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Multivariate analysis of geographically diverse rice germplasm for genetic improvement of yield, dormancy and shattering-related traits

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Abstract

A diverse set of 107 rice genotypes was evaluated for yield, shattering and dormancy traits. Analysis of variance revealed sizable variation while skewness and kurtosis values indicated near-normal distribution for most of the traits, thus quantitative nature controlled by many genes. A highly significant deviation from a normal distribution for dormancy and shattering % indicated their qualitative nature of inheritance. Four promising genotypes 'IRGC1723' (early with 65 days to flowering), 'IRGC 11108' and 'RNR 15459' (high grain number – 358 and low average shattering – <5%), 'RNR 11718' (high single plant yield – 56.73 g, low average shattering – <5% and dormancy period – 21 days) are identified. A significant positive correlation between shattering and dormancy confirms inter-relationship among domestication-related characteristics. The principal component analysis revealed the contribution of four PCs to maximum variability and hierarchical clustering grouped the genotypes into 18 divergent clusters. Five cultivars (Karimnagar Samba, Sheetal, PR 121, Pranahitha and Jagitial Samba) with a combination of low shattering ability (3.35–5.7%) and considerable dormancy period (13–20 days) falling in the same cluster can be used as donors for the improvement of rice genotypes with low shattering ability and incorporating a considerable period of dormancy so as to avoid pre-harvest sprouting due to delayed harvesting. Further, they can be crossed with 'Pratyumna' having less than 1 week dormancy period, a genotype of the cluster XVII with which they have a maximum genetic divergence of 51.4 and may serve as parents in the development of mapping populations for the identification of QTLs/genes for shattering and dormancy traits.

Keywords: augmented randomized complete block design, dormancy, multivariate analysis, rice, shattering, yield

Introduction

Rice is the most important human food crop in the world and is the staple food for more than half of the global population. Asia accounts for 90% of global rice consumption and the total rice demand continues to rise with the ever-increasing population (Rachana *et al.*, 2020). In India, it is grown in about 42.94 million hectares with a production of 115.9 million tonnes and productivity of 2585 kg/ha (INDIASTAT, 2018–19). Rice breeding programmes majorly focus on the development of modern rice varieties with high yield, wide adaptability, resistance to various biotic and abiotic stresses and improved grain quality (Dixit

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et al., 2020). However, two additional traits, grain shattering and pre-harvest sprouting (PHS) of matured grains in the standing crop, also result in reduced yields and economic loss to the farmers (Anusha *et al*., 2020).

Compared to other traits, little attention has been accorded to these traits, and part of the reason could be due to the lack of quality data on yield loss (Anusha *et al*., 2020). Yield losses in the range of 0–38% have been reported when varieties prone to severe shattering were grown (Jacobi *et al*., 1974; Sahu and Sahu, 1981; Agarwal *et al*., 1989). Dormancy is an important trait in rice breeding programmes because it is associated with resistance to PHS (Bewley and Black, 1982). PHS is a major constraint to rice production worldwide when long periods of hot, humid weather occur during harvesting seasons, leading to substantial losses of yield and quality.

Owing to the complex nature of agronomic traits, understanding genetic variability present in the germplasm *per se* for the trait, factors contributing to genetic variability and interaction among the component traits are of utmost importance. A critical understanding of genetic variability for the traits under improvement is a prerequisite for the success of any breeding programme. Thus, various selection criteria need to be employed in the identification of promising genotypes with a desirable combination of traits. Heritability estimates for the trait under improvement in a set of germplasm help in selecting superior genotypes as they measure the transmission of characters from generation to generation. Johnson *et al*. (1955) suggested that heritability estimates along with genetic advance would be more useful in predicting genetic gain under selection than heritability estimates alone since high heritability does not always indicate high genetic gain.

Correlation analysis determines the association among traits under study and help in designing selection strategies in the simultaneous improvement of a combination of traits. At the same time, an assessment of genetic diversity in a set of genotypes under study helps in the development of superior recombinants. While Mahalanobis' D^2, a powerful tool, quantifies the genetic divergence in germplasm, principal component analysis (PCA) helps in the identification of a set of genotypes capturing maximum genetic diversity of the collection (Noirot *et al*., 1996; Gireesh *et al*., 2017).

In view of the importance of shattering and dormancy-related traits in breeding for improved high-yielding rice varieties, the present investigation was undertaken to evaluate 107 genotypes and identify promising genotypes with desirable trait combinations of yield-related traits, low shattering and dormancy.

Materials and methods

The experimental material comprised 107 genotypes including 98 test entries and nine checks that included indigenous (83) and exotic (24) collections covering high-yielding *indica* cultivars suitable for various rice-growing ecologies of India, elite *indica* breeding lines, aromatic cultivars, tropical *japonica* accessions, landraces and selected backcross inbred lines (BILs) coded as 'SN' derived from the cross of 'Swarna', an elite *indica* cultivar, and 'CR100008', a wild accession of *Oryza nivara*. The details of the area of cultivation/geographical origin, source, cross-combination, grain type and other features are given in online Supplementary Table S1. The experiment was laid out at RRC during *Kharif* (wet season) 2019 in augmented randomized complete block design (ARCBD) in seven blocks. The checks (nine) were planted in seven replications such that each check appeared once in every block, thus the number of plots summed up to 161. The sowings in the nursery bed were completed by 18 July 2019 and plants were transplanted to the main field on 9 August 2019 with a spacing of 20 cm × 15 cm. Each plot was raised in one row of 4 m length. The plots were managed using standard recommended agronomic practices.

Mean data were collected on 11 traits related to yield, shattering and dormancy at appropriate stages of plant growth. Observations on yield traits were recorded at maturity. The traits included days to 50% flowering (DFF), plant height (PH; cm), panicle length (PL; cm), panicle number (PN) or ear bearing tillers (EBT), grain number (GN) or number of grains per panicle (NGP), 1000-grain weight or test weight (TW; g) in g, single plant yield (SPY; g), days to physiological maturity (PM), shattering by hand fist method (SHF) as % (Anusha *et al*., 2020), shattering by horizontal dropping method (SHD) (Voleti *et al*., 2013) as % and period of dormancy (DP) (Anusha *et al*., 2020). First flowered panicles were tagged and data on shattering were recorded after attaining physiological maturity. Panicles harvested at physiological maturity were sown in Petri plates at weekly intervals to assess the period of dormancy.

The augmented analysis of variance (ANOVA) was carried out using 'augmentedRCBD' R package (Aravind *et al*., 2020) in RStudio 1.3. (https://aravind-j.github.io/augmentedRCBD/ https://cran.r-project.org/package=augmentedRCBD). The contributing factors of the variance for traits under study were analysed under unidirectional elimination of heterogeneity separately for blocks and treatments. The ANOVA and genetic variability estimates [genotypic coefficient of variability (GCV), phenotypic coefficient of variability (PCV), broad sense heritability (Hb) and genetic advance as per cent mean (GA)] were obtained. The correlation and regression analyses were carried out in SAS 9.3 (2011). Stepwise regression analysis was performed to identify the traits influencing the SPY using traits considered in this experiment. Multivariate analyses such as diversity analysis and PCA were carried out using 'biotools' (Silva, 2017), 'FactoMineR' (Kassambara and Mundt, 2020) and 'factoextra' (Husson *et al*., 2020) R packages.

Results

ANOVA and mean performance of the genotypes

ANOVA both under treatment-adjusted and block-adjusted revealed highly significant differences among the genotypes for all the traits except for panicle number. In case of checks, mean sum of squares (MSS) was the same under both cases of heterogeneity elimination (adjustment) and non-adjustment for all the traits indicating some fixed effect stabilizing the performance of checks. The MSS of the test entries was significant and comparable both under adjustment of blocks and treatment adjustment. The critical difference (CD) of checks confirms the uniform contrast expression of traits across the blocks. CD between two test entries between the blocks is very slightly higher when compared to within the blocks for all the traits, indicating that environmental heterogeneity was insignificant within the blocks and also between the blocks for all the traits (online Supplementary Table S2).

Mean phenotypic distribution (online Supplementary Fig. S1) revealed a wide range for all the traits with near-normal distribution for most of the studied traits. Near-normal distribution with non-significant left-handed skewness was observed for DFF, TW and PM and non-significant right-handed skewness for PL, PN and GN. Near-normal distribution with significant right-handed skewness was observed for PH and SPY. Skewness and kurtosis values indicated a highly significant deviation from a normal distribution for dormancy and shattering % by both hand fist and horizontal dropping methods. Also, box plots (Fig. 1) revealed outliers for several traits including SPY. More than 10% coefficient of variation was recorded for all traits except for flowering duration and physiological maturity (online Supplementary Table S2). Tropical *japonica* accession 'IRGC1723' was very early with 65 days to 50% flowering and 'SR-7' had the highest number of productive tillers (30). 'IRGC 11108' and 'RNR 15459' recorded high grain number (358) and low average shattering (<5%). 'RNR 11718' recorded a high single plant yield of 56.73 g, low average shattering of <5% and dormancy period of 21 days after physiological maturity.

Heritability estimates

The estimates of PCV were slightly higher than the corresponding GCV estimates for all the studied traits (online Supplementary Table S2 and Fig. 2). The magnitude of PCV and GCV estimates was low for DFF and PM, moderate for PH, PL, PN and TW while it is high for GN, SPY, SHF, SHD and DP. The heritability estimates were low for PN, moderate for PL, SPY and SHD and high for DFF, PL, GN, TW and PM. While genetic advance (GA) was low for PN, moderate for DFF, PL and PM and high for PH, GN, TW, SPY, SHF, SHD and DP.

Correlation coefficients

Single plant yield had a highly significant positive correlation with PH, PL and TW and a significant positive correlation with GN (Table 1). A highly significant negative correlation for shattering trait was observed with DFF and GN, a significant negative correlation with PM and a highly significant positive correlation with PN and TW. Dormancy period recorded a highly significant negative correlation with GN and PM while a significant positive correlation with TW and shattering traits. Highly significant positive correlations were observed between two pairs of traits 'PH and PL' and 'DFF and PM', while a highly significant negative correlation between 'GN and PN', 'GN and TW' and 'PL and PM'.

Stepwise regression analysis of SPY over other traits

The SPY was influenced by PH (14.8%), TW (10.6%), GN (8.5%) and PN (2.2%); these four traits altogether explained 36.2% variability in the yield (Table 2).

Regression equation for SPY is expressed as;

$$\widehat{\mathrm{SPY}} = -0.22.84 + 0.48\mathrm{PH} + 0.06\mathrm{TW} + 0.12\mathrm{GN} + 1.09\mathrm{PN}.$$

With an increase in every one cm of PH, there is an increase of 0.48 g of SPY; with an increase in every 1 g of TW, there is an increase of 0.06 g of SPY; further for every one unit increase in GN and PN, there is an increase of 0.12 and 1.09 g of SPY, respectively. Also, the residual diagnosis also showed that the residuals of the model follow the normality assumption.

Principal component analysis

In the PCA, a total of 11 principal components (PCs) were extracted and it revealed four most informative PCs with Eigen values of 2.66, 1.96, 1.68 and 1.07 which accounted for 67.02% of the cumulative variance (online Supplementary Table S3 and Fig. 3(a)). As per the PCA-variables plot (Fig. 3(b)) and PCA Bi-plots (Fig. 3 (c)), five traits *viz.*, DFF, PM, TW, SHF and GN contributed maximum variations in PC1, while four traits *viz.*, PH followed by SPY, PL and GN contributed to the maximum variability in PC-2. Thirty-three genotypes in PC-1 had PC scores ranging from 1.05 (Warangal Rice 1) to 7.19 (Azhoghi), while in PC-2, 41 genotypes showed the PC score ranging from 1.007 (Bathukamma) to 6.93 (Jagtial

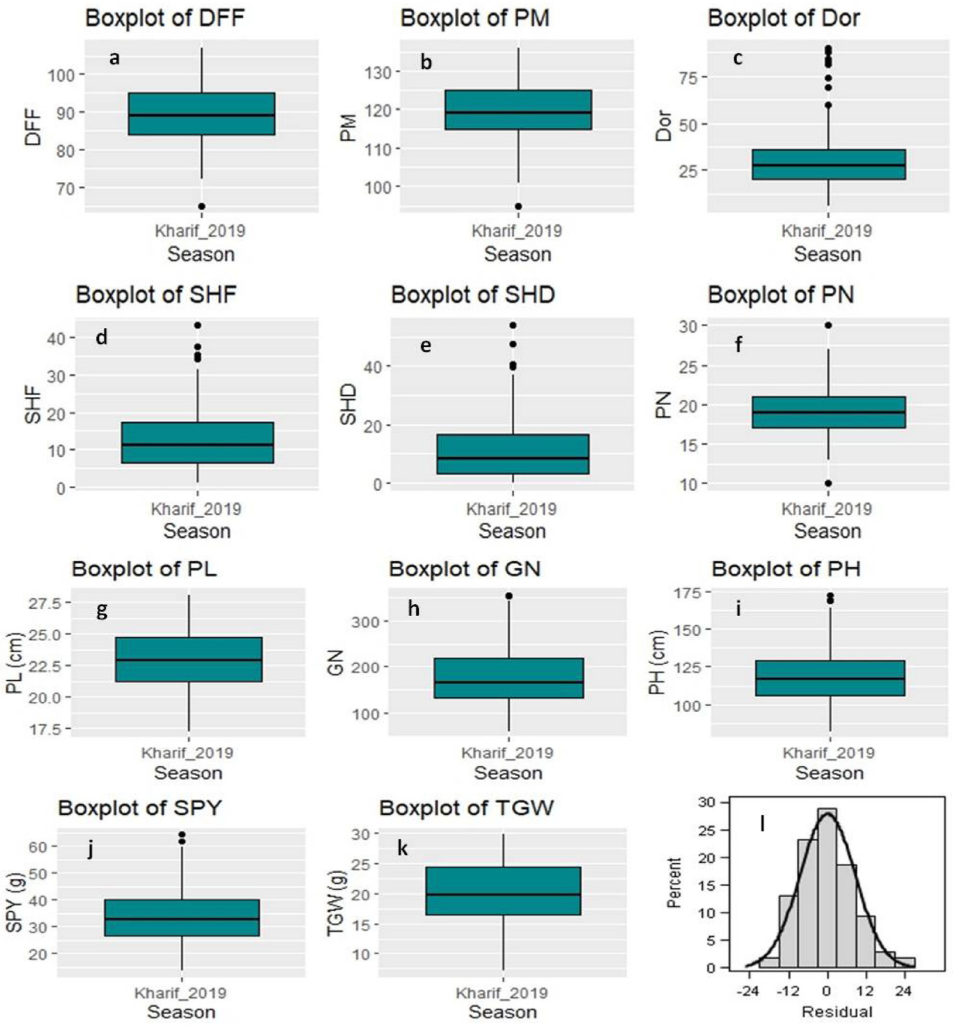

Fig. 1. Box-plots (a–k) showing variation in the data of 11 yield, shattering and dormancy-related traits in the studied rice germplasm. The upper, median and lower quartiles represent the 75th, 50th and 25th percentiles of the genotypes, respectively. The vertical lines represent the variation in the population. Dots represent the outliers. (l) Residual normality plot.

sannalu) (online Supplementary Table S4). Five genotypes (Azhoghi, SR-1, Rajendra, E2040, IRGC1723 and SR-6) in PC-1 and two genotypes (WGL 915 and RNR 11718) in PC-2 contributed to the maximum genetic diversity (Fig. 3 (c)).

Genetic diversity and clustering of genotypes based on D^2 *analysis*

Based on D^2 analysis, the 107 genotypes were grouped into 18 clusters (online Supplementary Table S5). Cluster I is the largest comprising 70 genotypes followed by cluster II with six genotypes, clusters III and VIII had four genotypes, clusters IV, VII and IX had three genotypes, clusters V, VI and X had two genotypes and the remaining eight clusters XI to XIII were single genotype clusters (online Supplementary Fig. S2). Cluster means for DFF is the lowest in clusters X and XVII. Low shattering % (<5%) based on the average of SHF and SHD was observed in four clusters (VI, XIV, XV and XVI). Cluster means for the traits PN, PL, GN, TW and SPY are the maximum in the clusters XVIII, XVI, VI, IX and XIV, respectively. Dormancy of 2–3 weeks was observed in clusters XII and XVI.

The average intra- and inter-cluster D^2 values among 18 clusters are presented in online Supplementary Table S6. The intra-cluster D^2 values ranged from 0 (XVIII, XVII, XVI, XV, XIV, XIII, XII and XI) to 17.2 in cluster X. The highest inter-cluster distance of 88.2 was observed between the pair of clusters 'XVII and XVIII' followed by 'XIV and XVII' (75.8), 'XI and XVII' (73.9), 'V and XVII' (68.9), 'X and XVI' (66.7) and 'XIII and XVII' (65.7), while the lowest was

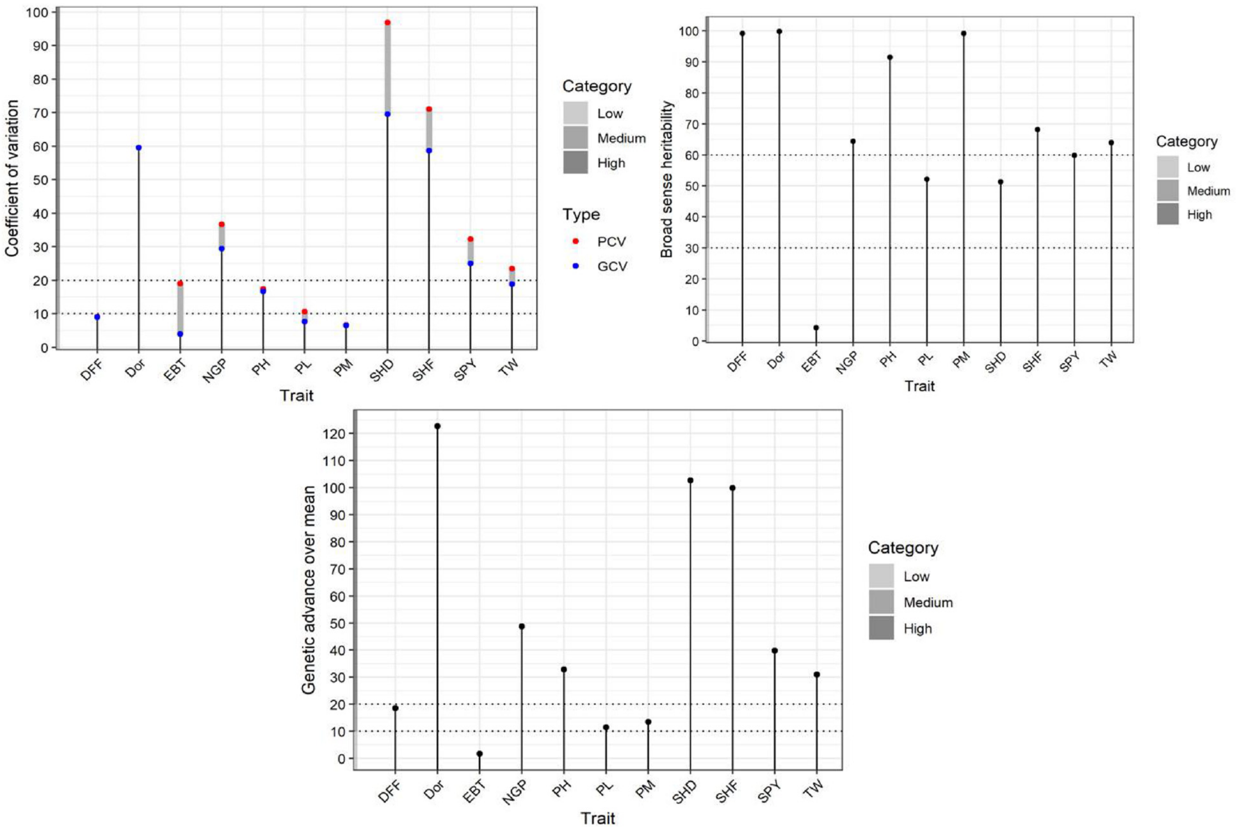

Fig. 2. GCV, PCV, heritability in broad sense and genetic advance as per cent of mean for 11 traits in 107 rice genotypes.

noticed between 'VIII and XVI' (19.1) and followed by 'XV and XVI' (19.4) and 'IV and XV' (19.6), 'I and II' (20.3) and 'II and XIII' (20.5).

Discussion

The constitution of the experimental material was made in such a way as to encompass maximum genetic diversity for the traits under study and ANOVA revealed ample genetic variance among the genotypes for all the traits except PN. A wide array of germplasm including high-yielding *indica* cultivars (47), aromatic cultivars (8), hybrid entries (6), IRRI collection (6), landraces (3), tropical *japonica* accessions (17), wild introgression lines (6), advanced elite breeding lines (5) and pre-release cultures under minikit testing (9) were included in the multivariate analysis (online Supplementary Table S1). Of the 108 genotypes studied, 83 are indigenous, 24 are exotic collections from the USA, Liberia, Argentina, Indonesia, Bolivia, Australia, Myanmar and unknown origin indicating extensive geographical diversity. Earlier reported BILs (BIL-SN13, BIL-SN25, BIL-SN163, BIL-SN108, BIL-SN38 and BIL-SN116) derived from Swarna/*O. nivara* with seed dormancy and low shattering (Anusha *et al.*, 2020), tropical *japonica* accessions known for low shattering ability and aromatic cultivars known for seed dormancy were included in the present study. Thus, this genetic material due to the presence of abundant variation is a valuable source to select the superior genotypes for traits under consideration. ARCBD is widely practised when a large number of genotypes have to be evaluated. Jyothi *et al.* (2018) evaluated 650 genetically diverse rice genotypes of tropical *japonica* and *indica* and established an initial core set for new plant type traits *viz.*, high grain number (GN), few unproductive tillers, strong culm and high biomass.

CD values under various conditions revealed the insignificant environmental heterogeneity and lesser micro-environment effect. Moreover, residual MSS under both systems of heterogeneity elimination was also lesser indicating the precision of the experimental methodology and research finding. Mean, range and standard deviation for all the traits revealed a wide range of phenotypic variation. Skewness and kurtosis values indicate near-normal distribution for most of the studied traits indicating the quantitative nature of traits that are controlled by many genes. A highly significant deviation from normal distribution was observed for the dormancy period and shattering %, indicating the qualitative nature of inheritance for these traits.

Table 1. Correlation coefficients among component yield, shattering and dormancy-related traits among 107 rice genotypes

Traits	DFF	PH	PL	PN	GN	TW	SPY	PM	SHF	SHD	DP
DFF	1	0.02	−0.22*	−0.004	0.21*	−0.21*	0.001	0.80**	−0.28**	0.18*	−0.11
PH		1	0.43**	0.06	0.21*	0.13	0.38**	−0.02	−0.11	−0.04	0.14
PL			1	0.15	0.02	0.25**	0.32**	−0.30**	−0.01	−0.16	0.07
PN				1	−0.31**	0.16	0.13	−0.08	0.32**	0.19*	0.06
GN					1	−0.39**	0.19*	0.19*	−0.30**	−0.03	−0.37**
TW						1	0.37**	−0.16	0.29**	0.05	0.19*
SPY							1	0.01	0.03	−0.05	−0.1
PM								1	−0.23*	0.24*	−0.25**
SHF									1	0.35**	0.20*
SHD										1	0.004
DP											1

*-significant at 0.05%; **-significant at 0.01%.

Table 2. Stepwise regression analyses of SPY and other traits in 107 rice genotypes

Variable	Estimates	SE	*F* value	*P*	Partial R^2	Model R^2
Intercept	−22.84	8.24	7.67	0.0067		0.362
PH	0.48	0.25	3.62	0.0598	0.148	
TW	0.06	0.015	16.72	<0.0001	0.106	
GN	0.12	0.04	7.25	0.0083	0.085	
PN	1.09	0.20	28.02	<0.0001	0.022	

Genetic variability is a prerequisite for any crop improvement programme and the range of variability for a particular trait is evident through PCV and GCV estimates. The present investigation revealed that the estimates of PCV were slightly higher than GCV for all the characters studied indicating less influence of environmental factors on the expression of traits. Similar such inferences were drawn by Rachana *et al.* (2018). Therefore, selection on the basis of phenotype alone can be effective for the improvement of these traits. Further, as the estimates of GCV and PCV are high for the traits GN, SPY, SHF, SHD and DP compared to the rest of the traits studied, direct selection for these traits would aid in genetic improvement. Heritability measures the contribution of genetic variability to the phenotypic variability and is a good index of the transmission of characters from parents to their offspring. However, heritability estimates along with genetic advance are normally more helpful in predicting the genetic gain under selection than heritability estimates alone. Thus, trait selection of PH, GN, TW, SPY, SHF, SHD and DP based on their high heritability and high genetic advance estimates would be more effective as these traits are under the control of additive gene action and least influenced by the environment.

Correlation studies are useful in understanding the association between grain yield and different traits (Ishwarya Lakshmi *et al.*, 2019), enabling plant breeders to select accessions possessing desirable traits that are related to grain yield. A highly significant positive correlation with PH, PL and TW and a significant positive correlation with GN was observed for SPY. Thus, these traits could be directly selected when breeding for high yield using the set of genotypes under study. Interestingly, for the set of genotypes under study, none of the component traits had a negative correlation with single plant yield in contrast to the general observation of a highly significant negative correlation between plant yield and plant height. Similar to our finding, Jambhulkar and Bose (2014) and Ronghua *et al.* (2019) reported a significant positive correlation between yield and plant height. Our findings are similar to the highly significant positive correlations between the pair of traits 'PH and PL' and 'DFF and PM' and highly significant negative correlation between 'GN and PN', 'GN and TW' and 'PL and PM' which is a common trend (Javed *et al.*, 2010; Ishwarya Lakshmi *et al.*, 2019). Further, a significant positive correlation between shattering and dormancy in the present investigation confirms the inter-relationship of weedy/domestication-related

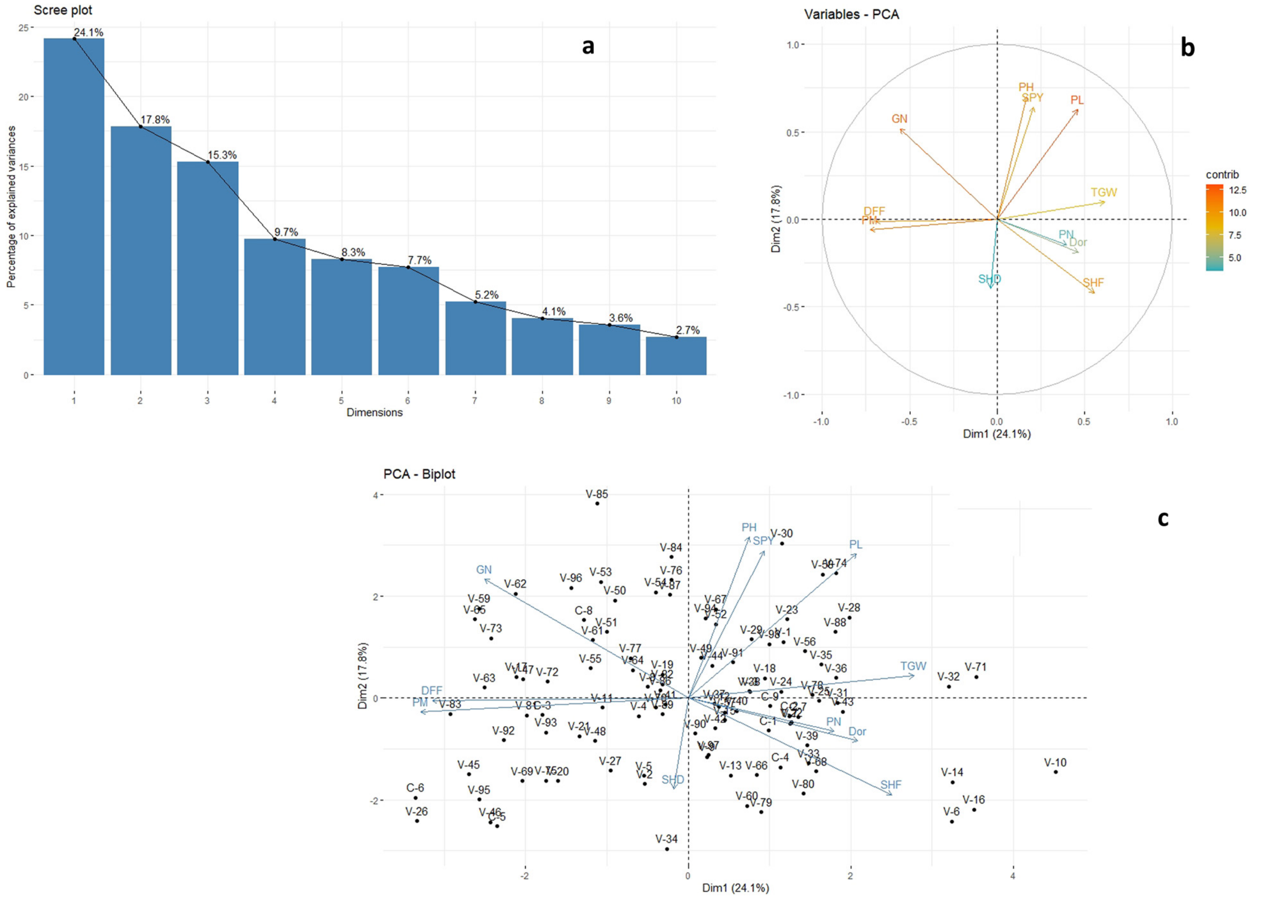

Fig. 3. (a) Scree Plot explaining the contribution of 11 various principal components, (b) PCA-Variables Plot, (c) PCA-Biplots explaining the contribution of 11 traits to the total variation in the 107 rice genotypes.

characteristics. Similar to our finding, Gu *et al.* (2005) reported a high shattering rate reducing germination percentage in weedy strain-derived BC_1F_1 populations. Seed shattering and dormancy have evolved as survival mechanisms in annual plant species. Shattering increases the survival ability and widespread distribution of a dormant seed making it thrive under unfavourable conditions. Seed shattering and dormancy QTLs have been found on chromosome 7 and a linkage among these traits has been demonstrated, even though they exist in indifferent regions of the chromosome (Sweeney *et al.*, 2006). Seed shattering and dormancy are the common morpho-physiological traits shared by weedy rice populations from different parts of the world, even though originating from multiple independent events (Huang *et al.*, 2017).

From stepwise regression analysis, it is clear that SPY was mainly influenced by PH, TW, GN and PN and altogether they contributed to 36.2% of the variability. The remaining variations may be explained by other factors or environmental variables which are not considered in this study. PCs explain the variability which could not be attributed to the other factors. In the present investigation, genetic variability was mainly explained by four PCs which accounted for 67.02% of the variance, while Worede *et al.* (2014) reported a similar amount of cumulative variance with two major PCs. Selection of traits via the traits that contribute to maximum morphological diversity through two major PCs would be beneficial. Five genotypes (Azhoghi, SR-1, Rajendra, E2040, IRGC1723 and SR6) in PC-1 and two genotypes (WGL915 and RNR11718) in PC-2 contributed to the maximum genetic diversity. Hence, utilizing these accessions as parents would be rewarding in rice breeding programmes.

Mahalanobis D^2 statistics is an effective statistical tool that gives a clear idea about the diverse nature of the population under evaluation. A wide range was observed for cluster means of all traits indicating a significant contribution of all the traits in genotypic clustering. The accessions were grouped into 18 diverse clusters with cluster I comprising 70 accessions accounting for 65.42% of the total genotypes evaluated indicating close relatedness among them. Majority of the genotypes belonging to cluster I are high-yielding popular varieties, hybrids and elite breeding lines. A high degree of heterogeneity was observed among eight of the clusters *viz*., *XI*, XII, XIII, XIV, XV, XVI, XVII and XVIII as they were represented by a single genotype, thus may be directly utilized as parents in future hybridization programmes to combine desirable characters. Highly divergent genotypes would produce a broad spectrum of variability in the subsequent generations enabling further selection and improvement and thus developed hybrids may produce a high magnitude of heterosis or desirable transgressive segregants, which would facilitate successful breeding. As the maximum inter-cluster distance was noticed between cluster XVII and XVIII followed by cluster XIV and XVII, cluster XI and XVII, cluster V and XVII, cluster X and XVI and cluster XIII and XVII crosses involving genotypes from these clusters would give wider and desirable recombinations. The greater the distance between two clusters, the greater the genetic diversity between the genotypes. The genotypes belonging to most divergent clusters may exploit the maximum amount of heterosis.

Five high-yielding varieties under cultivation (Karimnagar Samba, Sheetal, PR 121, Pranahitha and Jagtial Samba) with a combination of low shattering ability (3.35–5.7%) and considerable dormancy period (13–20 days) have been identified. Interestingly all the five promising genotypes are falling in the same cluster (Cluster I). They could be used as donors for the improvement of rice genotypes for low shattering ability and incorporating a considerable period of dormancy so as to avoid PHS due to delayed harvesting. Further, these five genotypes can be crossed with 'Pratyumna', a genotype of the cluster XVII with which they have a maximum genetic divergence of 51.4. 'Pratyumna' with the least dormancy period (<1 week) and high contrast in the trait values with the five identified varieties may serve as parents in the development of mapping populations for the identification of QTLs/genes for shattering and dormancy-related traits.

Conclusion

ANOVA revealed a considerable amount of genetic variance for all the traits except panicle number in the present study. Based on PCV, GCV, heritability and genetic advance estimates, selections based on plant height, grain number, test weight, grain yield and shattering and dormancy related traits can be effective for the improvement. Correlation and regression analyses indicate that grain number and thousand grain weight could be directly selected when breeding for high yield. The PC and D^2 cluster analyses attributed the variation due to traits and classified the variation existing in the germplasm accessions, respectively. The donors identified in the present investigation of geographically diverse germplasm will aid in the identification of QTLs/genes for shattering and dormancy-related traits for rice genetic improvement.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S1479262121000186

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