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ORIGINAL ARTICLE

Identification of promising genotypes and marker-trait associations for panicle traits in rice

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Abstract

Among various panicle traits, total number of spikelets, total number of grains and total grain filling % can be considered as main traits for determining yield in rice.Query To identify the genotypes with promising grain number at different positions of the panicle, a set of 72 germplasm comprising landraces and varieties were evaluated for 28 panicle traits across four environments. Correlation and regression analysis of 28 panicle traits highlighted the role of secondary panicle traits in contributing to the total grain yield. Three promising genotypes, viz. Badshahbhog, Ganjeikalli, Jeerigesanna for high SS (≥ 177), GS (≥ 143), and two genotypes, BR4_10, MO1 for GFS (93%) were identified. Interestingly, the same genotypes exhibited high STOT, GTOT and GFTOT. From G × E interactions, which won where view of GGE biplot, revealed that the genotypes Badshahbhog, Ganjeikalli, Jeerigesanna have won in different environments for grains total, and genotype BR4_10 for total grain filling %. Screening of the reported markers for cloned yield genes (*Dep1*, *Ghd7*, *Ghd8, PROG1* and *OsSPL14*) in 72 genotypes revealed 19 significant associations for 10 panicle traits in four environments with R^2 ranging from 5.4 to 20.2%. High significant association of *Ghd8* with SUS was detected with 20.2% R^2 value. The promising genotypes with high number of STOT, GTOT, GFTOT, SS, GS and GFS identified from the present study can be deployed in the breeding programmes of rice yield improvement.

Keywords Rice · Panicle traits · Cloned genes · Marker-trait associations

Abbreviations

SUP	Spikelets upper primary
GUP	Grains upper primary
GFUP	Grain filling percentage of upper primary
SUS	Spikelets upper secondary
GUS	Grains upper secondary
GFUS	Grain filling percentage of upper secondary
SLP	Spikelets lower primary
GLP	Grains lower primary
GFLP	Grain filling percentage of lower primary
SLS	Spikelets lower secondary
GLS	Grains lower secondary
GFLS	Grain filling percentage of lower secondary
SU	Spikelets upper
GU	Grains upper
GFU	Grain filling percentage of upper
SL	Spikelets lower
GL	Grains lower
GFL	Grain filling percentage of lower
SP	Spikelets primary
GP	Grains primary
GFP	Grain filling percentage of primary
SS	Spikelets secondary
GS	Grains secondary
GFS	Grain filling percentage of secondary
STOT	Spikelets total
GTOT	Grains total
GFTOT	Grain filling percentage total
PL	Panicle length

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Introduction

Rice (*Oryza sativa* L.) feeds more than half of the global population and plays a vital role in world's food security (Li et al. 2021). Enhancing yield levels to meet the demands of increasing global population under the decreasing cultivable area is a major challenge for rice breeding programmes. Rice yield is controlled by various factors such as direct (panicle number per unit area and/or per plant, grains per panicle and 1000 grain weight) and indirect (plant height, growth period, tillering ability, panicle length, grain length, grain filling rate and spikelets per panicle) (Huang et al. 2013). Panicle is the critical component for yield and panicle traits such as panicle length, panicle branching, number of primary branches and secondary branches determine the yield. Many high yielding rice cultivars possess longer primary branches and produce more secondary branches (Agata et al. 2020). The grain filling process differs for spikelets on primary branches and secondary branches of upper and lower portion of the rice panicle. Spikelets on primary rachis branches of upper half of the panicle show higher filling rate, whereas spikelets on secondary branches of lower half show relatively poor grain filling (Kato et al. 1993; Mohapatra et al. 1993; Rao et al. 2011). Wide genetic variability for various panicle traits has been reported in rice (Li et al. 2021). Significant genetic variation was also observed in the extent of grain filling across the panicle in the rice germplasm within a location (Kato et al. 2007; Kato 2010; Shiotsu et al. 2006) and in the same genotype at different locations (Kato et al. 2007) indicating the role of Genotype (G) × environment (E) interactions.

Many genes that regulate panicle traits have been functionally characterized/cloned such as *Gn1*-Grain number (Ashikari et al. 2005), *APO1-Aberrant Panicle Organization1* (Ikeda et al. 2007); *PROG1-Prostrate Growth* (Tan et al. 2008), *Ghd7-Grain number, plant height,* and *heading Date7* (Xue et al. 2008), *DEP1* (*Dense and Erect Panicle1*) (Huang et al. 2009), *IPA1/ WFP/ OsSPL14-Ideal Plant Architecture 1* (*IPA1*)/*Wealthy Farmer's Panicle* (*WFP*)/*Squamosa Promoter binding protein-Like 14* (*OsSPL14*) (Miura et al. 2010; Jiao et al. 2010). *LP-Larger Panicle* (Li et al. 2011), FUWA-an evolutionarily conserved gene (Chen et al. 2015) and CPB1-*Clustered Primary Branch 1* (Wu et al. 2016). In addition, several quantitative trait loci (QTLs), viz. *Ghd7, Ghd7.1 and Ghd8/DTH8-Days to Heading* were also reported to be associated with panicle traits besides other characters like heading date (Xue et al. 2008; Yan et al. 2011; Liu et al. 2013).

Gene-tagged markers/functional markers derived from the polymorphic sites within the genes were employed in mapping to detect variations in the target traits and also to identify QTLs responsible for these variations in rice (Pflieger et al. 2001). Based on the information derived from cloned genes, several candidate gene-based markers have been designed and deployed for marker assisted selection (MAS). Candidate gene-based markers for sucrose phosphate synthase gene and sugar transporter gene were found to be significantly associated with grain filling in primary and secondary branches of the rice panicle (Rao et al. 2011). Jang et al. (2018) identified 32 sequence variations in six panicle development genes that are significantly influencing spikelets per panicle. Three functional markers *Gn1a* (grain number), *GW2* (grain weight) and *SCM2* (strong culm) have been validated in 36 genotypes to identify QTLs associated with yield components (Mohanty et al. 2016). Genotypes with positive alleles for reported yield genes like *TGW6*, *Gn1a*, *SCM2* and *SPIKE* using gene-based functional markers were identified (Deepti et al. 2018) and candidate gene-based SSR markers from major yield genes, viz. *Gif1*, *Gn1a*, *GW2*, *Gs3* and *Dep1* (Zaharaddin et al. 2020).

Increasing yield by modifying the overall panicle architecture in terms of branching pattern and spikelet density has been reported. The secondary branch number is the most important contributor to spikelet number per panicle (Mei et al. 2006). Adriani et al. (2016) reported that the frequency of secondary branches is the most variable trait among the panicle traits.

In this study, we evaluated a panel of 72 germplasm, (1) to identify the genotypes with promising spikelets/grain number at different positions of the panicle, with special attention to total number of spikelets (STOT), total number of grains (GTOT) and total grain filling % (GFTOT) as they are the main panicle traits in determining yield, (2) to study the contribution of various panicle traits to total number of spikelets (STOT), total number of grains (GTOT) and total grain filling % (GFTOT) and (3) to identify significant marker-trait associations for panicle traits. The contribution of other panicle traits to STOT, GTOT and GFTOT has also been analysed which emphasized the importance of secondary panicle traits.

Materials and methods

Plant material and field screening

A set of 72 rice genotypes comprising 32 released varieties and 40 landraces (Supplementary Table S1) were evaluated in the Indian Council of Agricultural Research (ICAR)—Indian Institute of Rice Research (IIRR), Hyderabad, India (17.53° N and 78.27° E), for three consecutive wet seasons as three environments (E1, E2 and E3) and one wet

season as fourth environment (E4) at ICAR—National Rice Research Institute (NRRI) (20.45° N and 85.93° E) Cuttack, India. The field evaluation followed a randomized complete block design with two replications following standard crop management and protection practices. Each genotype was planted in three rows with spacing of 20 × 15 cm, and three panicles from tagged uniform plants from centre row were harvested at physiological maturity and air dried.

Phenotyping of panicle-related traits

The 72 genotypes were characterized for the 28 panicle-related traits. The distal half of the panicle was considered as the upper portion of the panicle and the proximal half was considered as lower portion of the panicle (Supplementary Fig. S1). The panicle length (PL) was measured using the scale (cm) from base to tip. The number of spikelets and grains on the upper and lower portion of primary and secondary branches were counted manually. The average of three panicles was considered for the analysis. The grain filling (GF) percentage was calculated based on the ratio of filled spikelets (grains) to the total number of spikelets. The 28 traits evaluated includes spikelets upper primary (SUP), grains upper primary (GUP), grain filling percentage of upper primary (GFUP), spikelets upper secondary (SUS), grains upper secondary (GUS), grain filling percentage of upper secondary (GFUS), spikelets lower primary (SLP), grains lower primary (GLP), grain filling percentage of lower primary (GFLP), spikelets lower secondary (SLS), grains lower secondary (GLS), grain filling percentage of lower secondary (GFLS), spikelets upper (SU), grains upper (GU), grain filling percentage of upper (GFU), spikelets lower (SL), grains lower (GL), grain filling percentage of lower (GFL), spikelets primary (SP), grains primary (GP), grain filling percentage of primary (GFP), spikelets secondary (SS), grains secondary (GS), grain filling percentage of secondary (GFS), spikelets total (STOT), grains total (GTOT) and grain filling percentage total (GFTOT).

Statistical analysis

Descriptive statistics, viz. minimum, maximum, average, CV (coefficient of variation) and standard deviation (SD) were performed using *statistix 8.1* (Analytical software 2003). The average data of each genotype across replications and environments were considered for density plots, correlation and regression analysis using R studio packages-*ggplot2, reshape2*, (Wickham 2007, 2016); *sjlabelled, sjPlot, ggcorrplot*, [Lüdecke, (2022); Kassambara, (2018)]; *ggplot2, gridExtra, ggpmisc, ggpubr* [Wickham, (2016); Auguie and Antonov (2017); Aphalo, (2022); Kassambara, (2018)].

Stability analysis

Three traits, viz. STOT, GTOT and GFTOT were analysed for additive main effect and multiplicative interactions (AMMI) and GGE biplots, mean versus stability, ranking genotype and Which Won Where/What plots (Dumble et al. 2017; Wright and Laffont 2018; Yaseen et al. 2018) using different packages in R (R Core Team 2018). The AMMI model used for the stability analysis is as follows:

$$Y_{ij} = \mu + g_i + e_j + \sum_{n=1}^{N} \gamma_n \beta_{in} \alpha_{ij} + \rho_{ij} + \varepsilon_{ij}$$

GGE biplots displayed the g and GE variation, which uses sites regression (SREG) linear–bilinear model as below

$$Y_{ij} - \mu_j = \sum_{k=1}^{t} \gamma_k \beta_{in} \alpha_{ij} + e_{ij}$$

where Y_{ij} = trait mean of *i*th genotype in *j*th environment, μ is grand mean, g_i genotypic effect of the *i*th genotype, e_j is environment effect of the *j*th environment, γ_n is eigenvalue of the *n*th IPCA, β_{in} is eigenvector for *i*th genotype for PC *n*, α_{ij} is eigenvector for *j*th environment for PC *n*, $\rho_{ij}$is AMMI residue, ε_{ij} is error associated with *i*th genotype in *j*th environment.

Genotyping and analysis

Candidate gene-based marker-trait associations

Reported markers for five cloned yield genes, viz. *Dep1*, *Ghd7*, *Ghd8, PROG1* and *OsSPL14* (Huang et al. 2009; Xue et al. 2008; Yan et al. 2011; Tan et al. 2008; Miura et al. 2010; Jiao et al. 2010) were used to study marker-trait associations. Total genomic DNA was isolated from fresh young leaves of 72 genotypes using cetyltrimethylammonium bromide (CTAB) protocol as per Doyle (1991). PCR amplification was carried out in a Veriti thermal cycler (Applied Biosystems, USA) in a 10 µl reaction volume containing 30 ng of template DNA, 10 × PCR buffer, 0.25 mM each of dNTPs, 0.5 pmol of forward and reverse primers, 1.0 U Taq polymerase (Bangalore Genei, India). PCR conditions were maintained as initial denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 45 s, annealing at 55 °C for 1 min, extension at 72 °C for 1 min and then a final extension at 72 °C for 10 min. Amplified products were resolved in 3% Metaphor agarose gel (Lonza, USA) and documented using Alpha Imager 1220 (Alpha Innotech, USA). Association between identified three polymorphic markers (Prb1, C8dsF/R and

M1) and 28 panicle traits was calculated using generalized linear model (GLM) in TASSEL v3.0 (Yu et al. 2006; Bradbury et al. 2007).

Results

Phenotyping statistics of 72 genotypes

Wide variation for the 28 panicle traits was observed among the 72 genotypes across the four environments (Table 1). Increase in panicle trait parameters from E1 to E3 environments was observed for most of the traits (Fig. 1). Marginal increase in 10 panicle trait values (PL, STOT, GTOT, SS, SLS, SL, GS, GLS, GLP and GL) was observed in E4 compared to E1, E2 and E3. Distribution of 28 panicle traits across four environments is shown in box plots (Fig. 1). From the average of four environments, STOT ranged from 76.67 (BR4_10) to 251.33 (Kalajira) with an average of 166.71, GTOT ranged from 71.42 (BR4_10) to 209.33 (IC115134) with an average of 131.88 and GFTOT ranged from 68.19 (BR4_10) to 94.89 (IC115134) with an average of 79.33%. Critical secondary panicle traits (for total grain yield) such as SS ranged from 36.50 (BR4_10) to 177.25 (Jeerigesanna) with an average of 99.71, the GS ranged from 34.25 (BR4_10) to 143.42 (Jeerigesanna) with an average of 76.41, and GFS ranged from 60.65 (BR4_10) to 93.84 (IC115134) with an average of 76.64%. The average panicle length ranged from 18.37 cm (KR1_24) to 30.32 cm (HRC205). Descriptive statistics of the 28 traits across four environments is given in Supplementary Table S2.

Based on the average of four environments, G3 (Badshahbhog) showed the STOT with 239.58 spikelets, and the highest GUS with 72.75 grains. G8 (BR4_10) showed the highest GFUP (98.42%), GFU (95.78%), GFL (94.27%), GFLS (94.38%), GFP (95.85%), GFS (93.84%) and GFTOT (94.89%). G13 (Ganjeikalli) has the highest SLS (102.08), SL (157.25), GLP (47.33), GLS (87.92), GL (135.25) and GTOT (209.33). G45 (IC5006) showed the highest number of SLP (57.50) and GP (75.42). G52 (Jeerigesanna)

Table 1 Phenotype variation (average of four environments) observed for 28 panicle traits in the 72 genotypes

Traits	Range	Mean ± SD	CV
Spikelets upper primary (SUP)	15.83–35.42	26.46 ± 4.75	17.95
Grains upper primary (GUP)	13.33–30.08	22.33 ± 3.88	17.39
Grain filling % upper primary (GFUP)	72.00–98.42	84.75 ± 6.62	7.81
Spikelets upper secondary (SUS)	14.83–89	41.26 ± 13.65	33.07
Grains upper secondary (GUS)	13.75–72.75	33.76 ± 11.91	35.27
Grain filling % upper secondary (GFUS)	66.26–94.5	81.80 ± 7.36	8.99
Spikelets lower primary (SLP)	24.33–57.5	40.62 ± 8.63	21.25
Grains lower primary (GLP)	18.75–47.33	33.14 ± 6.81	20.56
Grain filling % lower primary (GFLP)	64.47–94.46	82.01 ± 7.15	8.71
Spikelets lower secondary (SLS)	20.75–102.08	58.45 ± 15.54	26.59
Grains lower secondary (GLS)	17.42–87.92	42.66 ± 13.19	30.93
Grain filling % lower secondary (GFLS)	54.01–94.38	72.98 ± 9.51	13.02
Spikelets upper (SU)	31.58–117.83	67.72 ± 16.98	25.08
Grains upper (GU)	27.67–100	56.09 ± 14.33	25.54
Grains filling % upper (GFU)	71.11–95.78	83.08 ± 6.52	7.85
Spikelets lower (SL)	45.08–157.25	99.07 ± 22.29	22.50
Grains lower (GL)	37.92–135.25	75.79 ± 18.12	23.91
Grains filling % lower (GFL)	63.05–94.27	76.78 ± 7.78	10.14
Spikelets primary (SP)	40.17–92	67.08 ± 12.27	18.29
Grains primary (GP)	32.83–75.42	55.47 ± 9.83	17.72
Grain filling % primary (GFP)	67.76–95.85	83.04 ± 6.44	7.76
Spikelets secondary (SS)	36.50–177.25	99.71 ± 26.86	26.94
Grains secondary (GS)	34.25–143.42	76.41 ± 23.16	30.30
Grains filling % secondary (GFS)	60.65–93.84	76.64 ± 80.3	10.47
Spikelets total (STOT)	76.67–251.33	166.78 ± 36.24	21.73
Grains total (GTOT)	71.42–209.33	131.88 ± 30.06	22.79
Grain filling % total (GFTOT)	68.19–94.89	79.33 ± 6.84	8.62
Panicle length (PL)	18.37–30.32	25.12 ± 2.52	10.03

SD standard deviation, *CV* coefficient of variation

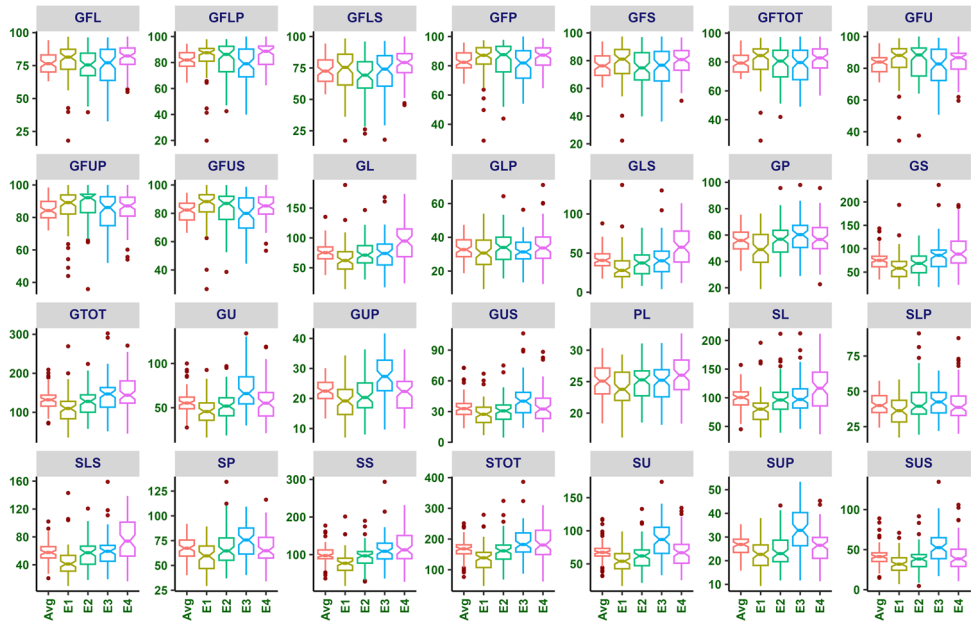


Fig. 1 Boxplots of 28 panicle traits in 72 genotypes with average of four environments. Spikelets upper primary (SUP), grains upper primary (GUP), grain filling percentage of upper primary (GFUP), spikelets upper secondary (SUS), grains upper secondary (GUS), grain filling percentage of upper secondary (GFUS), spikelets lower primary (SLP), grains lower primary (GLP), grain filling percentage of lower primary (GFLP), spikelets lower secondary (SLS), grains lower secondary (GLS), grain filling percentage of lower secondary (GFLS), spikelets upper (SU), grains upper (GU), grain filling percentage of upper (GFU), spikelets lower (SL), grains lower (GL), grain filling percentage of lower (GFL), spikelets primary (SP), grains primary (GP), grain filling percentage of primary (GFP), spikelets secondary (SS), grains secondary (GS), grain filling percentage of secondary (GFS), spikelets total (STOT), grains total (GTOT), grain filling percentage total (GFTOT) and panicle length (PL)

has the highest number of SS (177.25), SUS (89) and GS (143.42). G53 (Kalajira) showed the highest number of SUP (35.42), SP (92) and STOT (251.33) and G60 (MO1) showed the highest GFUS (94.50%) and GFLP (94.46%). It is noteworthy that three genotypes G52 (Jeerigesanna) > G3 (Badshahbhog) > G13 (Ganjeikalli) and showed highest GS (143.42, 137.42, 136.92) among the studied genotypes. Normal distribution was observed for SU, SUS, SLS, SL, SS, STOT, GU, GUS, GLS, GL, GS and GTOT as represented in density histograms (Supplementary Fig. S2).

Considering the average values of the total 28 traits of the study across four environments, average number of SS (99.71) was the highest across the genotypes followed by SL (99.07), SU (67.72), SP (67.08), SLS (58.45), SUS (41.26), SLP (40.62) and SUP (26.46), and the same pattern was also observed with grains. When the average values across four environments were considered, GFUP (84.75%) was the highest followed by GFU (83.08%), GFP (83.04), GFUS (81.8%), GFLP (82.01%), GFTOT (79.33%), GFL (76.78%), GFS (76.64%) and GFLS (72.98%).

Correlation and regression

Highest significant correlation was observed between SU with SUS; STOT with SS and GTOT with GUS. GTOT were significantly correlated with GS. Also, GFTOT was significantly correlated with GFL, GFS and GFLS (Fig. 2). For STOT, GTOT and GFTOT, higher significant correlations were observed with most of the secondary panicle traits.

In regression analysis, the average values of STOT, GTOT and GFTOT were analysed against the other 25 panicle traits. SS, SL, GTOT and SLS showed a direct positive effect on STOT with R^2 ranging from 0.94 to 0.84. GS, GL, SS and STOT were contributing to the GTOT with R^2 ranging from 0.93 to 0.88. For GFTOT, highest positive effect was observed for GFL, GFS, GFLS, GFU and GFUS with R^2 ranging from 0.94 to 0.81. (Fig. 3A–C).

Stepwise regression analysis

Stepwise regression analysis was performed to determine the panicle traits that contribute to STOT, GTOT and GFTOT (Supplementary Table S3). Three significant variables, viz. GLS (0.01%), SP (6.3%) and SS (93.6%) has positive effect on STOT, explaining 100% variation. The following model was obtained for STOT:

$$\widehat{\text{STOT}} = -0.01 + 0.001\ \text{GLS} + 1.0\ \text{SP} + 0.99\ \text{SS} \quad (1)$$

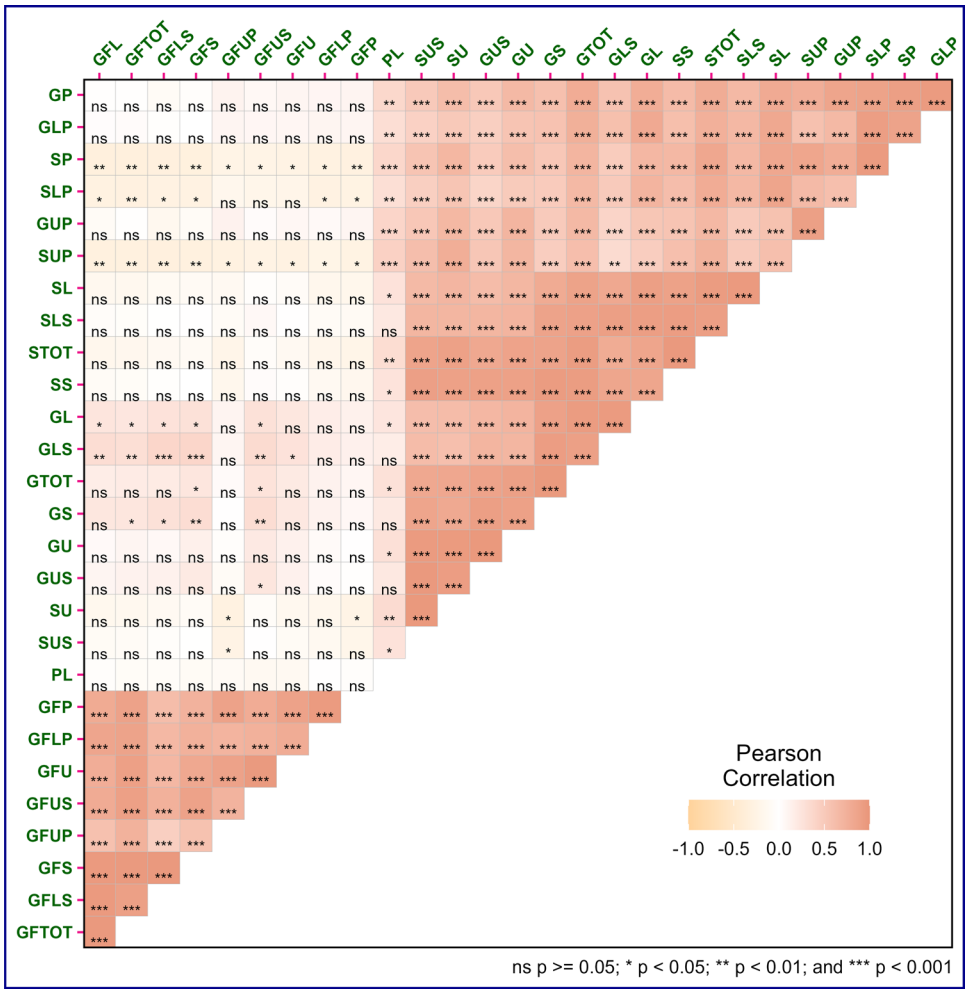


Fig. 2 Correlation among 28 panicle traits in 72 genotypes with average of four environments. Spikelets upper primary (SUP), grains upper primary (GUP), grain filling percentage of upper primary (GFUP), spikelets upper secondary (SUS), grains upper secondary (GUS), grain filling percentage of upper secondary (GFUS), spikelets lower primary (SLP), grains lower primary (GLP), grain filling percentage of lower primary (GFLP), spikelets lower secondary (SLS), grains lower secondary (GLS), grain filling percentage of lower secondary (GFLS), spikelets upper (SU), grains upper (GU), grain filling percentage of upper (GFU), spikelets lower (SL), grains lower (GL), grain filling percentage of lower (GFL), spikelets primary (SP), grains primary (GP), grain filling percentage of primary (GFP), spikelets secondary (SS), grains secondary (GS), grain filling percentage of secondary (GFS), spikelets total (STOT), grains total (GTOT), grain filling percentage total (GFTOT) and panicle length (PL)

For every number increase in GLS, SP and SS, there was an increase in 0.001 number of STOT with GLS; 1.0 number of STOT with SP and 0.99 number of STOT with secondary spikelets (SS).

GTOT was mostly influenced by GFUS (0.01%), GFLP (0.01%), GP (6.9%) and GS (93%) explaining 100% with the remaining variation explained by other factors. Stepwise regression Eq. (2) for GTOT is

$$\widehat{\text{GTOT}} = 0.009 + 0.0001\ \text{GFUS} + 0.0001\ \text{GFLP} + 1.0\ \text{GP} + 1.0\ \text{GS} \quad (2)$$

For every number increase in GFUS, GFLP, GP and GS, there was an increase in 0.0001 number of GTOT with GFUS; 0.0001 number of GTOT with GFLP; 1.0 number of GTOT with GP and 1.0 number of GTOT with GS.

GFTOT was influenced by STOT (0.03%), GFUP (0.01%), SUS (0.02%), GFUS (0.02%), GFLP (0.01%), GFLS (0.01%), SU (0.001%), GU (0.001%), GFU (5.89%), SL (0.001%), GL (0.01%), GFL (93.87%), GFP (0.04%) and GFS (0.01%) explaining 100% with the remaining variation explained by other factors. Stepwise regression Eq. (3) for GFTOT is

$$\begin{aligned}\widehat{\text{GFTOT}} = {} & -0.085 - 3.61\ \text{STOT} - 0.174\ \text{GFUP} - 0.009 \\ & \text{SUS} - 0.226\ \text{GFUS} - 0.197\ \text{GFLP} \\ & - 0.226\ \text{GFLS} + 3.64\ \text{SU} - 0.026 \\ & \text{GU} + 0.46\ \text{GFU} + 3.59\ \text{SL} + 0.018\ \text{GL} + 0.46 \\ & \text{GFL} + 0.39\ \text{GFP} + 0.49\ \text{GFS}\end{aligned} \quad (3)$$

GFTOT was positively controlled by SU, GFU, SL, GL, GFL, GFP and GFS; negative effect was shown by STOT, GFUP, SUS, GFUS, GFLP, GFLS and GU.

Stability analysis

Stability analysis of 72 genotypes across four environments (E1, E2, E3 and E4) has shown significant genotype × environment effects for the three traits, STOT, GTOT and GFTOT (Supplementary Table S4, Fig. 4A–C). For STOT,

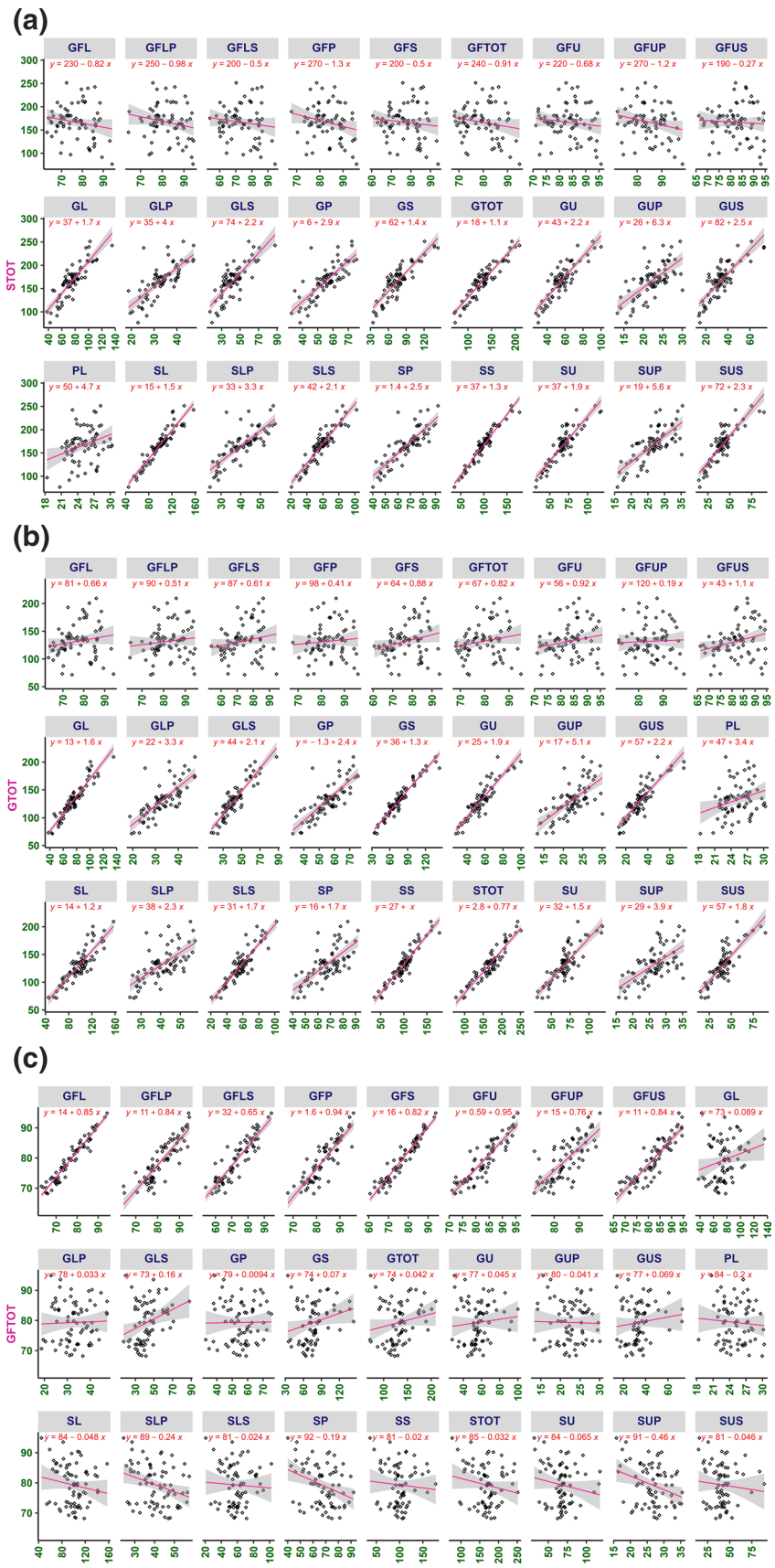


Fig. 3 Regression analysis for 28 panicle traits in 72 genotypes. **A** Spikelets total (STOT). **B** Grains total (GTOT). **C** Grains filling % total (GFTOT)

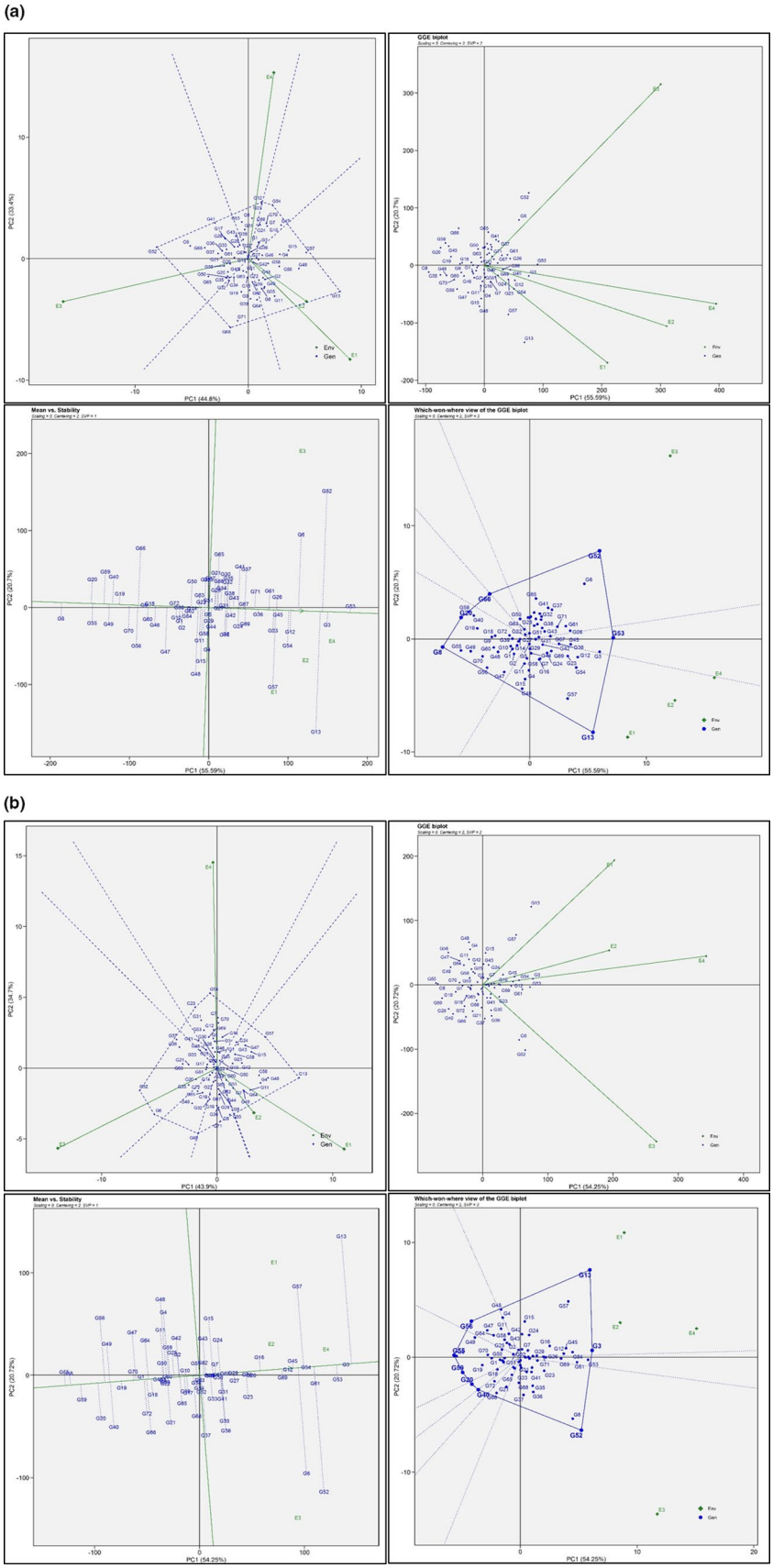
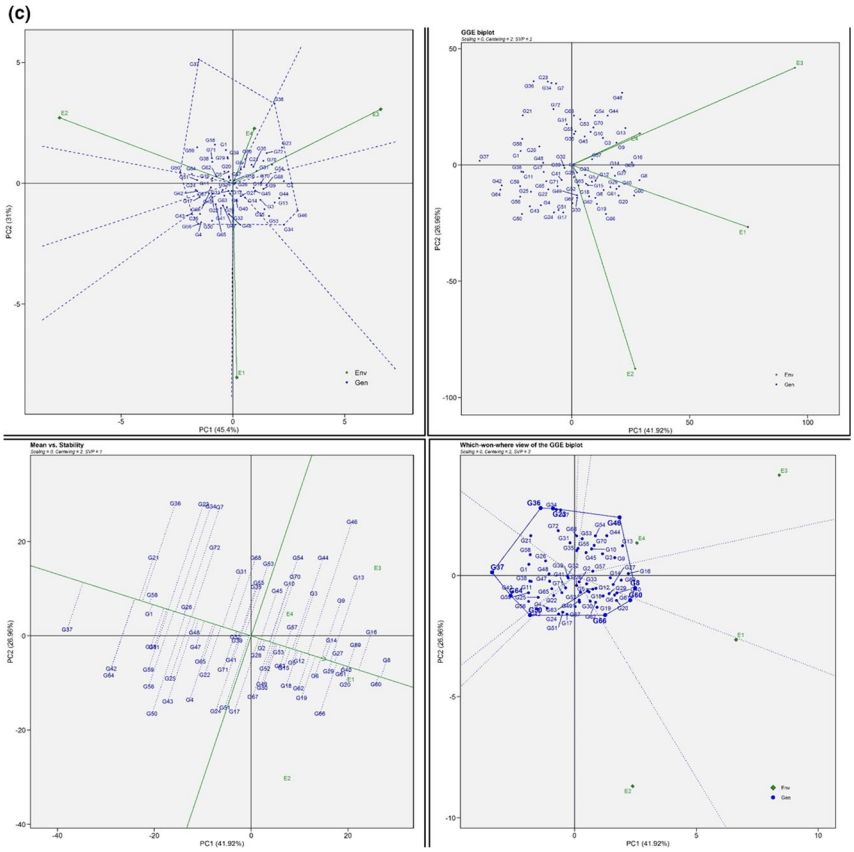


Fig. 4 AMMI biplot, GGE biplot, mean versus stability and Which Won Where/What for (**A**) spikelets total (STOT) (**B**) grains total (GTOT) (**C**) grains filling % total (GFTOT) across four environments in 72 genotypes

Fig. 4 (continued)



27.5% genotypic effect, 9.6% environment effect and 23.7% genotype environment effect was observed. According to AMMI analysis, PC1 contributed 44.8% variability, PC2 contributed 33.4% variability and PC3 contributed 21.8% variability. The AMMI biplot showed 78.2% of goodness of fit with 44.8% of PC1 and 33.4% of PC2 contribution from IPCA (interaction principal components axes) 1 and 2, respectively and with the highest mean values, E4 was found to be a favourable season. G42 (IC115134), G69 (Swarna) and G54 (Kalanamak) were found to be the best genotypes in E1, whereas G37 (IC114927) and G71 (Vibhava) in E3 and G45 (IC5006) and G3 (Badshahbhog) were found the best genotypes in E4. Based on the mean versus stability, G31 (IC114754) was more stable. As per the Which Won Where/What graph, G13 (Ganjeikalli) won in E2, G68 [SR6 (B)] in E1 and E3 and G12 (FR13A) won in E4. For GTOT, 26.3% genotypic effect, 8.2% environment effect and 24.1% genotype environment effect was observed. According to AMMI analysis, PC1 contributed 43.9% variability, PC2 contributed 34.7% variability and PC3 contributed 21.5% variability. The AMMI biplot showed 78.6% of goodness of fit with 43.9% of PC1 and 34.7% of PC2 contribution from IPCA1 and 2, respectively. G7 (BPT5204) was found to be the best genotype in E1, whereas G45 (IC5006) in E2 and G25 in E3 and G3 (Badshahbhog) and G54 (Kalanamak) were found to be the best genotypes in E4. Based on the mean versus stability, G5 (Basmati386), G71 (Vibhava) and G26 (IC114704) were more stable. As per the Which Won Where/What graph, G13 (Ganjeikalli) won in E1, G3 (Badshahbhog) in E2 and E4, G52 (Jeerigesanna) won in E3. For GFTOT, 18.72% genotypic effect, 1.60% environment effect, and 31.98% genotype environment effect was observed. According to AMMI analysis, PC1 contributed 45.4% variability, PC2 contributed 31.0% variability and PC3 contributed 23.7% variability. The AMMI biplot showed 76.4% of goodness of fit with 45.4% of PC1 and 31.0% of PC2 contribution from IPCA1 and 2. E3 and E4 showed the highest average values and were considered as the favourable environments. G52 (Jeerigesanna) was found to be the best genotype in E2, G57 (Madhukar) in E3 and G9 (CSR1) in E4. Based on the mean versus stability, G16 (Guddadani) was more stable. As per the Which Won Where/What graph, G60 (MO1) won in E1, G66 (RanbirBasmati) in E1 and E2, G8 (BR4_10) won in E1 and E4 and G46 (IC5968) in E3 and E4.

Marker-trait associations

Reported markers for five cloned yield genes were used to study marker-trait associations and three markers were polymorphic (Pr1b, C8dsF/R and M1) among the germplasm. These polymorphic markers were used for association analysis using GLM for 28 traits across four environments

(Supplementary Table S5). A total of 19 significant associations were detected for 10 traits in four environments with C8dsF/R and M1. Though polymorphic, Pr1b marker (*PROG1*) did not show any marker-trait association in the genotypes of the study. Majority (16) of the trait associations were found with marker C8dsF/R (*Ghd8*). SUS showed strong significant association with C8dsF/R (*Ghd8*) in E1 ($P \leq 0.003$), E2 ($P \leq 0.00009$) and E4 ($P \leq 0.005$) with 12%, 20% and 10.6% R^2. Likewise, GU, GUS, SU, SS and STOT were associated with C8dsF/R (*Ghd8*) in more than one environment. In E3, GP and SUP were associated with M1 (*OsSPL14*) (Table 2).

Discussion

Targeting higher yields in rice, many varieties and hybrids have been developed with larger panicles accommodating more number of spikelets in rice (Peng et al. 2008; Yang and Zhang 2010) targeting grain yield. The increase in spikelet number has not always been converted into increase in the number of grains because of the poor grain filling process, mostly in the spikelets secondary located in the lower portion of the panicle (Mohapatra et al. 1993). Wide genetic variation for panicle traits such as spikelets, grains and grain filling of primary and secondary branches of apical and basal portion of the panicle of rice (Kato 2010; Panda et al. 2020; Pasion et al. 2021). The contribution of grains from upper portion of the panicle towards the yield and quality is irrefutable, but the panicle structure of rice (being bottom heavy and tapering towards the top) is not very conducive for increasing the grain number in the top portion of the panicle. Hence, the lower portion of the panicle becomes important for improving the yield levels. Several studies underscored the importance of filling of spikelets resulting in the grains of lower portion of the panicle in realizing the total grain number and yield (Sekhar et al. 2015; Zhao et al. 2020). Similarly, the number of grains on primary branches in the panicle are more or less fixed, while the number of grains on secondary branches is variable, giving a scope for its increase. Screening of large sets of germplasm comprising landraces could be a promising approach to identify potential donors for various panicle traits, especially for secondary branches and lower portion. Three genotypes G3 (Badshahbhog), G13 (Ganjeikalli) and G52 (Jeerigesanna) showed highest SS and GS. Also, the genotype G13 showed highest SLS and GLS.

From the 72 germplasm characterized, promising genotypes have been identified with maximum trait values for the 28 traits of the study such as GUP (30.08 grains), GUS (72.75 grains), GLP (47.33 grains) and GLS (87.92 grains) suggesting the possibility of realizing a total number of potential grains 238.08 per panicle as against the observed maximum total grain number of 209.33 per panicle in a genotype (Table 1). This observation indicates the occurrence of promising natural variability for panicle traits in rice germplasm and its possible utility in the breeding programmes for the yield.

Table 2 Marker-trait associations of 72 genotypes in TASSEL using GLM method

S. No.	Trait	Marker	*F* value	*P* value	R^2	MS marker	DF error	MS error
1	E1_Spikelets upper (SU)	C8dsF/R (*Ghd8*)	6.16	0.015	8.46	1749.4	64	283.8
2	E1_Grains upper (GU)	C8dsF/R (*Ghd8*)	7.96	0.006	10.45	1856.9	64	233.3
3	E1_Grains upper secondary (GUS)	C8dsF/R (*Ghd8*)	11.13	0.001	14.30	1432.7	64	128.7
4	E2_Spikelets upper primary (SUP)	C8dsF/R (*Ghd8*)	7.39	0.008	9.99	304.4	64	41.2
5	E1_Spikelets upper secondary (SUS)	C8dsF/R (*Ghd8*)	9.07	0.003	12.19	1396.1	64	153.8
6	E2_Spikelets upper secondary (SUS)	C8dsF/R (*Ghd8*)	17.46	0.000	20.20	3561.0	64	204.0
7	E2_Spikelets primary (SP)	C8dsF/R (*Ghd8*)	4.21	0.044	5.75	1348.4	64	320.1
8	E2_Spikelets secondary (SS)	C8dsF/R (*Ghd8*)	8.91	0.004	11.52	8890.2	64	997.6
9	E2_Spikelets upper (SU)	C8dsF/R (*Ghd8*)	17.04	0.0001	19.84	5947.7	64	349.1
10	E2_Spikelets total (STOT)	C8dsF/R (*Ghd8*)	8.50	0.004	10.93	17,162.6	64	2018.8
11	E4_Spikelets secondary (SS)	C8dsF/R (*Ghd8*)	6.51	0.013	8.60	11,719.7	64	1798.9
12	E4_Spikelets total (STOT)	C8dsF/R (*Ghd8*)	4.12	0.046	5.59	11,941.2	64	2901.1
13	E4_Spikelets upper secondary (SUS)	C8dsF/R (*Ghd8*)	8.34	0.005	10.62	2993.9	64	358.9
14	E4_Grains lower secondary (GLS)	C8dsF/R (*Ghd8*)	4.70	0.033	6.52	3072.1	64	653.0
15	E4_Grains upper (GU)	C8dsF/R (*Ghd8*)	7.15	0.009	9.34	3056.4	64	427.5
16	E4_Grains upper secondary (GUS)	C8dsF/R (*Ghd8*)	11.21	0.001	13.91	3027.4	64	270.0
17	E3_Spikelets upper primary (SUP)	M1 (*OsSPL14*)	4.55	0.036	6.15	324.2	64	71.2
18	E3_Grains primary (GP)	M1 (*OsSPL14*)	4.07	0.0478	5.44	659.3	64	162.1
19	E1_Grains upper secondary (GUS)	M1 (*OsSPL14*)	4.03	0.048	5.72	572.9	64	142.2

Since, total number of spikelets and grains along with total grain filling % are the three main panicle traits determining the yield, using 72 germplasm set, the contribution of the remaining 25 panicle traits to the main traits was studied and the critical role of grains secondary in the lower portion of the panicle has been emphasized as reported in earlier studies (Liu et al. 2022; Zhou et al. 2017; Sekhar et al. 2021; Panigrahi et al. 2019). Among the 28 traits, the average number of spikelets secondary (SS) and grains secondary (GS) was the highest, and among the percentage wise panicle traits, the upper primary grain filling % was the highest and the secondary grain filling % was the second least and lower secondary grain filling % being the least. This observation highlights the importance of focused research efforts in deciphering the grain filling process of rice, so as to either increase the grain filling % of the secondary branches of lower portion or to increase spikelet number on the primary/secondary branches of the upper portion of the panicle.

The observed positive correlations of spikelets total (STOT) with spikelets secondary (SS); grains total (GTOT) with grains secondary (GS); GFTOT with grain filling % lower (GFL) and grain filling % secondary (GFS) are in congruence with the reports of the highest correlation between secondary branch number and total number of spikelets per panicle (Thapa et al. 2021; Ta et al. 2018). Panicle length (PL) showed negative correlation with GFTOT and positive correlation with total spikelets (STOT) and grains total (GTOT). Non-significant correlation between panicle length and number of spikelets per panicle was earlier reported by Rebolledo et al. (2016). In the study, especially some of the traits such as spikelets upper (SU), spikelets lower (SL), grains upper (GU), grains lower (GL), upper grain filling % (GFU), STOT, GTOT and GFTOT showed a correlation value of 0.97 and over for the secondary panicle traits, which led to emphasis more on secondary panicle traits.

Regression analysis of 28 traits revealed the relative importance of the role of spikelets secondary/grains of the lower portion of the panicle for STOT, GTOT and GFTOT in comparison to the traits from the upper portion of the panicle. Similar observations have been reported in panicle characterization of 20 Indonesian genotypes (Hastini et al. 2019). Another report of regression analysis by Ta et al. (2018) also showed 89–91% of the spikelet number variation was contributed by secondary branch number, while it was only 37–42% by primary branch number. Stability analysis, from which won where view of GGE biplot revealed the promising genotypes, viz. Badshahbhog, Ganjeikalli, Jeerigesanna and Kalajira for STOT, GTOT and BR4_10, MO1 for GFTOT across different environments.

Identification of QTLs (genomic regions) and candidate genes for yield and related traits supports the breeding objective of enhancing yield in rice. Cloning of the candidate genes associated with yield traits such as *Gn1a*, *Dep1*, *Ghd7*, *Ghd8, PROG1*, *OsSPL14* and others has provided the necessary impetus required for MAS, haplotype-based breeding and allele mining (Singh et al. 2022). Out of the three polymorphic markers evaluated in 72 genotypes, significant association of C8dsF/R marker derived from *Ghd8* with spikelets upper secondary (SUS) found to be stable across four environments. *Ghd8* is the prominent gene which positively regulates the primary and secondary branches (Yan et al. 2011; Sreenivasulu et al. 2021). The spatial location effect of *Ghd8* for the spikelets in the upper portion of the panicle has been identified in the present study in addition to confirming the reported role of *Ghd8* for the secondary branches. Markers developed based on the polymorphisms associated with Ghd8 gene have been utilized for the identifying natural allele variation (Yuan et al. 2022), hetero-allelic combinations (Xiong et al. 2021) and for the MAS (Hu et al. 2020). Similarly, the polymorphisms identified associated with OsSPL14 gene were deployed for characterizing natural allele variation (Hu et al 2021) and for marker assisted backcrossing for enhancing yield in two rice varieties (Pandit et al. 2021; Reyes et al. 2021; Punniakotti et al. 2023). The functional markers could also classify the core sets such of New Plant Type (NPT) core set of rice genotypes using yield related markers like *Ghd7, Ghd8*, *DEP1*, *GS3*, *Gn1a*, *PROG1* and *APO1* (Rachana et al. 2019). Functional markers associated with grain size (*GS3*), glutelin content (*Lgc1*gene), starch physicochemical properties (Waxy gene) and other agronomical traits were employed to genotype the USDA rice minicore constituting 217 accessions, which aided in the selection of the parental material with desirable allele/gene combinations (Li et al. 2022). Superior alleles identified can favourably be deployed for pyramiding (Tu et al. 2022) and also can be targeted for gene editing towards enhancing the yield levels in rice (Yadav et al. 2023). In summary, a comprehensive set of 72 genotypes were evaluated to identify the promising genotypes and marker-trait associations for 28 panicle traits with a specific emphasis on three key traits: STOT, GTOT, and GFTOT. Promising genotypes, viz. Badshahbhog, Ganjeikalli, Jeerigesanna and Kalajira for STOT, GTOT and BR4_10, MO1 for GFTOT were identified. Through correlation and regression analysis, the contribution of secondary panicle traits, especially SS, GS, GFS to STOT, GTOT and GFTOT has been highlighted. *Ghd8*, the prominent gene that regulates the branch number of the panicles showed significant association for SUS. The identified 10 promising genotypes can be deployed as donors for breeding rice with enhanced yield levels.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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