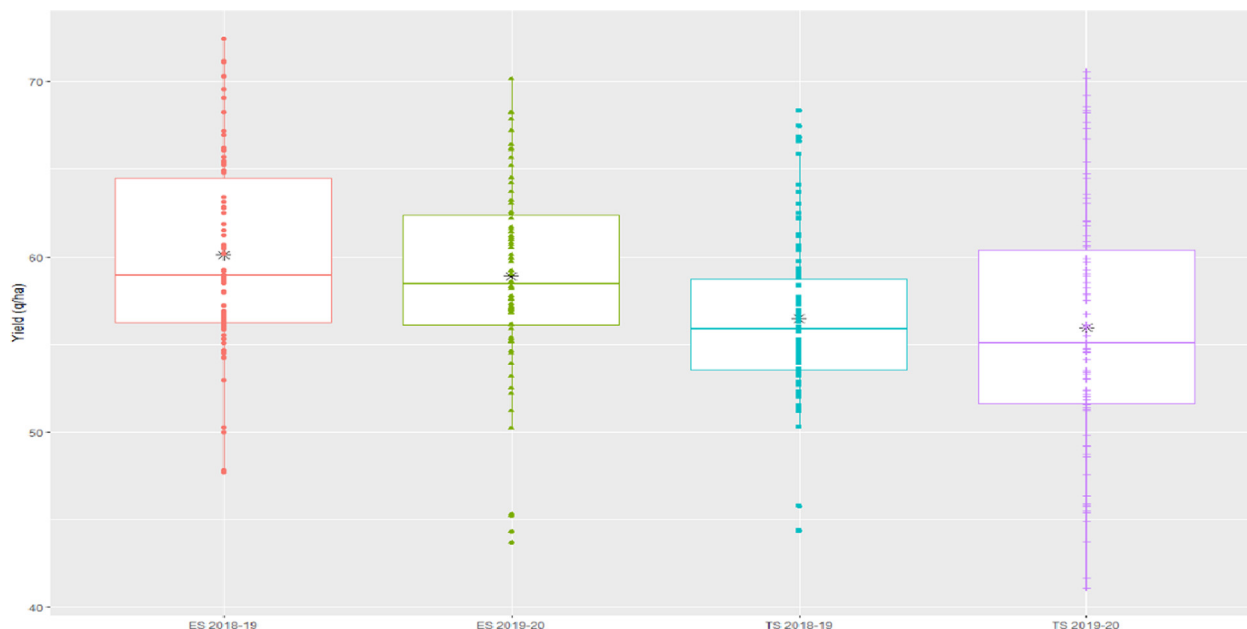


Fig. 1. Boxplot of grain yield (GY) across the early sown (ES) and timely sown (TS).

and SL in both sowing times. In factor analysis, it was observed that SATs namely SL, ISW, SPS, LGPS and UGPS were having significant effect with 0.35, 0.09, 0.40, 0.10, 0.11, respectively, in deciding the grain yield (GY) in ES, while, there was no such relationship significant effects were observed in TS (Table 3).

The generated heat map illustrates the creation of three major groups for traits understudy and two major groups of genotypes understudy in both sowing time (Supplementary Fig 3 a & b). The grouping pattern of traits has remained similar in both sowing conditions. However, the grouping of genotypes changes over the sowing condition. In ES, high GY genotypes were having two distinct patterns, some of them like WG 29, WG 18, WG 27, WG 7, WG 11 were having the high IGW, grain length (GL), grain width (GW), while, genotypes, WG 25, WG 33, WG 28 had high DF, SL, and SPS. In TS, WG 18, WG 27, WG 11, WG 38, and WG 29 were having high IGW, GL, GW, however, one high GY genotype i.e. WG25 had the high SL and SPS. Therefore, the exploitation of DF, SL, and SPS along with trait optimization with high IGW, GL, GW, and other un-accounted traits for yield maximization is more plausible in ES. In TS, trait optimization with high IGW, GL, GW, and other un-accounted traits is the right approach for yield maximization.

### 5. Genotype by environment interaction

The combined analysis with the AMMI model revealed the significant effects of G and E and GE on the GY, DF, and SATs. Combined analysis of variance indicated the presence of significant variations among the main effects of genotypes, sowing time and interaction effects between the genotypes and sowing time; and genotypes, sowing time and years for all the traits. However, broad-sense heritability was reduced drastically for most of the traits except ISW (0.78); LCGL (0.77); LCGW (0.79) and UCGL (0.71) (Table 3). The percent contribution of G and ST main effects was relatively higher than interaction effects. The GY, SPS, SL, UGPS, LSIGW, USIGW, UCIGW and LCGL with percent variation, 45%, 85.9%, 58.8%, 46.7%, 46.6%, 42.8%, 49.6% and 51% respectively, were affected by ST main effect, while, DF, LCIGW, and LCGW with percent variation 40.4%, 38.7%, and 75.2% respectively, were affected by G effect (Table 4). Therefore, the presence of variation

controlled by each factor including interaction effects allows their exploitation for maximizing the GY for target and unprecedented environmental conditions. AMMI 1 biplot is generated by placing the additive effects of G and E as a PC1 score against the performance of the trait under study (Gauch and Zobel, 1997). The genotypes and environments had the same sign on the PCA axis, their interaction is positive; and vice versa (Zobel et al., 1988). AMMI 1 of GY, indicated the superiority of ES over TS since the former fell right to average performance. Likewise, the placed genotypes into the right sector to average performance with WG18 and WG 11 as their extreme genotypes had superiority over left sector genotypes (Fig. 4). The genotypes, WG 11, and WG 18 having a high mean performance with low ASV values are suitable for wider adaptability (Supplementary Table 5).

The standardized GYT table was utilized to visualize the associations among the traits, trait profile of the genotypes with GGE biplot analysis. All GY-trait combinations were having a positive correlation because of shared GY as a common factor in both sowing times (Supplementary Fig. 4 a & b). The GY-trait combinations, two clusters in ES, while, three clusters in TS were formed. The

Table 2  
The per cent increase in GY, DF and SAT in early sown (ES) over timely sown (TS).

	Traits	Gain (%)
1	GY	5.83
2	DF	3.38
3	ISW	4.68
4	SPS	8.19
5	SL	2.88
6	LGPS	3.74
7	UGPS	7.57
8	LSIGW	6.35
9	USIGW	5.62
10	LCIGW	4.22
11	UCIGW	7.98
12	LCGL	4.56
13	LCGW	0.67
14	UCGL	3.44
15	UCGW	2.56

**Table 3**  
Combined analysis of variance over the environments for grain yield (GY), days to 50% flowering (DF) and spike architectural traits (SATs).

S.V	Df	DF	GY	ISW	SPS	SL	LGPS	UGPS	LSIGW	USIGW	LCIGW	UCIGW	LCGL	LCGW	UCGL	UCGW
Gen	42	25.193***	14.367***	0.118***	0.979***	0.385***	0.038***	0.07***	14.74***	11.041***	13.221***	9.403***	0.17***	0.048***	0.213***	0.05***
ST (Early & Timely)	1	3.244**	26.287***	0.116***	12.607***	1.191***	0.057*	0.11***	22.173***	17.05***	9.891***	21.59***	0.254***	0.003	0.314***	0.078*
Year	1	0.879*	0.218	0	0.018	0	0	0	0	0	0	0.233	0	0	0	0
Reps within (YEAR & ST)	4	0.005	0.051	0	0	0	0	0	0	0.012	0	0	0	0	0	0
ST × Gen	42	31.728***	6.985***	0.015	0.591***	0.195***	0.045***	0.027***	6.403***	5.688***	4.102***	8.313	0.05***	0.007***	0.046***	0.013***
Year × Gen	42	3.062*	0.006	0.006	0.162*	0.104***	0	0	1.197*	0.988***	1.402	0	0.004	0	0	0.001
Year × ST	1	0	0	0	0	0	0	0.001	0	0.236	0.081	0.026	0	0	0	0
Year × ST × Gen	42	1.022	6.211***	0.028	0.167***	0.069*	0.009***	0.02***	2.101***	2.79***	3.965***	2.248***	0.013***	0.003***	0.006**	0.005**
Residuals	168	0.355	1.245	0.001	0.152	0.081	0.01	0.007	0.995	2.012	1.468	1.693	0.007	0.003	0.016	0.011
Genotypic & Interactive variances	Gen	6.298	2.826	0.026	0.204	0.07	0.01	0.018	3.386	2.515	2.955	2.351	0.041	0.012	0.053	0.012
	ST × Gen	7.676	0.193	0	0.106	0.031	0.009	0.002	1.076	0.725	0.034	1.516	0.009	0.001	0.01	0.002
	Year:Gen	0	0.454	0.001	0.003	0.006	0	0	0.051	0	0	0	0	0	0	0
	Year × ST × Gen	0.333	2.483	0.014	0.008	0	0	0.007	0.553	0.389	1.249	0.278	0.003	0	0	0
Phenotypic variance		10.533	4.705	0.033	0.411	0.17	0.024	0.026	5.013	4.938	4.596	4.837	0.054	0.015	0.074	0.024
Heritability (Broad Sense)		0.598	0.601	0.78	0.496	0.415	0.401	0.667	0.675	0.509	0.643	0.486	0.773	0.797	0.719	0.501
Percent variation	Gen	40.4	24.6	42.7	6.7	19.0	24.0	29.8	31.0	27.7	38.7	21.6	34.2	75.2	35.8	31.6
	ST	5.2	45.0	40.0	85.9	58.8	35.6	46.7	46.6	42.8	29.0	49.6	51.0	5.3	52.6	49.3
	ST × Gen	50.8	12.0	5.1	4.0	9.6	28.3	11.5	13.4	14.3	12.0	19.1	10.1	10.8	7.8	8.0
	YEAR × ST × GEN	1.6	10.6	9.8	1.1	3.4	5.7	8.5	4.4	7.0	11.6	5.2	2.5	4.7	1.1	3.4

GY × ISW, GY × SL, GY × SPS, GY × LGPS, and GY × UGPS were fell into the same cluster irrespective of sowing time. The GY × DF<sup>M</sup> (inverse of original DF) was clustered with GY combinations of IGW, GL, and GW at all positions of the spike in ES, whereas, it came with GY × LCGL, GY × UCGL, GY × LCGW, and GY × UCGW in TS.

Fig. 5a represented the trait profiles of the genotypes with the “Which-won-where” pattern (Yan and Fréreau-Reid, 2018). The vertex genotype of the biplot has the largest values for the GY-trait combinations within the corresponding sector (Yan and Reid, 2018). In ES, WG 11 had the largest values for GY × LCIGW, GY × UCIGW, GY × LSIGW, GY × USIGW, GY × DF<sup>M</sup>, GY × LCGW, GY × UCGW, GY × UCGL, and GY × LCGL, indicating that WG 11 is best for high GY with high IGW, GL, GW at all positions and shorter DF<sup>M</sup>. Likewise, other genotypes were also identified for GY-trait combinations like WG 29 for GY × ISW and GY × SL; and WG 26 for GY × LGPS, GY × UGPS, and GY × SPS in ES(Fig. 5a). Based on the genotype-centered GGE, genotypes having an exclusively high value of specific GY-trait combination along with low values of remaining GY-Trait combinations were selected. The grain yield of these genotypes would be largely decided by a specific component trait. In ES, the genotypes namely WG 17, WG 6 for UGPS; WG 28, WG 42, WG 12 for LGPS; WG 26, WG 33 for SPS, WG 43, WG 25 for SL; WG 2, WG 14 for UCIGW etc., were identified for these traits which largely influence the GY (Fig. 5b).

In TS, out of two sectors, a large sector was having all the GY-Trait combinations with WG 40 and WG 11 as best genotypes, and in the second sector, WG 33 was found best for GY × SPS, which are overlapping with the 1<sup>st</sup> sector also (Supplementary Fig. 5a). Likewise, genotypes having the high value of specific GY-trait were identified in TS (Supplementary Fig. 5b). In ES and TS, the best genotypes were identified based on genotype-focused (row centric) SVP and GY-trait combination/tester-centered G + GE biplot (Supplementary Fig 6a and 6b).

### 6. Discussion

Wheat being a staple crop is classified as a major source of protein and one-fifth of the dietary calorie intake across the continents (Cao et al. 2020; <http://www.fao.org/faostat/en/#data/CC>). The gap in projected wheat grain demand and supply by 2050 due to stagnation of genetic gain and changing climatic conditions are the real future challenges (Cao et al., 2020; Ray et al., 2013; Yadav et al., 2017b). Therefore, designing the more efficient selection criteria like spike fertility along with grain yield (Alonso et al., 2018) and incorporation of fine-tuned traits under prevailing and projected climate are the necessity. Since spring wheat can germinate a wide range of temperatures, ranging from 4 to 25 °C, early sowing in the 3rd phase of October allows higher biomass accumulation and escaping from the terminal heat stress ultimately higher grain yield (Yadav et al., 2017b, 2018). To understand the impact of early sowing vs. timely sowing on grain yield and spike architectural traits, and to find avenues of designing the breeding strategies for the wheat improvement were carried out. We found that ES was having superiority over TS for GY with 5.83%, SATs range from 0.67% to 8.18%. This small difference of average gain i.e. 1.03%, between GY and SATs indicates that the SATs play a very crucial role in deciding GY. The spread of variability between the first quartile and third quartile for most of the traits was higher in ES than TS, which indicates that ES gives more plasticity in the expression of traits. In ES, the increment in the value of SATs representing the sink size directly or indirectly along with other unaccounted traits is responsible for this yield gain. The assimilation of photosynthates in the source and their acquisition and allocation of photosynthates in sink organs define the grain yield (Wolde

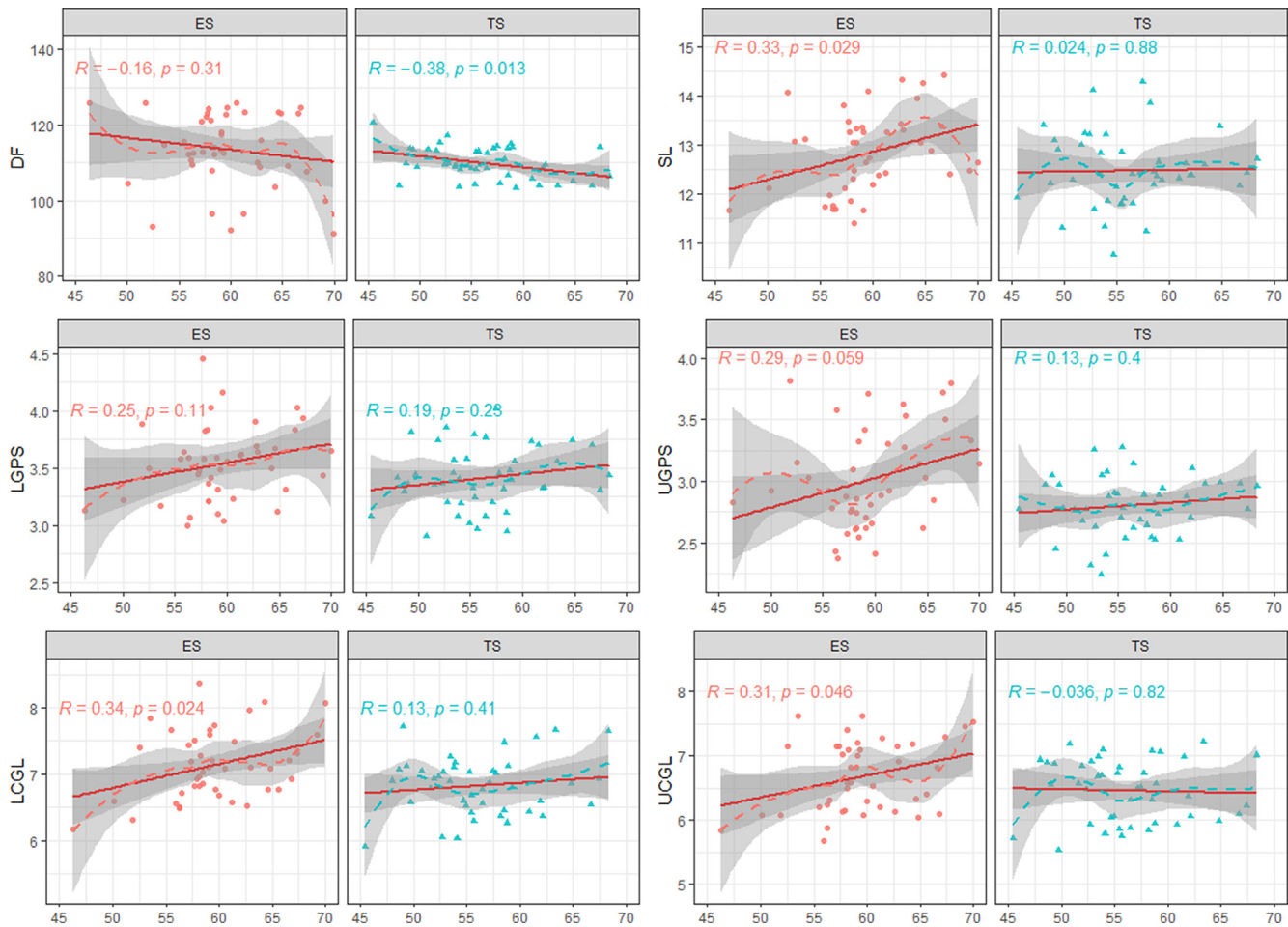


Fig. 2. Regression of DF, SL, LGPS, UGPS, LCGL and UCGL over GY in early sown (ES) and timely sown (TS).

Correlation matrix under Early sown condition

		r value											r value		
p value	DF	-0.19	0.09	0.32	0.28	0.13	-0.03	-0.44	-0.36	-0.38	-0.27	-0.25	-0.49	-0.28	-0.53
	-0.219	GY	0.25	-0.04	0.36	0.29	0.31	0.16	0.15	0.1	0.19	0.38	0.16	0.34	0.33
	-0.575	-0.109	ISW	0.13	0.32	0.18	0.43	0.22	0.1	0.42	0.29	0.34	0.18	0.31	0.22
	-0.034	-0.799	-0.415	SPS	0.56	0.41	0.11	0.07	0.08	-0.01	0.14	0	0.06	0.05	0.12
	-0.066	-0.019	-0.036	0.000	SL	0.5	0.35	0.25	0.25	0.31	0.31	0.33	0.26	0.27	0.25
	-0.388	-0.059	-0.256	-0.006	0.000	LGPS	0.47	0.12	0.06	0.07	0.16	-0.03	0.16	0.03	0.2
	-0.833	-0.040	-0.003	-0.483	-0.023	-0.001	UGPS	0.02	0.01	-0.03	-0.07	-0.04	-0.07	0.13	0.03
	-0.003	-0.303	-0.152	-0.646	-0.101	-0.456	-0.899	LSIGW	0.84	0.76	0.7	0.81	0.73	0.71	0.72
	-0.018	-0.343	-0.530	-0.618	-0.100	-0.683	-0.941	0.000	USIGW	0.74	0.77	0.58	0.77	0.53	0.78
	-0.012	-0.520	-0.005	-0.931	-0.041	-0.67	-0.833	0.000	0.000	LCIGW	0.89	0.49	0.84	0.58	0.78
	-0.079	-0.231	-0.063	-0.362	-0.046	-0.29	-0.638	0.000	0.000	0.000	UCIGW	0.46	0.72	0.6	0.79
	-0.102	-0.012	-0.025	-0.985	-0.03	-0.866	-0.809	0.000	0.000	0.000	-0.002	LCGL	0.39	0.88	0.59
	0.000	-0.302	-0.236	-0.692	-0.098	-0.315	-0.662	0.000	0.000	0.000	0.000	-0.009	LCGW	0.45	0.9
	-0.067	-0.024	-0.045	-0.753	-0.076	-0.83	-0.407	0.000	0.000	0.000	0.000	0.000	-0.002	UCGL	0.64
	0.000	-0.033	-0.158	-0.452	-0.111	-0.202	-0.825	0.000	0.000	0.000	0.000	0.000	0.000	0.000	UCGW
		p value											p value		

Fig. 3a. Genetic correlation matrix of grain yield (GY), day to 50% flowering (DF) and spike architectural traits (SATs) over early sown (ES).



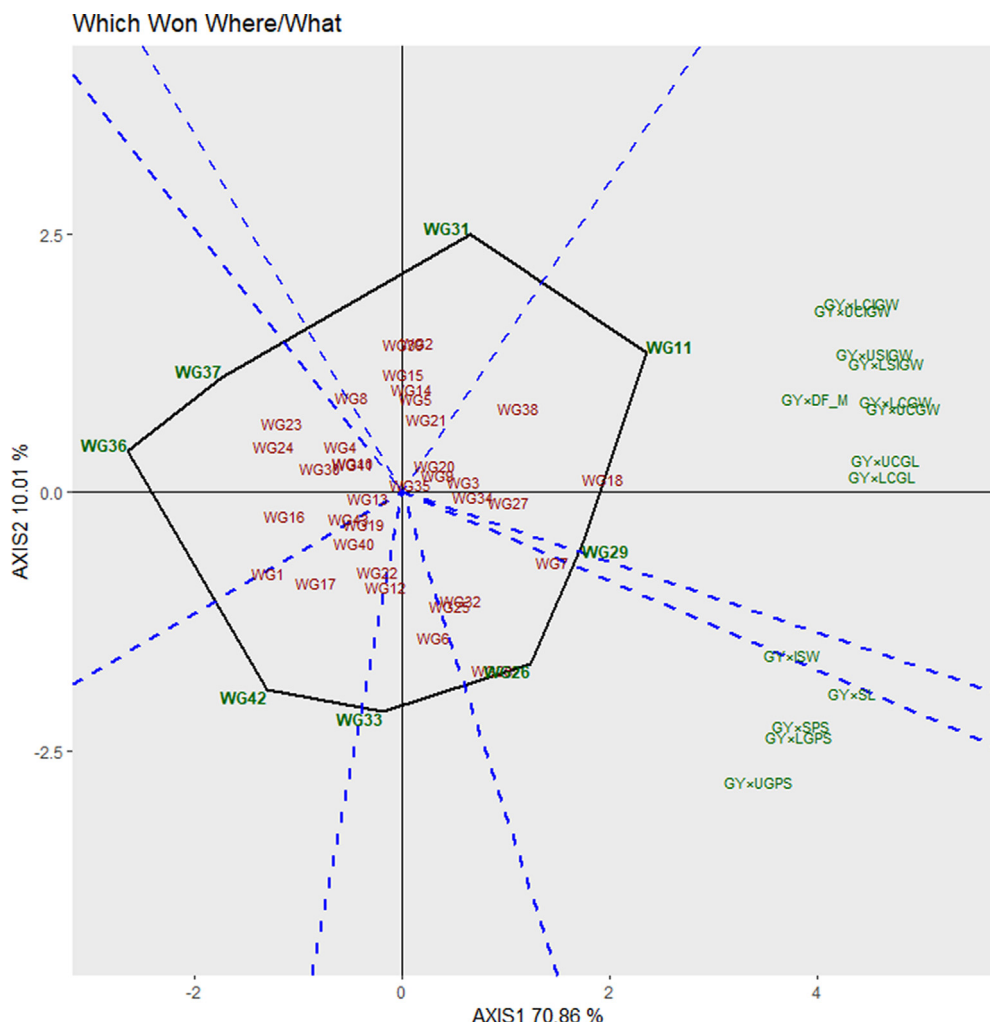


Fig. 5a. Which-won-where pattern under GGE analysis of GY\_trait combinations in early sown (ES).

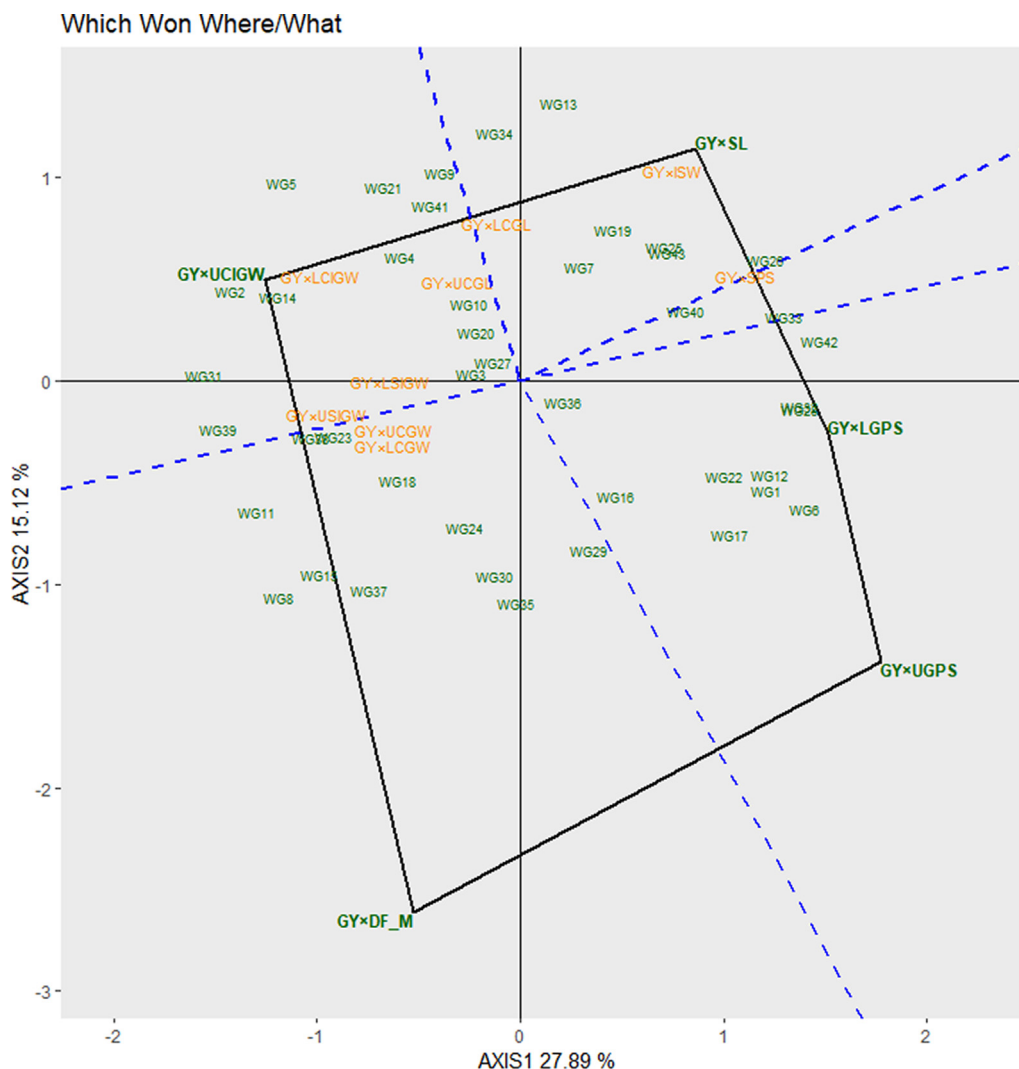
et al., 2019). Several reports suggested that kernel growth in modern wheat cultivars is not limited by the source, but is sink limited (Borrás et al., 2004; Miralles and Slafer, 2007; Pedro et al., 2011; Serrago et al., 2013; Zhang et al., 2010). However, source-limited grain growth leading to weight reduction was reported in wheat (Sandaña et al., 2009; Serrago et al., 2013). The co-limitation of source and sink capacity in a modern cultivar of durum wheat had also been reported (Royo et al., 2008). The reasons for the reduction in sink limitation because of improved grains per unit area (De Vita et al., 2007; Royo et al., 2007) and enhanced grain weight potential (Royo et al., 2008). Modern wheat cultivars are sink limited because shriveled grain entries due to source limitation have been discarded at the early stage of selection (Alonso et al., 2018). Entries of high yield potential having a large number of grains per unit area and high potential TGW show the source limitation (Alonso et al., 2018).

The percent reduction in the LGSK vs. UGSK; and IGW and GW of lower vs. upper spike portions comparatively was lower in ES indicating more differential acquisition and allocation of photosynthates in ES & TS. Simply by exposing the material in ES i.e. high production environment, the sink strength has been improved significantly, therefore, the generalization of source/sink/co-limitation is not possible unless and until the test material is exposed to a high production environment. It was hypothesized

based on several published reports that differences in the degree of source limitation might be related to the environmentally determining limitation (Calderini et al., 2006). The presence of significant difference and high broad-sense heritability of GY, DF and SATs in each environment provides the opportunity to get a high response to selection under respective environment.

The differential regression relationship with low to moderate magnitude of GY with DF and SATs in ES and TS, indicated the clear-cut effect of sowing time on their contribution in GY. The DF was having a negative relationship with GY with a lower magnitude ( $R^2 = 0.026$ ) in ES and a higher magnitude ( $R^2 = 0.144$ ) in TS (Fig. 2). Therefore, the probability to enhance the biomass accumulation for yield gain through increased crop duration by selecting genotypes with a breached negative correlation is comparatively high in ES. The positive relationship of SATs namely SL, LGPS, UGPS, LCGL, UCGL, LSIGW, USIGW, LCIGW, UCIGW, LCGW, and UCGW with GY in ES (Fig. 2 and Supplementary Fig. 3), have been due to the high production environment enhanced the sink capacity at individual plant spike level. Whereas, in TS, no such relationship except the weak relationships of GY with LCGL, LGPS, and UGPS was observed (Fig. 2). The SPS had a significant negative relationship with GY in TS ( $R = -0.29$ ;  $R^2 = 0.078$ ), while, no relationship in ES (Supplementary Fig. 2). This regression relationship indicates that the expression of SATs was having more influence in deciding





GGE Biplot showing components 1 and 2 explaining 43.01% of the total variation using Column Metric Preserving SVP and Tester-Centered G+GE with scaling by standard deviation

**Fig. 5b.** Unique Which-won-where pattern under GGE analysis of GY\_trait combinations in early sown ((ES).

the GY only in ES. The DF had negative correlations for most of the SATs except the positive correlation with SPS and SL in both sowing times (Fig. 2). It was also reported the SL, SPS was also positively correlated with days to heading (Würschum et al., 2018). The high correlation of LCGL and UCGL with GY in ES than TS indicated that ES provides the congenial condition for the growth of middle florets of the spike. In TS, very little to no relationship of SATs with GY indicates that these traits decide the GY in combinations with each other and other unaccounted traits under this study. This difference is due to the number of grains per spikelet depending on floret primordia survival at anthesis than the number of initiated floret primordia per spikelet at the early stage (González-Navarro et al., 2015). Moreover, generation and degeneration of floret primordia are variable along with spikes, and chances of the fertility of more distal florets are less in the apical or basal spikelets (González-Navarro et al., 2015; Prieto et al., 2018).

The generated a distinct pattern in the heatmap of ES than TS allows the effective exploitation of traits under study for further GY enhancement. In ES, high GY genotypes having distinctively high DF, SL, and SPS; and IGW, GL, GW, which can be exploited along with trait optimization for yield maximization in more plau-

sible (Supplementary Fig 3 a & b). The exploratory and confirmatory factor analysis revealed that component traits namely SL, ISW, SPS, LGPS and UGPS significantly influence the GY in ES, therefore, we can give more emphasis on the exploitation of these traits in yield consolidation in ES. The per cent gain of these traits in ES over TS was 2.88% (SL), 4.68% (ISW), 8.19% (SPS) 3.74% (LGPS) and 7.57% (UGPS) indicating their significance in yield consolidation in ES. However, the absence of such significant effects of component traits with GY restricts their exploitation in TS (Table 4). The E and G main effects comparatively were having the major percent contribution of total GEI for GY, DF, and SATs (Supplementary Table 5). The high PC1 score i.e. 70.92% for GY representing the non-crossover GE, which means majority of the genotypes perform in a proportional response across the environments. While, only less percentage of genotypes had cross-over interaction represented by PC2 score, 17.65% (Yan et al., 2000). Practically GEI is most consequential in presence of high cross-over interaction in the selection of genotypes for a specific environment (Elias et al., 2016; Gauch and Zobel, 1997). Though, significant GEI having no or little crossover GE could still influence the accuracy of absolute estimates of variety performance across production environments (George and Lundy, 2019). The generated biplot of GY over PC1 i.e.

AMMI 1 indicated the superiority of ES having higher values than average. Similarly, genotypes with the extreme of them, WG18 were having superiority over others since they fell into the right sector (Fig. 4). Among the genotypes, WG 11 and WG 18 having the high GY with low ASV values, are suitable for ES and TS. (Supplementary Table 5).

The novel approach to select the genotypes based on multiple traits other than the breeder's personal judgment of setting weights and truncation points in selection indices (Yan and Frégeau-Reid, 2018). This approach is based on the yield-trait combination, the superiority of a genotype would be not only on individual traits but its combining with yield or other target traits (Yan and Frégeau-Reid, 2018). Due to its quite effectiveness in the selection of genotypes based on the graphical representation of GY-trait combination, and to understand combining of SATs and DF with GY, this method was employed for this study. The vertex genotype of the G + GE biplot has the largest values for the GY-trait combinations within the corresponding sector (Yan and Frégeau-Reid, 2018). In ES, WG 11 was identified best for high GY with IGW, GL, GW, and shorter DF. Likewise, WG 29 for high GY with ISW and SL; and WG 26 for high GY with LGPS, UGPS, and SPS were the best (Fig. 5a). Since these SATs and DF<sup>M</sup> have the positive to no significant negative correlation in ES. Therefore, three genotypes namely WG 11, WG 29, and WG 26 were having the high GY with different trait combinations, therefore, by making crosses among them, traits can be combined to have transgressive segregants for high GY along with the high value of all traits. However, in TS, all GY-trait combinations were fell in one sector with WG 40 and WG 11 as winners, it means the absence of major influence of individual trait separately on GY (Supplementary Fig. 5a). A genotype focused "which won where" of GGE with standardized GYT data, in which genotypes were used as a tester to do tester-centered G + GE to focus on the genotype selection based on GY-trait combinations. The vertex GY-trait combinations represent the presence of the highest exploitable variability in comparison to others located in the middle of biplot. The selected genotypes were selected for specific component traits, which would have the high value of target trait, and largely defines the high yield along with the low value of other remaining component traits. This approach would be of very much use in the quantification of the effect of individual traits on defining the grain yield. Since all identified genotypes based on individual GY-trait combinations are having the high yield exclusively due to specific traits, therefore, these genotypes can be utilized for making the mapping populations or as parents in yield enhancement program.

## 7. Conclusion

To meet the projected demand for wheat grain, the yield gain must be at the same pace by manipulating the source-sink capacity. As we know, the cause of happening of wheat green revolution was the agronomic interventions and responsive genotypes. Therefore, deciphering the influence of DF and SATs over GY will give insights into their effective exploitation in early and timely sown conditions for further yield gain. The correlation, regression and confirmatory factor analysis indicated that positive response of SATs viz., SL, SPS, ISW, LSGS and UGPS over GY in early sowing (ES) gives clarity that greater emphasis on the exploitation of these SATs would be more rewarding only in early sowing. The presence of genotype by environment interactions of SATs and GY allows exploitation of these traits by making fine-tunes with the prevailing environment for further yield enhancement. The GGE approach proposed by Yan and Reid (2018) would be very useful in the selection of genotypes based on yield-trait combinations and making fine-tunes with the environment.

## Author contributions

**MK:** Wrote the initial manuscript. **MK, NKB, PB, KBG, AAC:** Analyzed data. **RY:** Provided the breeding material. **MK, PD, RA:** Managed field trials and recorded phenotypic data. **MK, NKB, PB, KBG, PD, AAC, RA, RY:** Revised the manuscript. **MK, RY:** Designed the experiment, supervised the research project.

All authors have read and approved the final manuscript.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgement

The facilities and financial support provided by FOSU unit and Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi and ICAR-BMGF project are duly acknowledged.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.sjbs.2022.01.007>.

## References

- Alonso, M.P., Mirabella, N.E., Pano, J.S., Cendoya, M.G., Pontaroli, A.C., 2018. Selection for high spike fertility index increases genetic progress in grain yield and stability in bread wheat. *Euphytica* 214 (7). <https://doi.org/10.1007/s10681-018-2193-4>.
- Boden, S.A., Cavanagh, C., Cullis, B.R., Ramm, K., Greenwood, J., Jean Finnegan, E., Trevaskis, B., Swain, S.M., 2015. Ppd-1 is a key regulator of inflorescence architecture and paired spikelet development in wheat. *Nat. Plants* 1, 1–6. <https://doi.org/10.1038/nplants.2014.16>.
- Borrás, L., Slafer, G.A., Otegui, M.E., 2004. Seed dry weight response to source-sink manipulations in wheat, maize and soybean: A quantitative reappraisal. *F. Crop. Res.* 86 (2–3), 131–146. <https://doi.org/10.1016/j.fcr.2003.08.002>.
- Brown, T.A., 2015. *Confirmatory factor analysis for applied research*. Guilford, publications.
- Calderini, D.F., Reynolds, M.P., Slafer, G.A., 2006. Source-sink effects on grain weight of bread wheat, durum wheat, and triticale at different locations. *Aust. J. Agric. Res.* 57, 227–233. <https://doi.org/10.1071/AR05107>.
- Cao, S., Xu, D., Hanif, M., Xia, X., He, Z., 2020. Genetic architecture underpinning yield component traits in wheat. *Theor. Appl. Genet.* 133 (6), 1811–1823. <https://doi.org/10.1007/s00122-020-03562-8>.
- De Vita, P., Nicosia, O.L.D., Nigro, F., Platani, C., Riefolo, C., Di Fonzo, N., Cattivelli, L., 2007. Breeding progress in morpho-physiological, agronomical and qualitative traits of durum wheat cultivars released in Italy during the 20th century. *Eur. J. Agron.* 26 (1), 39–53. <https://doi.org/10.1016/j.eja.2006.08.009>.
- Dia, M., Wehner, T.C., Arellano, C., 2017. RGXe: An R program for genotype x environment interaction analysis. *American Journal of Plant Sciences* 08 (07), 1672–1698.
- Dixon, L.E., Greenwood, J.R., Bencivenga, S., Zhang, P., Cockram, J., Mellers, G., Ramm, K., Cavanagh, C., Swain, S.M., Boden, S.A., 2018. TEOSINTE BRANCHED1 regulates inflorescence architecture and development in bread wheat (*Triticum aestivum*). *Plant Cell* 30 (3), 563–581. <https://doi.org/10.1105/tpc.17.00961>.
- Elias, A.A., Robbins, K.R., Doerge, R.W., Tuinstra, M.R., 2016. Half a century of studying genotype × Environment interactions in plant breeding experiments. *Crop Sci.* 56 (5), 2090–2105. <https://doi.org/10.2135/cropsci2015.01.0061>.
- Ferrante, A., Cartelle, J., Savin, R., Slafer, G.A., 2017. Yield determination, interplay between major components and yield stability in a traditional and a contemporary wheat across a wide range of environments. *F. Crop. Res.* 203, 114–127. <https://doi.org/10.1016/j.fcr.2016.12.028>.
- Fischer, R.A., 2008. The importance of grain or kernel number in wheat: A reply to Sinclair and Jamieson. *F. Crop. Res.* 105 (1–2), 15–21. <https://doi.org/10.1016/j.fcr.2007.04.002>.
- Foulkes, M.J., Slafer, G.A., Davies, W.J., Berry, P.M., Sylvester-Bradley, R., Martre, P., Calderini, D.F., Griffiths, S., Reynolds, M.P., 2011. Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *J. Exp. Bot.* 62 (2), 469–486. <https://doi.org/10.1093/jxb/erq300>.
- Gabriel, K.R., 1971. The biplot graphic display of matrices with application to principal component analysis. *Biometrika* 58 (3), 453–467.

- Gao, X.Q., Wang, N., Wang, X.L., Zhang, X.S., 2019. Architecture of Wheat Inflorescence: Insights from Rice. *Trends Plant Science* 24 (9), 802–809. <https://doi.org/10.1016/j.tplants.2019.06.002>.
- Gauch, H.G., 2006. Statistical Analysis of Yield Trials by AMMI and GGE. *Crop Sci.* 46 (4), 1488–1500. <https://doi.org/10.2135/cropsci2005.07-0193>.
- Gauch, H.G., Zobel, R.W., 1997. Identifying mega-environments and targeting genotypes. *Crop Sci.* 37 (2), 311–326. <https://doi.org/10.2135/cropsci1997.0011183X003700020002x>.
- Gauch, H.G., Zobel, R.W., 1988. Predictive and postdictive success of statistical analyses of yield trials. *Theor. Appl. Genet.* 76 (1), 1–10. <https://doi.org/10.1007/BF00288824>.
- George, N., Lundy, M., 2019. Quantifying genotype × environment effects in long-term common wheat yield trials from an agroecologically diverse production region. *Crop Sci.* 59 (5), 1960–1972. <https://doi.org/10.2135/cropsci2019.01.0010>.
- Gerard, G.S., Crespo-Herrera, L.A., Crossa, J., Mondal, S., Velu, G., Juliana, P., Huerta-Espino, J., Vargas, M., Rhandawa, M.S., Bhavani, S., Braun, H., Singh, R.P., 2020. Grain yield genetic gains and changes in physiological related traits for CIMMYT's High Rainfall Wheat Screening Nursery tested across international environments. *F. crop. Res.* 249, 107742. <https://doi.org/10.1016/j.fcr.2020.107742>.
- González-Navarro, O.E., Griffiths, S., Molero, G., Reynolds, M.P., Slafer, G.A., 2015. Dynamics of floret development determining differences in spike fertility in an elite population of wheat. *F. Crop. Res.* 172, 21–31. <https://doi.org/10.1016/j.fcr.2014.12.001>.
- <https://www.wheatinitiative.org/vision-paper>, n.d. Vision Paper – Wheat initiative [WWW Document]. URL <https://www.wheatinitiative.org/vision-paper> (accessed 12.13.20). <http://www.fao.org/faostat/en/#data/CC> <https://www.quantitative-plant.org/software/smartgrain>
- McSteen, P., 2009. Hormonal regulation of branching in grasses. *Plant Physiology* 149 (1), 46–55. <https://doi.org/10.1104/pp.108.129056>.
- Miralles, D.J., Slafer, G.A., 2007. Paper presented at international workshop on increasing wheat yield potential, CIMMYT, Obregon, Mexico, 20–24 March 2006 Sink limitations to yield in wheat: how could it be reduced? *J. Agric. Sci.* 145 (02), 139. <https://doi.org/10.1017/S0021859607006752>.
- Parry, M.A.J., Reynolds, M., Salvucci, M.E., Raines, C., Andralojc, P.J., Zhu, X.-G., Price, G.D., Condon, A.G., Furbank, R.T., 2011. Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *J. Exp. Bot.* 62 (2), 453–467. <https://doi.org/10.1093/jxb/erq304>.
- Pedro, A., Savin, R., Habash, D.Z., Slafer, G.A., 2011. Physiological attributes associated with yield and stability in selected lines of a durum wheat population. *Euphytica* 180 (2), 195–208. <https://doi.org/10.1007/s10681-011-0352-y>.
- Poursarebani, N., Seidensticker, T., Koppolu, R., Trautewig, C., Gawroński, P., Bini, F., Govind, G., Ruten, T., Sakuma, S., Tagiri, A., Wolde, G.M., Youssef, H.M., Battal, A., Ciannamea, S., Fusca, T., Nussbaumer, T., Pozzi, C., Börner, A., Lundqvist, U., Komatsuda, T., Salvi, S., Tuberosa, R., Uauy, C., Sreenivasulu, N., Rossini, L., Schnurbusch, T., 2015. The genetic basis of composite spike form in barley and 'miracle-wheat'. *Genetics* 201, 155–165. <https://doi.org/10.1534/genetics.115.176628>.
- Prieto, P., Ochagavía, H., Savin, R., Griffiths, S., Slafer, G.A., 2018. Physiological determinants of fertile floret survival in wheat as affected by earliness per se genes under field conditions. *Eur. J. Agron.* 99, 206–213. <https://doi.org/10.1016/j.eja.2018.07.008>.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ray, D.K., Mueller, N.D., West, P.C., Foley, J.A., Hart, J.P., 2013. Yield Trends Are Insufficient to Double Global Crop Production by 2050. *PLoS One* 8 (6), e66428. <https://doi.org/10.1371/journal.pone.0066428>.
- Reynolds, M., Foulkes, J., Furbank, R., Griffiths, S., King, J., Murchie, E., Parry, M., Slafer, G., 2012. Achieving yield gains in wheat. *Plant, Cell Environ.* 35, 1799–1823. <https://doi.org/10.1111/j.1365-3040.2012.02588.x>.
- Reynolds, M., Foulkes, M.J., Slafer, G.A., Berry, P., Parry, M.A.J., Snape, J.W., Angus, W. J., 2009. Raising yield potential in wheat. *J. Exp. Bot.* <https://doi.org/10.1093/jxb/erp016>
- Royo, C., Álvaro, F., Martos, V., Ramdani, A., Isidoro, J., Villegas, D., García Del Moral, L. F., 2007. Genetic changes in durum wheat yield components and associated traits in Italian and Spanish varieties during the 20th century. *Euphytica* 155, 259–270. <https://doi.org/10.1007/s10681-006-9327-9>
- Royo, C., Martos, V., Ramdani, A., Villegas, D., Rharabti, Y., García del Moral, L.F., 2008. Changes in Yield and Carbon Isotope Discrimination of Italian and Spanish Durum Wheat during the 20th Century. *Agron. J.* 100 (2), 352–360. <https://doi.org/10.2134/agronj2007.0060>.
- Sadras, V.O., Slafer, G.A., 2012. Environmental modulation of yield components in cereals: Heritabilities reveal a hierarchy of phenotypic plasticities. *F. Crop. Res.* 127, 215–224. <https://doi.org/10.1016/j.fcr.2011.11.014>.
- Sakuma, S., Golan, G., Guo, Z., Ogawa, T., Tagiri, A., Sugimoto, K., Bernhardt, N., Brassac, J., Mascher, M., Hensel, G., Ohnishi, S., Jinno, H., Yamashita, Y., Ayalon, I., Peleg, Z., Schnurbusch, T., Komatsuda, T., 2019. Unleashing floret fertility in wheat through the mutation of a homeobox gene. *Proc. Natl. Acad. Sci. U. S. A.* 116 (11), 5182–5187. <https://doi.org/10.1073/pnas.1815465116>.
- Sandaña, P.A., Harcha, C.L., Calderini, D.F., 2009. Sensitivity of yield and grain nitrogen concentration of wheat, lupin and pea to source reduction during grain filling. A comparative survey under high yielding conditions. *F. Crop. Res.* 114 (2), 233–243. <https://doi.org/10.1016/j.fcr.2009.08.003>.
- Serrago, R.A., Alzueta, I., Savin, R., Slafer, G.A., 2013. Understanding grain yield responses to source-sink ratios during grain filling in wheat and barley under contrasting environments. *F. Crop. Res.* 150, 42–51. <https://doi.org/10.1016/j.fcr.2013.05.016>.
- STAR, version 2.0.1, 2014. Biometrics and Breeding Informatics. PBGB Division, International Rice Research Institute, Los Baños, Laguna.
- Wickham, H., 2016. *ggplot2—Elegant Graphics for Data Analysis*. Springer International Publishing, Cham, Switzerland.
- Wolde, G.M., Mascher, M., Schnurbusch, T., 2019. Genetic modification of spikelet arrangement in wheat increases grain number without significantly affecting grain weight. *Mol. Genet. Genomics* 294 (2), 457–468. <https://doi.org/10.1007/s00438-018-1523-5>.
- Würschum, T., Leiser, W.L., Langer, S.M., Tucker, M.R., Longin, C.F.H., 2018. Phenotypic and genetic analysis of spike and kernel characteristics in wheat reveals long-term genetic trends of grain yield components. *Theor. Appl. Genet.* 131 (10), 2071–2084. <https://doi.org/10.1007/s00122-018-3133-3>.
- Yadav, R., Gaikwad, K., Kumar, M., Kumar, N., 2017a. 'HDCSW 18' wheat the first ever variety for conservation agriculture in India. *Indian Farming* 67, 3–4.
- Yadav, R., Gaikwad, K.B., Bhattacharyya, R., 2017b. Breeding wheat for yield maximization under conservation agriculture. *Indian J. Genet. Plant Breed.* 77, 185–198. <https://doi.org/10.5958/0975-6906.2017.00026.8>.
- Yadav, R., Gaikwad, K., Bhattacharyya, R., Bainsla, N.K., Kumar, M., Yadav, S.S., 2018. Breeding New Generation Genotypes for Conservation Agriculture in Maize-Wheat Cropping Systems under Climate Change, in: Yadav, S.S., Redden, R.J., Hatfield, J.L., Ebert, A.W., Hunter, D. (Eds.). *Food Secur. Clim. Chang.* 189–228. <https://doi.org/10.1002/9781119180661.ch10>.
- Yadav, R., Gupta, S., Gaikwad, K.B., Bainsla, N.K., Kumar, M., Babu, P., Ansari, R., Dhar, N., Dharmateja, P. and Prasad, R., 2021. Genetic Gain in Yield and Associated Changes in Agronomic Traits in Wheat Cultivars Developed Between 1900 and 2016 for Irrigated Ecosystems of Northwestern Plain Zone of India. *Frontiers in plant science*, p.1957.
- Yan, W., 2002. Singular-value partitioning in biplot analysis of multi-environment trial data. *Agron. J.* 94, 990–996. <https://doi.org/10.2134/agronj2002.0990>
- Yan, W., 2001. GGEbiplot—A Windows Application for Graphical Analysis of Multi-environment Trial Data and Other Types of Two-Way Data. *Agron. J.* 93 (5), 1111–1118. <https://doi.org/10.2134/agronj2001.9351111x>.
- Yan, W., Fréreau-Reid, J., 2018. Genotype by Yield×Trait (GYT) Biplot: A Novel Approach for Genotype Selection based on Multiple Traits. *Sci. Rep.* 8 (1). <https://doi.org/10.1038/s41598-018-26688-8>.
- Yan, W., Hunt, L.A., Sheng, Q., Szlavnics, Z., 2000. Cultivar Evaluation and Mega-Environment Investigation Based on the GGE Biplot. *Crop Sci.* 40 (3), 597–605. <https://doi.org/10.2135/cropsci2000.403597x>.
- Yan, W., Tinker, N.A., 2006. Biplot analysis of multi-environment trial data: Principles and applications. *Can. J. Plant Sci.* 86 (3), 623–645.
- Zhang, H., Turner, N.C., Poole, M.L., 2010. Source-sink balance and manipulating sink-source relations of wheat indicate that the yield potential of wheat is sink-limited in high-rainfall zones. *Crop Pasture Sci.* 61, 852–861. <https://doi.org/10.1071/CP10161>.
- Zobel, R.W., Wright, M.J., Gauch, H.G., 1988. Statistical Analysis of a Yield Trial. *Agron. J.* 80 (3), 388–393. <https://doi.org/10.2134/agronj1988.0002196200800030002x>.