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Research Article

Assessment of variability in phenological, morphological and yield traits in a biparental RIL population in wheat (*Triticum aestivum* L)

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Abstract

A HUW-234 x HUW-468 RIL population in wheat comprising 160 RIL's along with two parents and two released varieties were evaluated for phenological, morphological and seed traits in an augmented block design and variability was assessed through principal component analysis. PCA concentrated variability in first five principal components. The total variance explained with the first six PC's was 76.65 per cent. Latent roots (Eigen values) for significant PCs ranged from 3.39 (PC1) to 1.05 (PC5). The first two PC's that were used for constructing biplot graphs explained 42.77 %. The first PC contributed 25.48 per cent of total variation mainly contributed by the grain yield per plant (30.59 per cent), seed growth rate (30.44 per cent), spikelets per spike (16.15 per cent) and 1000-grain weight (16.03 per cent). The second component explained 17.29 per cent of variation contributed largely by days to seed fill (38.31 per cent), days to flowering (35.68 per cent) and seed length (11.41 per cent), while as the third, fourth and fifth component explained 15.29, 9.95 and 8.63 per cent of variations respectively. Six variables including seed yield per plant, seed growth rate, days to seed fill, spikelets per spike, 1000-grain weight and days to flowering contributed above the expected average to the variability in PC1 and PC2. Grain yield was positively correlated with seed growth rate followed by spikelets per spike, 1000-grain weight and seed breadth. A number of RILs were identified based on their superior performance for various phenological and yield traits. RILs 3, 11, 89 and 150 had superior performance for multiple traits indicating desirable segregation for various traits.

Keywords

Wheat, RILs, Augmented Block Design, Principal Component Analysis, GT (Genotype x Trait) Biplot

INTRODUCTION

Wheat (*Triticum spp.*) is one of the principal food grains of the world and contributes to the international food security. It is the most traded cereal grain, with 10% of total production sold in the international markets (Marathe and MacPherson 2001), and is the most widely grown of all the cereals; production spans the equator to latitudes of more than 60°N and 50°S, and altitudes of up to 3,000 m above the sea level. The first cultivation of wheat occurred about 10,000 years ago, as a part of "Neolithic Revolution". These earliest cultivated forms were diploid and tetraploid wheat and their genetic relationships

indicates that they are originated from south-east part of Turkey. It is the most widely grown cereal in temperate and some tropical environments, where it is often cultivated as the winter season crop in rotation with a number of other crops. Wheat belongs to the family Poaceae, sub-family Pooideae, tribe Triticeae and genus *Triticum*. Global wheat demand is increasing as the population of the world is increasing which is expected to grow by 30 % by the year 2050 (9 billion from current 7 billion). Estimated demand of wheat in 2010 reached 666 million metric tons (MMT) and projected up to 880 MMT by 2050 (Weigand, 2011).

Wheat is the staple food and main source of energy and nutrition in the Indian diet. Wheat is an important source of carbohydrates. Globally, it is the leading source of protein in human food, having a protein content of about 13%, which is relatively high compared to other major cereals, but relatively low in protein quality for supplying essential amino acids. When eaten as the whole grain, wheat is a source of multiple nutrients and dietary fiber. Wheat being major staple food crop providing around 20 % of calories and proteins in human diet, therefore, it play an important role in food security in India. Annual increase of at least 1.6 % in grain yield is required in the coming years in order to fulfil the demand. As a cool season crop, wheat has as an optimal daytime growing temperature during reproductive development of 15 °C and for every degree Celsius above this optimum a reduction in yield of 3% to 4% has been observed.

With a global yearly production of more than 750 million tons, wheat (*Triticum aestivum* L.) has become the world's greatest and most significant food crop for direct consumption (FAO, 2017). High nutritional value, good storing ability, and simple transporting ability make this cereal crop an important food source. Cereal crops like wheat have provided mankind with its primary source of calories since, the beginning of agriculture (Feuillet *et al.* 2008). Wheat is cultivated on more land area than any other food crop with a cropped area of 220.4 million hectares in 2016. As a major cereal crop, wheat accounts for about 30% of the world's cereal area to provide food for 36 % of the global population. World trade in wheat is greater than for any other crops combined. In 2016, world production of wheat was 749 million tonnes making it the second most produced cereal after maize (FAO, 2017). India recorded a production of 93.50 million tonnes in 2016 which contributes to ~36% to national food basket (Anonymous, 2017). The major wheat producing states are Uttar Pradesh, Punjab, Haryana, Madhya Pradesh, Rajasthan, Bihar, Maharashtra, Gujarat, Karnataka, West Bengal, Uttarakhand, Himachal Pradesh and Jammu & Kashmir. These states contribute about 99.5 per cent of total wheat production in the country. Remaining States, namely, Jharkhand, Assam, Chhattisgarh, Delhi and other North Eastern States contribute only about 0.5 per cent of the total wheat production in the country (Anonymous, 2017). The cultivation of wheat is so widely distributed geographically that the crop is being harvested in one country or the other all the year round (Tiwari and Shoran, 2011).

In J&K the wheat is grown on an area of 2.85 million hectares with the production of 5.40 million tonnes having the productivity of 1.94 tonnes per hectare (Anonymous, 2016). In the state of J&K wheat is mostly confined to Jammu region and very meagre area in Kashmir valley mostly because of the climatic constraints and lack of early maturing varieties that could fit in rice-wheat rotation. Moreover the effects of climatic change are going to negatively impact the yield in Jammu region as well as other parts of world due to drought and terminal

heat stress. There is a need to develop early maturing varieties that could fit in rotation with rice to augment the food production in state as well as varieties that are resilient to terminal heat stress.

The major limitation with using seed yield *per se* as the selection criteria for crop improvement is less reliability of results on account of the complexity of its inheritance as well as low heritability and therefore, the realised gains for yield have not been very encouraging by direct selection for yield. As a result, there has been greater emphasis across breeding programmes to elucidate the nature of relationship and trait associations between yields and other traits which are relatively less complex and have comparatively better heritability for using as an indirect selection criterion for improving yield. The phenotypic correlation among traits reflects the observed relationship between the traits arising out of both genetic and environmental factors; while as the genotypic correlations arise from linkage and pleiotropy. The knowledge of trait associations in breeding materials is essential for a variety of reasons: (i) it enables us to perceive the diversity of breeding material and identify the trait through which a crop plant is able to grow successfully in a given ecological condition with optimum productivity and to avoid characters that have a little or no breeding value in combination with PCA; (ii) it also enables us to narrow down to a very few traits that not are only accountable for large amount of variation but have a breeding value correlated with seed yield. The principal component analysis (PCA), one of multivariate analysis methods elucidates among a set of the traits which ones are decisive in genotypic differentiation (Kovacic, 1994). PCA enables easier understanding of impacts and connections among different traits by identifying them and explaining their roles. This method is a powerful multiple method to apply for evaluating yield component (Guertin and Bailey, 1982), identify biological relationships among traits (Acquaah *et al.* 1992), decrease associated-traits to a few factors (Johnson and Wichern, 1996) and description of correlations among variables.

MATERIALS AND METHODS

Location: The present study was undertaken in *Kharif* 2018 at experimental farm of Faculty of Agriculture at Wadura in J&K, India (34° 17' North and 74° 33' E at an altitude of 1594 metres above the sea level). The minimum and maximum temperature during experimental period was 14.87 and 28.97 degrees Celsius, the minimum and maximum relative humidity was 55.68 and 80.14 per cent and the total rainfall recorded was 336.2 mm.

The material used in the present study comprised of 164 genotypes including 160 biparental RILs derived from a cross of HUW-234 x HUW-468 and four checks namely Shalimar Wheat-1, Shalimar Wheat-2, HUW-234 and HUW-468. Shalimar Wheat-1 and Shalimar Wheat-2 are the varieties released by SKUAST-Kashmir, while, HUW-234 and HUW-468 are the parents of RIL population.

The material was evaluated in augmented block design (Federrer, 1956). The design consisted of 8 blocks containing 24 genotypes in each with 20 test entries and four check entries. Each genotype was represented by a single line of 1.5 meter length. Recommended agronomic practices were followed to ensure a good crop. Data was collected from five randomly selected competitive plants on 12 phenological, morphological, and yield traits viz., Days to flowering (DF), Days to maturity (DM), Plant height (PH), Spike length (SPL), Number of tillers (NT), Seed length (SL), Seed breadth (SB), 100-grain weight (1000GW), Spikelets per spike (SP/S), Days to seed fill (DSF), Seed growth rate (SGR), Grain yield per plant (GYPP). In each block the checks were allotted randomly. Days to seed fill was estimated as the duration from flowering to maturity while as seed growth rate was estimated as ratio of seed yield and days to seed fill.

Principal component analysis was done using JMP SAS. The fact that Eigen values are above 1 indicates that the evaluated principle component weight values are reliable (Mohammadi and Prasanna, 2003). In the principal components where the values of Latent roots (Eigen values) was reduced to less than unity, which in the present study occurred after the sixth principal component together accounting for more than 80 % of the total variance and as such, the rest of the components were not considered.

RESULTS AND DISCUSSION

The descriptive statistics pertaining to morphological, phenological and yield traits are presented in **table 1**. Among phenological traits, days to flowering ranged from 129 to 149 with mean value of 141.30, days to maturity ranged from 215 to 236.25 with mean value of 220.99, days to seed fill ranged from 71 to 93 with mean value of 79.69 while as seed growth rate ranged from 30.28 to 78.54 mg/day with mean value of 50.19 mg/day. Among the morphological traits plant height ranged from 80.50 to 155.50 cm with mean value of 113.24 cm and the number of tillers ranged from 6.00 to 20.00 with mean value of 11.99, the number of spikelets per plants ranged from 6.40 to 19.60 with a mean of 11.55. Among yield contributing traits, seed length ranged from 0.37 to 0.94 cm with a mean of 0.86 cm, seed breadth ranged from 0.23 to 0.81 cm with a mean of 0.35 cm, 1000-grain weight ranged from 27.80 to 69.70 g with a mean of 43.20, while grain yield per plant ranged from 2.37 to 6.29 g with a mean of 4.02 g. Similarly, broad range of variation was observed in other yield contributing traits. High CV was recorded in the number of tillers, spike length, grain yield and days to seed fill while as low CV was observed in case of days to maturity, days to flowering and seed growth rate. Broader range and high CV in most of the traits has also been reported in wheat by Ahmad et al (2018) and Guo et al (2018).

Table 1. Descriptive statistics for 12 morphological and yield traits in a wheat RIL population

| Traits | Minimum | Maximum | Mean | St. Dev. (SD) | SE mean (SEm) | CV (%) |
|-------------|---------|---------|--------|---------------|---------------|--------|
| DF | 129.00 | 149.00 | 141.30 | 3.51 | 0.27 | 2.43 |
| DM | 215.00 | 236.25 | 220.99 | 2.52 | 0.16 | 0.94 |
| PH (cm) | 80.50 | 155.50 | 113.24 | 13.23 | 1.04 | 11.57 |
| SPL | 6.40 | 19.60 | 11.55 | 2.52 | 0.20 | 21.87 |
| NT | 6.00 | 20.00 | 11.99 | 3.09 | 0.24 | 25.83 |
| SL (cm) | 0.37 | 0.94 | 0.86 | 1.28 | 0.01 | 11.92 |
| SB (cm) | 0.23 | 0.81 | 0.35 | 0.07 | 0.001 | 19.15 |
| 1000GW (g) | 27.80 | 69.70 | 43.26 | 6.46 | 0.51 | 14.95 |
| SP/S | 13.00 | 24.00 | 18.41 | 2.49 | 0.19 | 13.65 |
| DSF | 71.00 | 93.00 | 79.69 | 2.73 | 0.06 | 20.48 |
| SGR (g/day) | 30.28 | 78.54 | 50.19 | 10.27 | 0.18 | 2.92 |
| GYPP (g) | 2.37 | 6.29 | 4.02 | 0.81 | 0.81 | 20.60 |

Trait legend: DF: Days to flowering, DM: Days to maturity, PH: Plant height, SPL: Spike length, NT: Number of tillers, SL: Seed length, SB: Seed breadth, 1000GW: 100-grain weight, SP/S: Spikelets per spike, DSF: Days to seed fill, SGR: Seed growth rate, GYPP: Grain yield per plant

The principal component analysis is an extremely useful tool for extracting desirable information from large number of data sets. It is sequentially done with subjective decisions being made at many of these steps (Kavithamani et al. 2019). In the present study principal component analysis (PCA) was done for 12 traits (phenological, morphological and seed traits) scored in the field experiment laid in an augmented block design. The number of principal components calculated from

correlation matrix is 12 which are similar to number of observed traits. PCA concentrated variability in first six principal components. The total variance explained with the first five PC's was 76.65 per cent (**Table 2**). The variance explained with last seven PC's is irrelevant. In the principal components where the values of latent roots (Eigen values) was reduced to less than unity, which in the present study occurred after the fifth principal component together accounting for more than 76 per cent

Table 2. Eigen values (Latent roots) and rotated component loadings (values of principal component traits of wheat)

| Component | Eigen value | Variability (%) | Cumulative % |
|-----------|-------------|-----------------|--------------|
| PC1 | 3.05 | 25.48 | 25.48 |
| PC2 | 2.07 | 17.29 | 42.77 |
| PC3 | 1.83 | 15.29 | 58.06 |
| PC4 | 1.19 | 9.95 | 68.01 |
| PC5 | 1.03 | 8.63 | 76.65 |
| PC6 | 0.89 | 7.41 | 84.06 |
| PC7 | 0.81 | 6.80 | 90.86 |
| PC8 | 0.68 | 5.72 | 96.58 |
| PC9 | 0.345 | 2.87 | 99.45 |
| PC10 | 0.05 | 0.44 | 99.89 |
| PC11 | 0.01 | 0.11 | 100.00 |
| PC12 | 0.01 | 0.00 | 100.00 |

of total variance in the present experimental material, the rest of the components were not considered. Latent roots (Eigen values) for significant PCs ranged from 3.05 (PC1) to 1.05 (PC5). The first two PC's that were used for constructing biplot graphs explained 42.77 per cent of variation. The first PC contributed 25.48 per cent of total variation mainly contributed by grain yield per plant (30.59 per cent), seed growth rate (30.44 per cent), spikelets per spike (16.15 per cent) and 1000-grain weight (16.03 per cent). The second component explained 17.29 per cent of variation contributed largely by days to seed fill (38.31 per cent), days to flowering (35.68 per cent) and seed length (11.41 per cent), while as the third, fourth and fifth component explained 15.29, 9.95 and 8.63 per

cent of variation respectively. In the present study, if the contribution of the variables were uniform, the expected value would be $1/\text{length of variables } 1/12 = 8.33$ per cent. The total contribution of a given trait (contribution), on explaining the variations retained by two PCs (PC1 and PC2) is given by $\text{contribution} = [(C1 \times \text{Eig1}) + (C2 \times \text{Eig2})] / (\text{Eig1} + \text{Eig2})$, where: C1 and C2 are the contributions of the variable on PC 1 and PC 2, respectively and Eig 1 and Eig 2 are the eigen values of PC1 and PC2, respectively (Kassambara, 2017). In the present study, six variables including seed yield per plant, seed growth rate, days to seed fill, spikelets per spike, 1000-grain weight and days to flowering contributed above the expected average to the variability in PC1 and PC2 (**Table 3**).

Table 3. Trait contributions to Principal components and total contribution to PC1 and PC2

| Trait | PC1 | PC2 | PC3 | PC4 | PC5 | Total contribution to PC1 and PC2 |
|--------|--------------|--------------|--------------|--------------|--------------|-----------------------------------|
| DF | 0.19 | 35.68 | 11.41 | 0.52 | 0.76 | 14.54 |
| DM | 0.02 | 2.63 | 44.17 | 2.57 | 0.28 | 1.07 |
| PH | 0.10 | 2.38 | 8.65 | 1.32 | 26.08 | 1.02 |
| SPL | 1.14 | 2.40 | 0.16 | 4.22 | 55.10 | 1.65 |
| NT | 0.13 | 0.01 | 5.54 | 30.99 | 6.56 | 0.08 |
| SL | 0.31 | 11.41 | 25.80 | 2.33 | 2.68 | 4.80 |
| SB | 4.66 | 2.33 | 0.03 | 11.43 | 3.66 | 3.72 |
| 1000GW | 16.03 | 2.48 | 0.40 | 18.43 | 2.66 | 10.55 |
| SP/S | 16.15 | 0.27 | 0.57 | 26.36 | 1.73 | 9.73 |
| DSF | 0.19 | 38.31 | 3.19 | 0.30 | 0.40 | 15.60 |
| SGR | 30.44 | 2.05 | 0.03 | 0.05 | 0.03 | 18.96 |
| GYPP | 30.59 | 0.02 | 0.02 | 1.40 | 0.03 | 18.24 |

Trait legend: DF: Days to flowering, DM: Days to maturity, PH: Plant height, SPL: Spike length, NT: Number of tillers, SL: Seed length, SB: Seed breadth, 1000GW: 100-grain weight, SP/S: Spikelets per spike, DSF: Days to seed fill, SGR: Seed growth rate, GYPP: Grain yield per plant

The Pearson correlations among the traits are presented in **Table 4**. Grain yield was positively correlated with seed growth rate (0.93) followed by spikelets per spike

(0.74), 1000-grain weight (0.61) and seed breadth (0.26). Similar results have been reported in wheat by Akram *et al.* (2008), Mecha *et al.* (2017) and Kumar *et al.* (2020).

The GT data are approximately displayed in a GT biplot (Fig. 1a and 1b), which can be used to visualize the trait associations and the trait profiles of the genotypes. In terms of the trait-standardized GT data, when two vectors are close, forming a small angle (acute, $< 90^\circ$), the two variables they represent are strongly positively correlated. If vector rays meet each other at 90° , they are not likely to be correlated. Similarly, if the rays diverge and form a large angle (close to 180°), they are negatively correlated. In the present study, based on the factor loading graph (Fig. 1a and 1b), seed yield per plant is

strongly correlated with the number of seed growth rate, spikelets per spike, 1000-grain weight and seed breadth. Seed yield per plant is negatively correlated with spike length, while as no correlation with seed length and days to maturity can be visualized. Similar results have also been reported in GT biplot analysis in common bean by Beheshtizadeh et al (2013) who reported the first four PCs contributed about 76 per cent of total variation. Bhanupiya et al (2014) also reported that first two PCs accounted for about 46 per cent of variation with weight of grains, the number of spikelets spike, spike length,

Table 4. Correlation matrix for 12 traits in Wheat RIL mapping population

| Traits | DF | DM | PH | SPL | NT | SL | SB | 1000GW | SP/S | DSF | SGR | GYPP |
|--------|----|---------------|-------|-------|-------|---------------|-------|--------------|-------|----------------|---------------|---------------|
| DF | 1 | 0.63** | 0.04 | 0.14 | -0.05 | -0.07 | -0.16 | 0.09 | -0.09 | -0.70** | 0.08 | -0.07 |
| DM | | 1 | -0.16 | 0.10 | -0.13 | 0.45** | -0.09 | 0.05 | -0.04 | 0.11 | -0.01 | -0.01 |
| PH | | | 1 | -0.04 | 0.06 | -0.18 | -0.02 | -0.08 | 0.03 | -0.20* | -0.01 | -0.03 |
| SPL | | | | 1 | 0.09 | -0.13 | -0.04 | -0.09 | -0.08 | -0.08 | -0.11 | -0.11 |
| NT | | | | | 1 | -0.09 | -0.05 | -0.14 | 0.10 | -0.05 | -0.02 | -0.02 |
| SL | | | | | | 1 | 0.12 | -0.06 | 0.08 | 0.51** | 0.01 | 0.08 |
| SB | | | | | | | 1 | 0.25* | 0.10 | 0.12 | 0.24* | 0.26* |
| 1000GW | | | | | | | | 1 | 0.03 | -0.06 | 0.74** | 0.61** |
| SP/S | | | | | | | | | 1 | 0.08 | 0.66** | 0.74** |
| DSF | | | | | | | | | | 1 | -0.11 | 0.08 |
| SGR | | | | | | | | | | | 1 | 0.93** |
| GYPP | | | | | | | | | | | | 1 |

Trait legend: DF: Days to flowering, DM: Days to maturity, PH: Plant height, SPL: Spike length, NT: Number of tillers, SL: Seed length, SB: Seed breadth, 1000GW: 100-grain weight, SP/S: Spikelets per spike, DSF: Days to seed fill, SGR: Seed growth rate, GYPP: Grain yield per plant

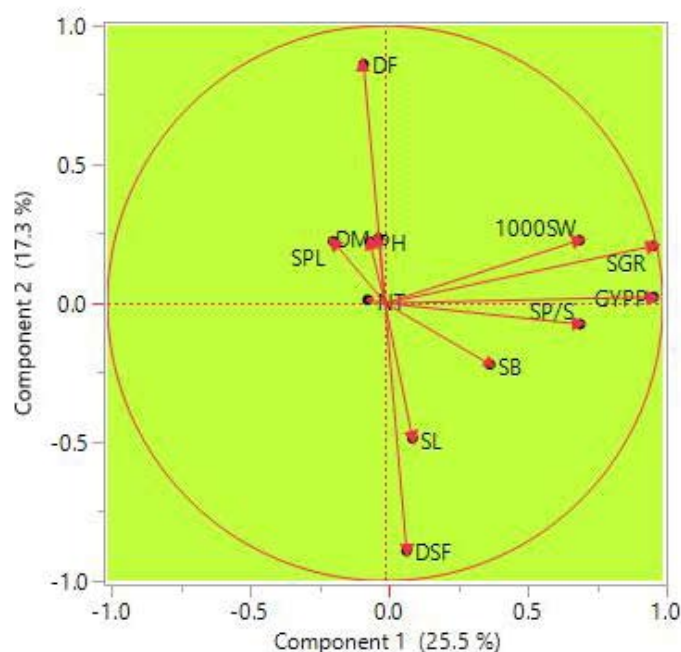


Fig. 1a

and grain yield as major contributors to PC1 and PC2 in wheat. Similarly Kumar et al (2016) reported that first six principal components showed Eigen values more than one and cumulatively they explained 81.75% variability. Pooja et al (2018) reported that in a RIL population of

wheat the first four principal components (PC-I, PC-II, PC-III and PC-IV) contributed about 78.34 per cent of the total variability with high positive component loading for all variables except 100-grain weight, harvest index and days to 50% heading.

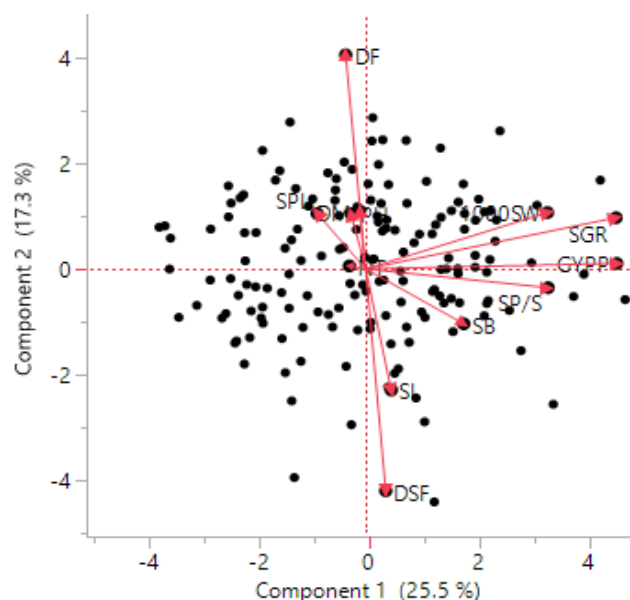


Fig. 1b

Fig. 1a and 1b. Trait biplot and GT biplot based on PC1 and PC2

Table 5. Best RILs identified for various traits (values in parentheses are mean values of RIL)

| TRAIT | BEST RILS IDENTIFIED |
|--------|--|
| DF | 8(129), 14(133), 11(134), 3(134), 1(134), 5(135), 16(136), 2(136), 24(137), 7(137), 13(137), 57(137), 60(137), 66(137), 74(137), 94(137), 120(137) |
| DM | 54(215), 8(215), 14(216), 3(216), 86(216), 1(217), 57(217), 60(217), 85(217), 119(217), |
| PH | 87(155.5), 93(142.5), 52(141.5), 45(140), 104(139.5), 75(137.5), 108(135), 94(133), 73(132.5), 27(131.5) |
| SPL | 121(19.6), 36(18.75), 116(18.125), 19(18), 127(17.775), 113(17.625), 29(17.25), 109(16.975), 104(16.475), 145(16.175) |
| NT | 113(20), 109(19), 62(19), 57(18), 32(18), 63(18), 89(18), 92(18), 56(16), 40(16) |
| SL | 56(0.78994), 150(0.7874), 62(0.77724), 153(0.7747), 2(0.77216), 71(0.77216), 60(0.76454), 93(0.76454), 143(0.76454), 115(0.762) |
| SB | 6(0.80772), 25(0.69342), 4(0.49624), 11(0.4953), 86(0.48194), 13(0.4683), 44(0.46736), 58(0.46228), 1(0.44798), 2(0.44958) |
| 1000GW | 25(62.40), 158(57.6), 62(56.1), 159(57.6), 4(53.2), 21(52.6), 125(52.4), 154(52.3), 140(52.1), 160(51.9) |
| SP/S | 150(24), 125(24), 1(24), 18(24), 138(23), 142(23), 89(23), 110(23), 112(23), 63(23), 11(23), 21(23) |
| GYPP | 125(6.288), 21(6.049), 158(6.048), 18(5.524), 11(5.428), 4(5.32), 25(5.304), 53(5.284), 57(5.28), 86(5.269) |

The Genotype by Trait (GT) biplot also enables us to compare genotypes on the basis of the measured multiple variables and also identifies genotypes that are particularly superior in certain traits. The GT biplot can thus be effectively used as an independent selection criteria based on several traits and in yield trials for grain yield evaluation (Yan and Rajcan, 2002). The vector length (i.e., the distance to the biplot origin) of a trait indicates how well the trait is represented in the biplot; a relatively short vector indicates that the variation of the trait across genotypes is either small or not well presented in the biplot, which is due to its weak or lack of correlation with other traits (Yan and Fregeau-Reid, 2018). This invariably occurs due to poor goodness of fit of the biplot as the two PCs (PC1 and PC2) account for only a part of total variation (the goodness of fit of the GT biplot in **Fig. 1a** and **1b** is 42.77 per cent). The vector length of a genotype indicates whether it is intermediate for all traits or has clear strengths and/or weaknesses in its trait profile. The GT biplot in **Fig. 1a** and **1b** also shows the trait profiles of the genotypes, the accuracy of which also depends on the goodness of fit of the biplot. **Figure 1b** represents differential genotypic profiles having higher values for traits accounting for variation and correlated with grain yield. The GT biplot substantiates the correlation results as the angle of vector lines depicts the strength of relationship. In our case, the vectors of SGR, SP/S, 1000SW and SB are main contributors of grain yield in wheat (acute angle). Similarly, grain yield has no relation with DF and DSF (almost right angles). This is especially true in case of Kashmir valley where these two parameters have no relevance. In fact, the taken after flowering is very important and wheat being a long duration crop in Kashmir spanning over 220 days, gets enough time for photosynthetic accumulation and remobilisation. A number of RILs were identified based on their superior performance for various phenological and yield traits (**Table 5**). These lines can be further evaluated for the stability of performance across locations. RILs 3, 11, 89 and 150 had superior performance for multiple traits indicating desirable segregation for various traits.

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