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GENOME-WIDE ASSOCIATION STUDY FOR MORPHOLOGICAL AND GRAIN TRAITS IN RICE LANDRACES

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SUMMARY

Rice (*Oryza sativa* L.) landraces represent a valuable genetic resource that can play an important role in sustainable crop production and biodiversity conservation for the future. However, the cultivation and genetic diversity of these landraces in the Mekong Delta have been unacceptable due to widespread adoption of high-yielding rice cultivars and intensive farming practices, leading to environmental degradation and biodiversity losses. The following study evaluated the morphological and grain traits of 65 rice landraces from the Mekong Delta, conserved in the Gene Bank of Can Tho University, Vietnam. The landraces underwent cultivation in field conditions and assessment based on the evaluation system of the International Rice Research Institute (IRRI), Philippines. Grain quality analysis focused on grain size and shape. The genome-wide association study was successful in identifying the genomic regions linked to the morpho-agronomic traits in landraces of the Mekong Delta using single nucleotide polymorphisms (SNPs). Correlation analysis helped link the genetic characteristics with 11 traits, and candidate genes associated with 681 significant SNPs attained identification using the Rice SNP-Seek Database. The findings provided valuable insights into the genetic and phenotypic diversity of rice landraces for further improvement and germplasm conservation in the Mekong Delta, Vietnam.

Keywords: Rice (*O. sativa* L.), landraces, genetic variations, biodiversity, agronomic traits, candidate genes, GWAS

Key findings: This study identified 46 candidate SNPs within 32 genes associated with 11 agronomic traits in 65 rice (*O. sativa* L.) landraces. Plant height and brown rice shape are the key traits for breeding, with new candidate SNPs linked to them.

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INTRODUCTION

Rice (*Oryza sativa* L.) landraces represent a rare and valuable genetic resource (Hour *et al.*, 2020) that provides justification for its conservation, expansion, and further development (Corrado and Rao, 2017; Marone *et al.*, 2021). However, in previous years, the cultivation area and genetic diversity of rice landraces have been facing rejection due to the widespread adoption of high-yielding rice cultivars and intensive farming practices in the Mekong Delta, Vietnam (Van-Kien *et al.*, 2020). Additionally, intensive rice cultivation has contributed to environmental degradation, including soil, water, and air pollution, posing risks to public health (Tran *et al.*, 2024).

For balancing crop productivity with ecological sustainability, it is crucial to establish designated areas for cultivating landraces and specific rice cultivars (Mohapatra and Sahu, 2022). This type of strategy would promote the production of region-specific rice products, as well as help in maintaining ecological balance, preserving biodiversity, and sustaining the natural habitats of various plant species (Dulloo *et al.*, 2010). Despite their agronomic and ecological significance, rice landraces are rare, as farming communities have shifted toward cultivation of high-yielding rice cultivars. The few remaining rice landrace cultivars primarily emphasize productivity over grain quality, limiting their market competitiveness compared with modern high-yielding cultivars (Sarfaraz, 2023). Moreover, the absence of distinctive characteristics hinders their potential for branding and geographical indication development (Corrado and Rao, 2017).

With these challenges and the present threats of climate change, characterizing the morphological, agronomic, and grain quality traits of rice landraces is imperative for establishing a comprehensive database to support germplasm conservation, varietal improvement, and climate-adaptive breeding programs (Marone *et al.*, 2021). Moreover, such characterization facilitates genome-wide association studies (GWAS) to analyze correlation between morphological and genetic traits (Beena *et al.*, 2021). However, earlier studies have performed sequencing and identified single nucleotide polymorphisms (SNPs) in the rice landraces (Tam *et al.*, 2019); yet, the morphological traits data remain insufficient for phenotype-genotype correlation analysis.

Therefore, assessment based on the morphological and quality traits of rice landraces provides an opportunity to investigate phenotype-genotype relationships. It will considerably contribute to the development of the phenotypic and genetic traits database for rice landraces in the Mekong Delta, Vietnam. These efforts will aid in rice breeding, genotypes' genetic improvement, and germplasm conservation. Furthermore, this study will serve as a scientific base for future research on the genetic diversity and sustainable utilization of the rice plant genetic resources.

MATERIALS AND METHODS

Plant material

This study utilized 65 rice (*O. sativa* L.) landraces collected from coastal provinces in the Mekong Delta, currently preserved in the Gene Bank at the Can Tho University, Can Tho, Vietnam. These landraces incurred selection based on their prior whole-genome sequencing data (Tam *et al.*, 2019). The availability of genetic sequence data, including nucleotide sequences, enables efficient identification of single nucleotide polymorphisms (SNPs) without incurring additional sequencing costs.

Experimental design and cultivation

The 65 rice landraces proceeded to cultivation under field conditions following a randomized complete block design with three replications. Each plot measured 5 m², with a planting density of 30 cm × 30 cm. Standard agronomic practices, including soil preparation, irrigation, fertilization, and pest control, continued according to regional rice production guidelines.

Morphological and grain traits characterization

The data on morphological traits entailed recording at different growth stages using descriptors established by the International Rice Research Institute (IRRI), Philippines (SES, 2013). For data collection, using the randomly selected three plants ensued in each experimental unit and within each replication.

Plant height (cm), as recorded, commenced from the soil surface to the tip of the tallest panicle in each selected rice plant. The leaf angle studied were erect, horizontal, and droopy. For flag leaf angle, the studied shapes were erect, intermediate, horizontal, and descending. The studied collar colors were light green, green, and purple. The 100-grain weight (g) measurement transpired by weighing 100 rice grains, then, adjusting for moisture content using the following formula:

$$100 - grain\ weight\ (g) = \frac{W_0 \text{ x } (100 - \mathrm{H}_0)}{100 - 14}$$

Where, W_0 = the weight of 100 grains (g) and H_0 = the sample moisture content (%).

Rice grain size and shape determination was by measuring the length and width of 10 grains (brown rice) in each landrace and averaging over three replications. Ten grains, as aligned on Caro paper, had their total length measured to calculate the average grain length. The same 10 grains' arrangement side by side had their width measurement.

Data analysis

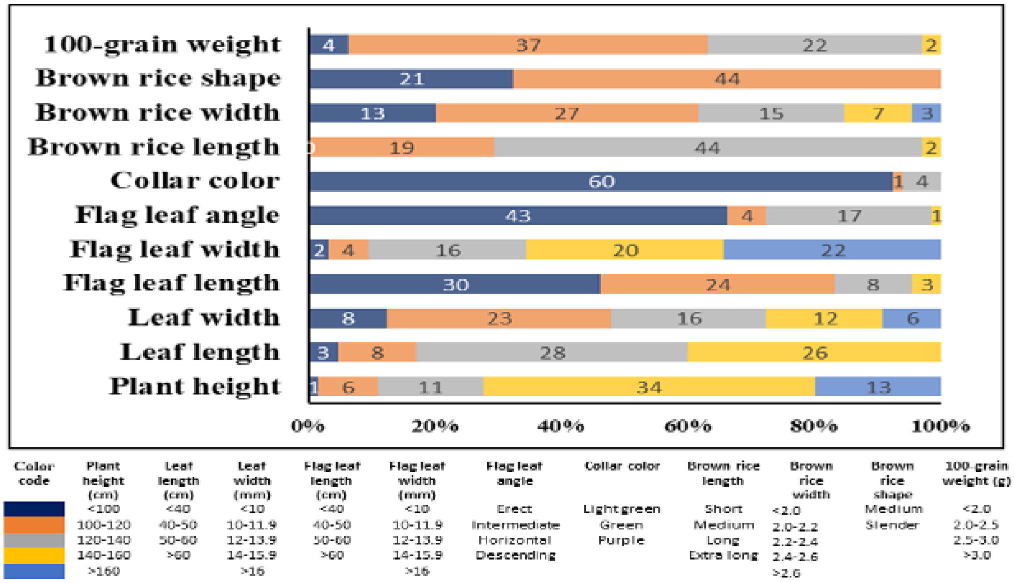
The data based on various morphological and grain traits underwent analysis using R software. Dendrogram analysis using R classified the 65 rice landraces based on 11 traits. Extracting SNPs totaled 37,643 from the dataset of Tam *et al.* (2019). SNP filtering succeeded in using TASSEL v5.2.73 with the following selection criteria: a missing allele rate of 0%, a maximum minor allele frequency of 20%, and a maximum heterozygous allele rate of 10%. As a result, selecting 24,946 SNPs proceeded for correlation analysis. The genome-wide association study (GWAS) continued using the general linear model (GLM) in TASSEL v5.2.64. Candidate SNPs with a significance threshold of $-\log10$ (P-value) $\geq$ 4.0 were choices for candidate gene identification. The identification of candidate genes associated with significant SNPs used the Rice SNP-Seek Database (Mansueto *et al.*, 2016).

RESULTS

Morphological and grain traits

In rice (*O. sativa* L.) landraces, the plant height assessment under uniform production conditions revealed a range from 94 to 175 cm, with an average plant height of 146 cm (Figure 1). The 34 rice landraces (52.3%) had plant heights between 140 and 160 cm; 13 out of 65 landraces had plant heights more than 160 cm, with 11 landraces measuring 120–140 cm. However, one rice landrace had the plant height below 100 cm. Flag leaf angle is a fundamental trait in rice genotypes, exhibiting distinct variations. As illustrated in Figure 1, 43 rice landraces (66.2%) had an erect flag leaf angle, followed by 17 other landraces with a horizontal angle. However, only one landrace displayed a droopy leaf angle. Most studied rice genotypes (60) exhibited light green leaf collars. Four landraces had purple collars, while only one rice genotype had a standard green collar (Figure 1).

The most common category comprised 28 landraces (43.1%) with leaf lengths of 50–60 cm. The least common category included three landraces with leaf lengths of less than 40 cm (Figure 1). Leaf width varies across rice landraces as mostly influenced by cultivation techniques and the existing environmental conditions. The distribution of leaf width followed a normal pattern (Figure 1). The most common category included 23 landraces (35.4%) that were visible with leaf widths of 10–11.9 mm, followed by 16 other landraces measuring 12–13.9 mm and 12 landraces measuring 14–15.9 mm. The least common group, comprising six landraces (9.2%), had leaf width exceeding 16 mm.



Color code	Plant height (cm)	Leaf length (cm)	Leaf width (mm)	Flag leaf length (cm)	Flag leaf width (mm)	Flag leaf angle	Collar color	Brown rice length	Brown rice width	Brown rice shape	100-grain weight (g)
🟦	<100	<40	<10	<40	<10	Erect	Light green	Short	<2.0	Medium	<2.0
🟧	100-120	40-50	10-11.9	40-50	10-11.9	Intermediate	Green	Medium	2.0-2.2	Slender	2.0-2.5
⬜	120-140	50-60	12-13.9	50-60	12-13.9	Horizontal	Purple	Long	2.2-2.4		2.5-3.0
🟨	140-160	>60	14-15.9	>60	14-15.9	Descending		Extra long	2.4-2.6		>3.0
🟦	>160		>16		>16				>2.6		

Figure 1. Morphological and grain quality traits of 65 rice landraces.

Grain length varied among the 65 rice landraces, ranging from 5.7 to 7.6 mm, and the average brown rice grain length was 6.7 mm (Figure 1). None of the studied rice landraces appeared in the short-grain category. Nineteen rice landraces (29%) had medium-length grains, 44 landraces had long grains, and two landraces had very long grains. The brown rice width of 65 rice landraces exhibited considerable variations, ranging from 1.83 to 2.63 mm, with an average width of 2.17 mm. Most brown rice landraces' (42) width occurred within the range of 2.0–3.0 mm. Notably, three landraces had exceptionally large brown rice widths (> 2.6 mm), while 13 landraces had widths smaller than 2.0 mm (Figure 1).

In the presented study, the brown rice shape determination depended on the length-to-width ratio. The average length-to-width ratio was 3.14, ranging from 2.27 to 3.76. The results revealed the rice landraces examined predominantly exhibited medium to slender grain shapes. Most rice genotypes (44) had slender grains, while the remaining 21 rice landraces had medium-sized grains (Figure 1). The 100-grain weight spanned from 1.7 to 3.1 g, and the average 100-grain weight was 2.4 g. The majority of rice landraces (59) had a grain weight between 2.0 and 3.0 g. Two landraces were evident with grain weights of more than 3.0 g, while four landraces had grain weights of less than 2.0 g (Figure 1).

Genetic diversity in rice landraces

The genetic diversity analysis of the 65 rice landraces used the dendrogram method based on 11 agronomic traits. The results indicated the height of five on the dendrogram chart; the rice landraces' classification resulted in 32 distinct groups, demonstrating significant diversity (Figure 2). At a similarity height of 10, the 65 rice landraces clustered into 10 main groups, with Cluster 1 containing the largest number of landraces (47), while four clusters contained only a single landrace. At the similarity height of 15, the rice landraces bore categories of five groups. Group 1 had 58 landraces; Group 2, three landraces; Group 3, one landrace; Group 4, two landraces; and Group 5, one landrace. At the similarity height of 20, the rice landraces proceeded to group into three main categories—Group 1: 62 landraces, Group 2: two landraces, and Group 3: one landrace. Notably, the rice landrace 'Voi' exhibited distinct characteristics compared with other landraces, while the rice landraces 'Lun Hen' and 'Nang Lon Luc' also displayed unique variations (Figure 2).

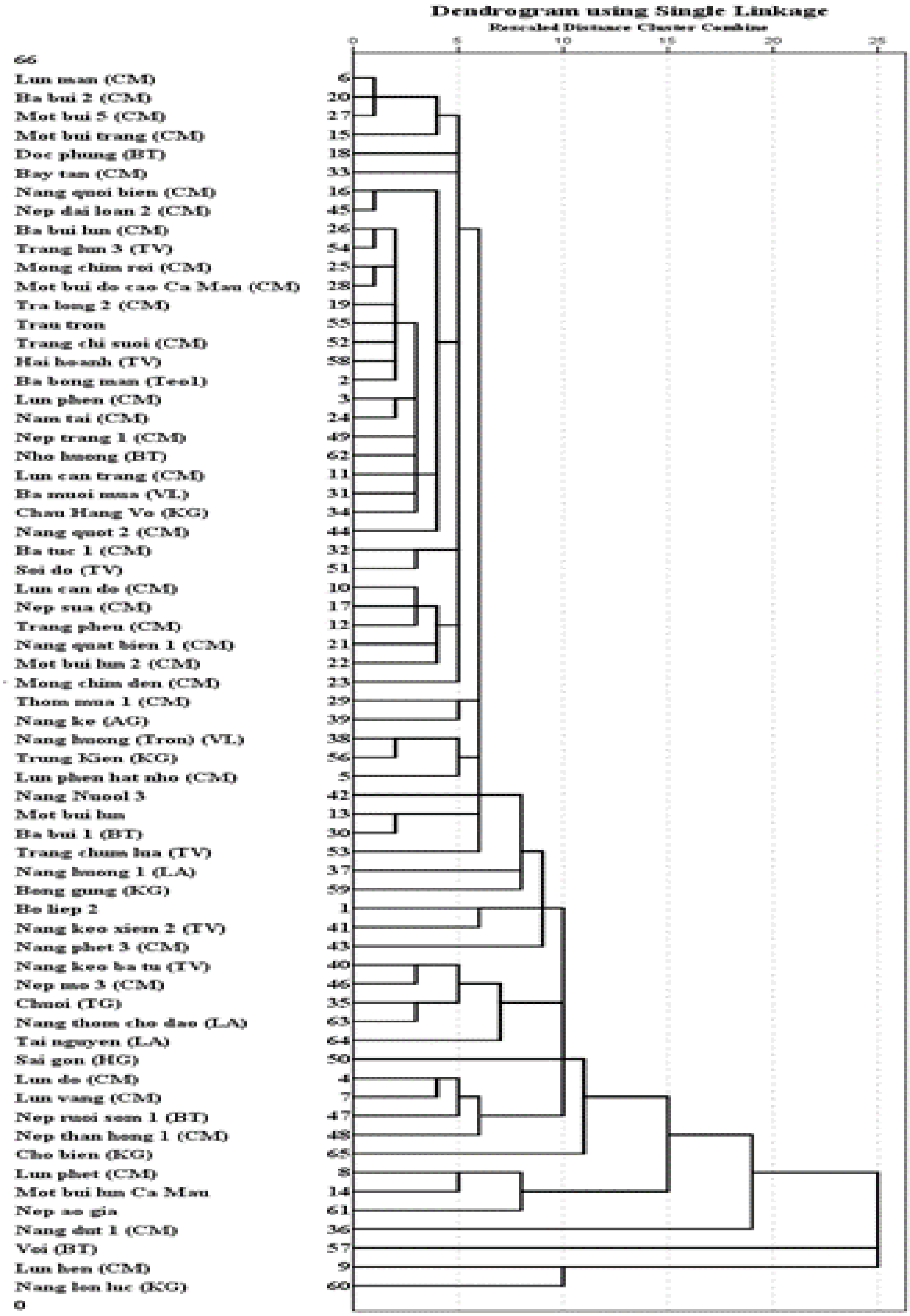


Figure 2. The correlation of 65 rice landraces based on 11 agronomic traits.

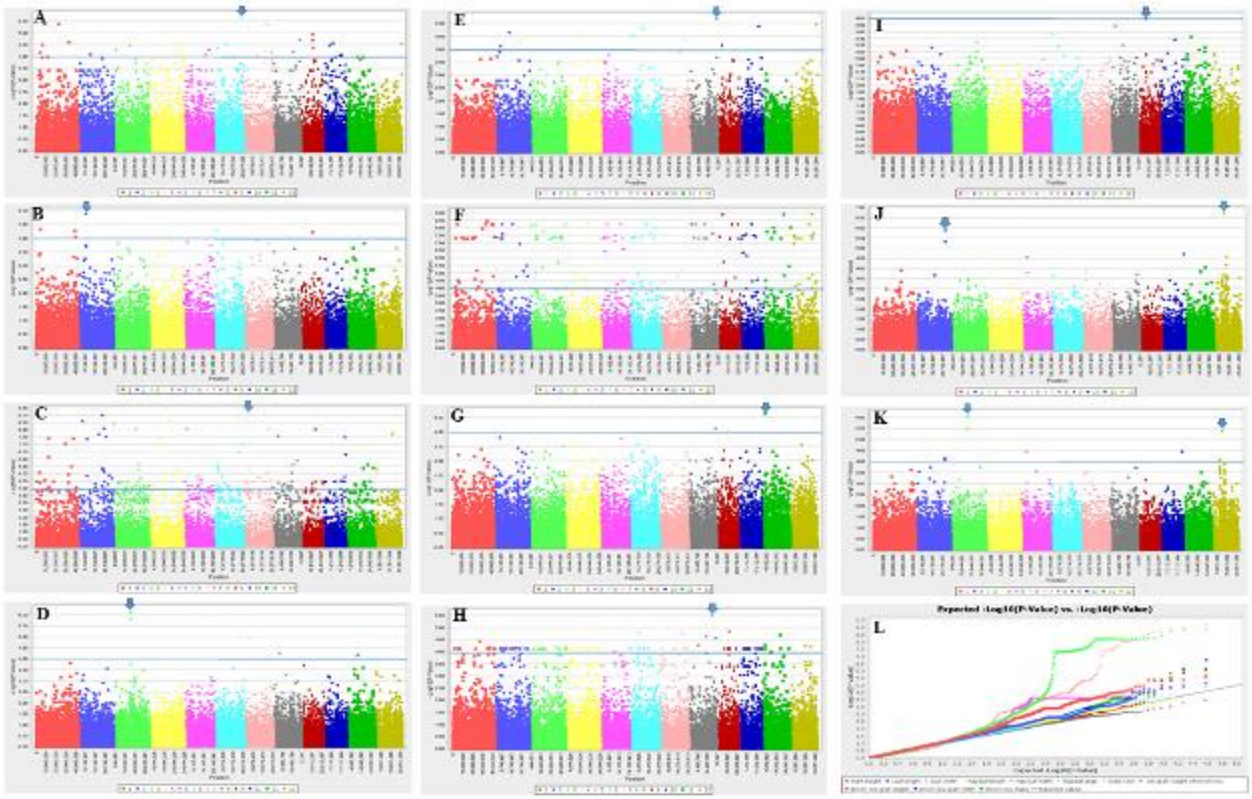


Figure 3. Manhattan plot for 11 traits, A. Plant height; B. Flag leaf angle; C. Collar color; D. 100-grain weight of brown rice; E. Leaf length; F. Leaf width; G. Flag leaf length; H. Flag leaf width; I. Brown rice grain length; J. Brown rice grain width; K. Brown rice shape; and L. QQ-Plots for 11 traits. Utilizing 24,946 SNPs derived from 65 rice landraces, a GWAS proceeded to investigate the relationship between SNPs and 11 traits across all 12 chromosomes.

Genome-wide association study

Manhattan plot analysis of 24,946 SNPs across 12 chromosomes identified associations for 11 traits. Plant height emerged to be linked to SNPs on 11 chromosomes, excluding Chr11, with 37 candidate SNPs detected, the highest on Chr01 (seven SNPs). The most significant SNP was on Chr06 at S06_28580644 (Figure 3A). Flag leaf angle showed an association with SNPs on five chromosomes, peaking on Chr02 at S02_7568240, with Chr01 containing the most (three SNPs) (Figure 3B). For collar color, the identification of 157 SNPs was notable across all chromosomes, with Chr02 showing the strongest association (Figure 3C). Leaf length had 10 SNPs across eight chromosomes, with the peak on Chr08 (S08_27336090) (Figure 3E). Leaf width had 182 SNPs across all chromosomes, requiring further validation (Figure 3F). For flag leaf length, two SNPs were noticeable (Chr08, Chr11), with the peak on Chr11 (S11_3102603) (Figure 3G). However, for flag leaf width with 237 SNPs, only one remained significant on Chr08 (S08_23330936) under a stricter threshold (Figure 3H).

For grain traits, five SNPs revealed links to rice grain length (Chr03, Chr07, Chr08, and Chr11) (Figure 3I), while nine SNPs across five chromosomes influenced the rice grain width, with Chr02 and Chr12 being the key (Figure 3J). Eight SNPs across the five chromosomes showed associations with brown rice shape, particularly on Chr02 and Chr12 (Figure 3K). However, no significant SNPs were distinct for 100-grain weight (Figure 3D).

Identification of candidate SNPs and genes

The GWAS analysis of 11 traits identified candidate SNPs totaling 681 distributed across most of the rice chromosomes. Notably, no significant SNPs materialized for the 100-grain weight. However, three traits (collar color, leaf width, and flag leaf width) exhibited the highest number of significant candidate SNPs, ranging from 157 to 237 SNPs (Table 1). Despite numerous significant SNPs, the varied distribution hindered candidate gene identification for collar color, leaf width, and flag leaf width, leading to their exclusion from this study.

Several distinct SNPs were in apparent association with multiple traits, such as rice grain width and shape, as well as plant height, leaf length, and flag leaf length. The study further examined seven agronomic traits, utilizing 108 SNPs in total to identify candidate genes. Forty-two candidate SNPs within 29 genes across multiple chromosomes were successful for identification (Table 1). In chr01, three genes contained four SNPs linked to the plant height and flag leaf angle. Chr02 had two genes with two SNPs associated with the leaf length and flag leaf angle. In chr03, two genes harbored four SNPs related to the plant height, rice grain width, and the grain length-to-width ratio. Chr04 included three genes with four SNPs linked to plant height, while chr05 had one gene with a single SNP for the same trait. Multiple genes in chr06 contained SNPs for plant height, flag leaf angle, and leaf length. Chr07 had one gene with four SNPs for plant height, leaf length, and brown rice grain length. Additional SNPs were distinct in chr09, chr10, and chr11, while chr12 was the most relevant for grain traits, harboring SNPs linked to grain width, length-to-width ratio, and plant height (Table 1).

The identification of candidate genes containing SNPs for the nine analyzed traits showed that plant height had the highest number of SNPs within genes (19 SNPs across 15 genes), followed by the grain shape (11 SNPs in three genes) and brown rice width (six SNPs in four genes). Two traits, including leaf length and flag leaf angle, had four SNPs distributed across four different genes. Notably, for 100-grain weight, flag leaf length, and brown rice length, no gene was noticeable with candidate SNPs (Table 1).

Genotypes identification for traits

For plant height, identifying 19 candidate SNPs resulted across nine chromosomes, with eight being particularly significant and considerable. These SNPs classified rice landraces into six allele patterns, the most common being CGGCTGGT (54 landraces) (Figure 4). Four SNPs linked to flag leaf angle showed two allele types, with homozygous genotypes associated with an erect angle and heterozygous genotypes linked to a droopy angle (Figure 4).

Leaf length had seven candidate SNPs across six chromosomes, with the ACCG allele pattern being the most frequent (57 rice landraces). One SNP on chr11 influenced the flag leaf length, whereas the minor T allele correlated with shorter flag leaves (Figure 4). For grain traits, one SNP on chr07 influenced the brown rice length, while six SNPs on chr03, chr11, and chr12 affected the brown rice width, with CCGTGC (28 landraces) being most common. Eleven SNPs, mainly on chr12, expressed linkage to brown rice shape, with CCGTAGGACCG (31 landraces) as the dominant allele pattern (Figure 4).

DISCUSSION

Genome-wide association studies (GWAS) play a crucial role in identifying candidate SNPs for breeding and selecting new rice (*O. sativa* L.) cultivars (Yu *et al.*, 2014; Pantaliao *et al.*, 2016; Nayyeripasand *et al.*, 2021). Several studies have analyzed the relationship among the various agronomic traits in different rice landraces and their SNPs (McNally *et al.*, 2009; Beena *et al.*, 2021). GWAS on agronomic traits also provides a foundation for further research (Huang *et al.*, 2010; Yano *et al.*, 2016). Rice landraces play an important role in rice breeding due to their valuable traits, which enable them to adapt to local environmental

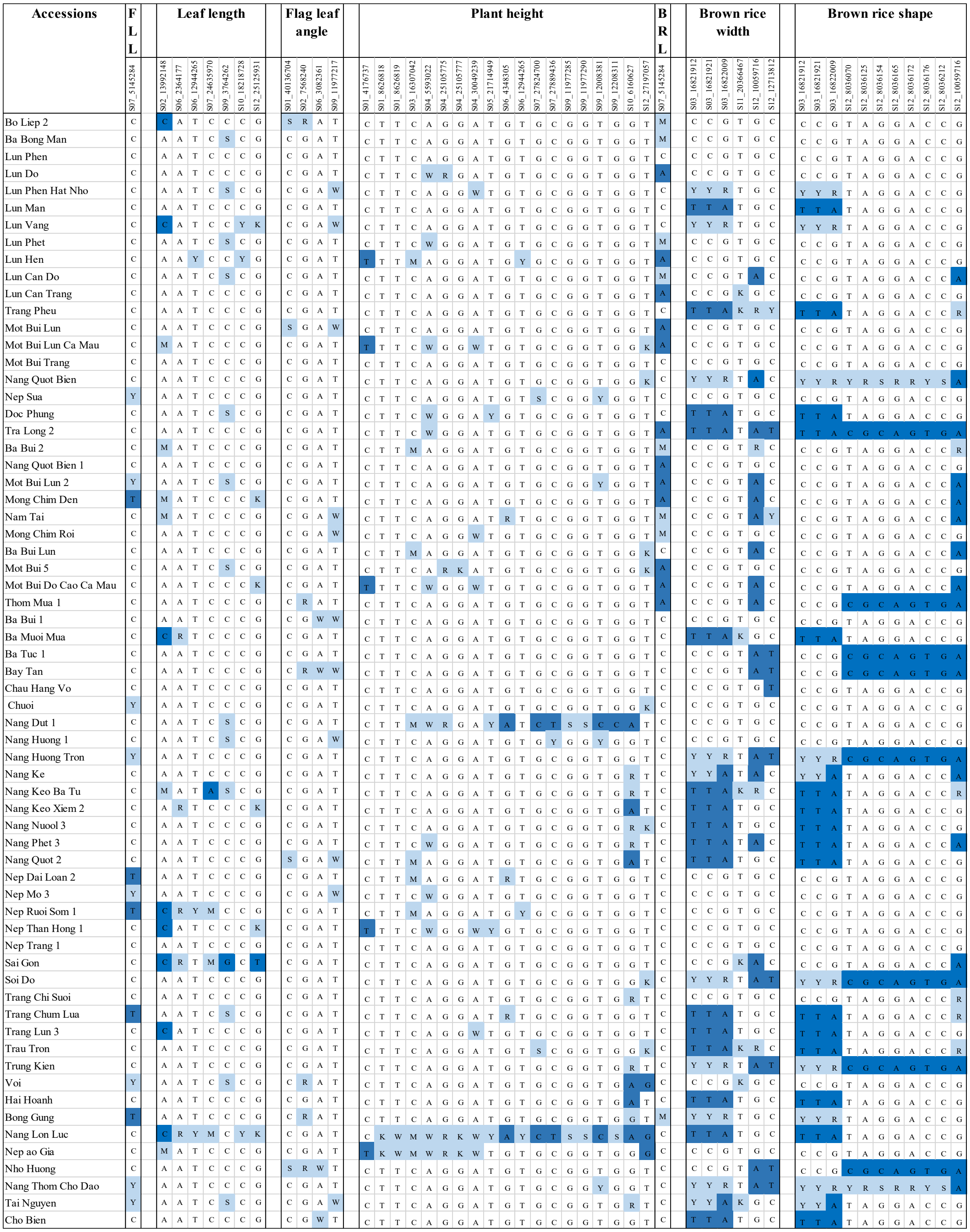
Table 1. Candidate SNP and genes.

No.	Traits	Chromosome	Position	Candidate SNP	P_Value	Candidate gene
1	PH	1	4176737	S01_4176737	6.96E-05	*Os01g0179901*
2	PH	1	8626818	S01_8626818	4.31E-06	*Os01g0257900*
3	PH	1	8626819	S01_8626819	4.31E-06	
4	FLA	1	40136704	S01_40136704	9.19E-05	*LOC_Os01g69060*
5	FLA	2	7568240	S02_7568240	1.31E-05	*LOC_Os02g13910*
6	LL	2	13992148	S02_13992148	2.26E-05	*Os02g0437901 chr02*
7	PH	3	16307042	S03_16307042	3.42E-05	*LOC_Os03g28330*
8	BRW, BRS	3	16821912	S03_16821912	7.27E-07	*LOC_Os03g29520*
9	BRW, BRS	3	16821921	S03_16821921	7.27E-07	
10	BRW, BRS	3	16822009	S03_16822009	1.50E-06	
11	PH	4	5593022	S04_5593022	3.53E-05	*OsNippo04g061500*
12	PH	4	25105775	S04_25105775	1.29E-05	*LOC_Os04g42420*
13	PH	4	25105777	S04_25105777	6.63E-05	
14	PH	4	30049239	S04_30049239	8.42E-05	*LOC_Os04g50790*
15	PH	5	21714949	S05_21714949	8.29E-05	*LOC_Os05g37160*
16	LL	6	2364177	S06_2364177	2.93E-05	*LOC_Os06g05240*
17	FLA	6	3082361	S06_3082361	5.33E-05	*OsNippo06g045350*
18	PH	6	4348305	S06_4348305	4.53E-05	*Os06g0186400*
19	PH	6	12944265	S06_12944265	4.74E-04	*OsNippo06g142600*
20	BRL	7	5145284	S07_5145284	1.06E-05	*LOC_Os07g09680*
21	LL	7	24635970	S07_24635970	4.71E-05	*LOC_Os07g41160*
22	PH	7	27824700	S07_27824700	6.08E-05	*OsNippo07g275900*
23	PH	7	27889436	S07_27889436	7.03E-05	*LOC_Os07g46670*
24	LL	9	3764262	S09_3764262	7.14E-05	*OsNippo09g043400*
25	FLA	9	11977217	S09_11977217	6.13E-05	*LOC_Os09g20000*
26	PH	9	11977285	S09_11977285	1.14E-05	
27	PH	9	11977290	S09_11977290	1.14E-05	
28	PH	9	12008381	S09_12008381	2.06E-05	*LOC_Os09g20040*
29	PH	9	12208311	S09_12208311	1.49E-05	
30	PH	10	6160627	S10_6160627	3.35E-05	*Os10g0189001*
31	FLL	11	3102603	S11_3102603	2.35E-05	*LOC_Os11g06420*
32	BRW	11	20366467	S11_20366467	8.97E-05	*LOC_Os11g34750*
33	BRS	12	8036070	S12_8036070	8.88E-05	*Os12g0245100*
34	BRS	12	8036125	S12_8036125	8.88E-05	
35	BRS	12	8036154	S12_8036154	8.88E-05	
36	BRS	12	8036165	S12_8036165	8.88E-05	
37	BRS	12	8036172	S12_8036172	8.88E-05	
38	BRS	12	8036176	S12_8036176	8.88E-05	
39	BRS	12	8036212	S12_8036212	8.88E-05	
40	BRW, BRS	12	10059716	S12_10059716	1.83E-07	*LOC_Os12g17550*
41	BRW	12	12713812	S12_12713812	2.71E-05	*LOC_Os12g22520*
42	PH	12	27197057	S12_27197057	2.93E-05	*LOC_Os12g43790*

The number of candidate SNPs in 65 rice varieties for agronomic traits, as follows: plant height (37); flag leaf angle (7); collar color (157); leaf length (10); leaf width (182); flag leaf length (2); flag leaf width (237); and brown rice of 100-grain weight (0). PH: Plant height; FLA: Flag leaf angle; LL: Leaf length; FLL: Flag leaf length; BRL: Brown rice length; BRW: Brown rice width; and BRS: Brown rice shape.

conditions. Utilizing the Rice SNP-Seek database (Mansueto *et al.*, 2016), 46 candidate SNPs within 32 genes resulted in association with plant height, flag leaf angle, leaf length, and brown rice traits. The findings provide a considerable genetic basis for trait selection in rice breeding programs.

Plant height, as determined by the genetic makeup of the rice genotypes, also sustained influences from cultivation



Accessions	FLL	Leaf length							Flag leaf angle				Plant height																			BRL	Brown rice width						Brown rice shape										
	S07_5145284	S02_13992148	S06_2364177	S06_12944265	S07_24635970	S09_3764262	S10_18218728	S12_25125931	S01_40136704	S02_7568240	S06_3082361	S09_11977217	S01_4176737	S01_8626818	S01_8626819	S03_16307042	S04_5593022	S04_25105775	S04_25105777	S04_30049239	S05_21714949	S06_4348305	S06_12944265	S07_27824700	S07_27889436	S09_11977285	S09_11977290	S09_12008381	S09_12208311	S10_6160627	S12_27197057	S07_5145284	S03_16821912	S03_16821921	S03_16822009	S11_20366467	S12_10059716	S12_12713812	S03_16821912	S03_16821921	S03_16822009	S12_8036070	S12_8036125	S12_8036154	S12_8036165	S12_8036172	S12_8036176	S12_8036212	S12_10059716
Bo Liep 2	C	C	A	T	C	C	C	G	S	R	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Ba Bong Man	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Lun Phen	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Lun Do	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	W	R	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Lun Phen Hat Nho	C	A	A	T	C	S	C	G	C	G	A	W	C	T	T	C	A	G	G	W	T	G	T	G	C	G	G	T	G	G	T	C	Y	Y	R	T	G	C	Y	Y	R	T	A	G	G	A	C	C	G
Lun Man	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Lun Vang	C	C	A	T	C	C	Y	K	C	G	A	W	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	Y	Y	R	T	G	C	Y	Y	R	T	A	G	G	A	C	C	G
Lun Phet	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	W	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Lun Hen	C	A	A	Y	C	C	Y	G	C	G	A	T	T	T	T	M	A	G	G	A	T	G	Y	G	C	G	G	T	G	G	T	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Lun Can Do	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	A	C	C	C	G	T	A	G	G	A	C	C	A
Lun Can Trang	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	K	G	C	C	C	G	T	A	G	G	A	C	C	G
Trang Pheu	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	T	T	A	K	R	Y	T	T	A	T	A	G	G	A	C	C	R
Mot Bui Lun	C	A	A	T	C	C	C	G	S	G	A	W	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Mot Bui Lun Ca Mau	C	M	A	T	C	C	C	G	C	G	A	T	T	T	T	C	W	G	G	W	T	G	T	G	C	G	G	T	G	G	K	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Mot Bui Trang	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nang Quot Bien	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	K	C	Y	Y	R	T	A	C	Y	Y	R	Y	R	S	R	R	Y	S	A
Nep Sua	Y	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	S	C	G	G	Y	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Doc Phung	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	W	G	G	A	Y	G	T	G	C	G	G	T	G	G	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Tra Long 2	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	W	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	T	T	A	T	A	T	T	T	A	C	G	C	A	G	T	G	A
Ba Bui 2	C	M	A	T	C	C	C	G	C	G	A	T	C	T	T	M	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	R	C	C	C	G	T	A	G	G	A	C	C	R
Nang Quot Bien 1	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Mot Bui Lun 2	Y	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	Y	G	G	T	A	C	C	G	T	A	C	C	C	G	T	A	G	G	A	C	C	A
Mong Chim Den	T	M	A	T	C	C	C	K	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	A	C	C	C	G	T	A	G	G	A	C	C	A
Nam Tai	C	M	A	T	C	C	C	G	C	G	A	W	C	T	T	C	A	G	G	A	T	R	T	G	C	G	G	T	G	G	T	M	C	C	G	T	A	Y	C	C	G	T	A	G	G	A	C	C	A
Mong Chim Roi	C	A	A	T	C	C	C	G	C	G	A	W	C	T	T	C	A	G	G	W	T	G	T	G	C	G	G	T	G	G	T	M	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Ba Bui Lun	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	M	A	G	G	A	T	G	T	G	C	G	G	T	G	G	K	C	C	C	G	T	A	C	C	C	G	T	A	G	G	A	C	C	A
Mot Bui 5	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	A	R	K	A	T	G	T	G	C	G	G	T	G	G	K	A	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Mot Bui Do Cao Ca Mau	C	A	A	T	C	C	C	K	C	G	A	T	T	T	T	C	W	G	G	W	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	A	C	C	C	G	T	A	G	G	A	C	C	A
Thom Mua 1	C	A	A	T	C	C	C	G	C	R	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	A	C	C	G	T	A	C	C	C	G	C	G	C	A	G	T	G	A
Ba Bui 1	C	A	A	T	C	C	C	G	C	G	W	W	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Ba Muoi Mua	C	C	R	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	T	T	A	K	G	C	T	T	A	T	A	G	G	A	C	C	G
Ba Tuc 1	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	A	T	C	C	G	C	G	C	A	G	T	G	A
Bay Tan	C	A	A	T	C	C	C	G	C	R	W	W	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	A	T	C	C	G	C	G	C	A	G	T	G	A
Chau Hang Vo	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	T	C	C	G	T	A	G	G	A	C	C	G
Chuoi	Y	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	K	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nang Dut 1	C	A	A	T	C	S	C	G	C	G	A	T	C	T	T	M	W	R	G	A	Y	A	T	C	T	S	S	C	C	A	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nang Huong 1	C	A	A	T	C	S	C	G	C	G	A	W	C	T	T	C	A	G	G	A	T	G	T	G	Y	G	G	Y	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nang Huong Tron	Y	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	Y	Y	R	T	A	T	Y	Y	R	C	G	C	A	G	T	G	A
Nang Ke	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	Y	Y	A	T	A	C	Y	Y	A	T	A	G	G	A	C	C	A
Nang Keo Ba Tu	C	M	A	T	A	S	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	T	T	A	K	R	C	T	T	A	T	A	G	G	A	C	C	R
Nang Keo Xiem 2	C	A	R	T	C	C	C	K	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	A	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Nang Nuool 3	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	K	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Nang Phet 3	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	W	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	T	T	A	T	A	C	T	T	A	T	A	G	G	A	C	C	A
Nang Quot 2	C	A	A	T	C	C	C	G	S	G	A	W	C	T	T	M	A	G	G	A	T	G	T	G	C	G	G	T	G	A	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Nep Dai Loan 2	T	A	A	T	C	C	C	G	C	G	A	T	C	T	T	M	A	G	G	A	T	R	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nep Mo 3	Y	A	A	T	C	C	C	G	C	G	A	W	C	T	T	C	W	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nep Ruoi Som 1	T	C	R	Y	M	C	C	G	C	G	A	T	C	T	T	M	A	G	G	A	T	G	Y	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nep Than Hong 1	C	C	A	T	C	C	C	K	C	G	A	T	T	T	T	C	W	G	G	W	Y	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nep Trang 1	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Sai Gon	C	C	R	T	M	G	C	T	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	K	A	C	C	C	G	T	A	G	G	A	C	C	A
Soi Do	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	K	C	Y	Y	R	T	A	T	Y	Y	R	C	G	C	A	G	T	G	A
Trang Chi Suoi	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	R
Trang Chum Lua	T	A	A	T	C	S	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	R	T	G	C	G	G	T	G	G	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	R
Trang Lun 3	C	C	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	W	T	G	T	G	C	G	G	T	G	G	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Trau Tron	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	S	C	G	G	T	G	G	K	C	T	T	A	K	R	C	T	T	A	T	A	G	G	A	C	C	R
Trung Kien	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	Y	Y	R	T	A	T	Y	Y	R	C	G	C	A	G	T	G	A
Voi	Y	A	A	T	C	S	C	G	C	R	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	A	G	C	C	C	G	K	G	C	C	C	G	T	A	G	G	A	C	C	G
Hai Hoanh	C	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	A	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Bong Gung	T	A	A	T	C	C	C	G	C	R	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	M	Y	Y	R	T	G	C	Y	Y	R	T	A	G	G	A	C	C	G
Nang Lon Luc	C	C	R	Y	M	C	Y	K	C	G	A	T	C	K	W	M	W	R	K	W	Y	A	Y	C	T	S	S	C	S	A	G	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G
Nep ao Gia	C	M	A	T	C	C	C	G	C	G	A	T	T	K	W	M	W	R	K	W	T	G	T	G	C	G	G	T	G	G	G	C	C	C	G	T	G	C	C	C	G	T	A	G	G	A	C	C	G
Nho Huong	C	A	A	T	C	C	C	G	S	R	W	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	C	C	G	T	A	T	C	C	G	C	G	C	A	G	T	G	A
Nang Thom Cho Dao	Y	A	A	T	C	C	C	G	C	G	A	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	Y	G	G	T	C	Y	Y	R	T	A	T	Y	Y	R	Y	R	S	R	R	Y	S	A
Tai Nguyen	Y	A	A	T	C	S	C	G	C	G	A	W	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	R	T	C	Y	Y	A	K	G	C	Y	Y	A	T	A	G	G	A	C	C	G
Cho Bien	C	A	A	T	C	C	C	G	C	G	W	T	C	T	T	C	A	G	G	A	T	G	T	G	C	G	G	T	G	G	T	C	T	T	A	T	G	C	T	T	A	T	A	G	G	A	C	C	G

Figure 4. SNP haplotype of agronomic traits of 65 rice landraces. The dark blue alleles represent minor alleles, the light blue alleles represent heterozygous alleles, and the white alleles represent the major alleles of the SNPs. Heterozygous alleles indicate the presence of both alleles at the SNP position in specified landraces. R (A:G), Y (C:T), S (C:G), W (A:T), K (G:T), and M (A:C). PLL: Flag leaf length, BRL: Brown rice length.

techniques and the existing environmental conditions. Therefore, the genetic basis underlying rice plant height remains incompletely understood (Peng *et al.*, 2023). Historically, breeding rice landraces aimed to be taller (Khan *et al.*, 2015), allowing them to thrive in deep-water environments. However, high-yielding rice cultivars require shorter plant heights, as excessive plant height enhances the risk of lodging and, eventually, yield loss (Hedden, 2003). In this study, the 65 rice landraces were remarkable with higher plant height, making them unsuitable for intensive cultivation in the Mekong Delta. GWAS analysis identified 37 candidate SNPs associated with plant height, a considerably higher number than reported by Ma *et al.* (2016). Previous studies have indicated that plant height is a polygenic trait influenced by both genetic and environmental factors (Huang *et al.*, 2010).

The presented study identified a candidate gene, *Os01g0179901*, located near the dwarf gene (*Os01g0177400, d18*), which was associated with gibberellins biosynthesis. Additionally, the dwarf gene (*Os01g0178500*, *OsIAA1*) showed distinction in influencing the leaf angle, while the dwarf gene (*osa-miR156b*, *OsmiR156b*) displayed linkages in increasing plant height. These findings highlight that the candidate SNP located on chr01 at position 4,176,737 can be favorable in rice breeding to improve the plant height trait. Furthermore, a quantitative trait locus (QTL) on dwarf (ph1.1) reached detection as contributing to plant height (Mansueto *et al.*, 2016).

Flag leaf angle categorization consisted of erect, intermediate, horizontal, and droopy (SES, 2013). Erect flag leaves enhance the light absorption efficiency while reducing the pest infestation, making them beneficial for breeding programs (Khan *et al.*, 2015). In this study, most rice landraces had erect flag leaves, which is beneficial for cultivation. This study identified that landraces with homozygous genotypes at these SNPs generally exhibited erect flag leaves, whereas heterozygous genotypes correlated with more horizontal and droopy leaves. These findings align with the past research highlighting the genetic basis of flag leaf architecture in rice (Yano *et al.*, 2016).

Based on the IRRI classification, the leaf collar color consisted of three main groups (SES, 2013). These results confirm that light green leaf collars were the dominant characteristic among the studied rice landraces. A few landraces displayed distinctive purple collars, which can aid in landrace identification. Leaf length is a distinguishing trait among the rice cultivars (Tari *et al.*, 2009), categorized into four groups by IRRI (SES, 2013). GWAS identified 10 candidate SNPs, with the peak SNP located on Chr08 at position S08_27336090, and these results emerged consistent with the findings of Yang *et al.* (2015). The presence of polymorphic SNPs suggests that leaf length is a highly variable trait influenced by multiple genetic loci. Leaf width received influences from both genetic and environmental factors in rice genotypes (Fabre *et al.*, 2016). In this study, the average weight of 100 brown rice was 2.4 g. Past studies revealed that most rice landraces have a 1000-grain weight with a range of 23–30 g (Kanchana *et al.*, 2012).

In rice, the grain size is a crucial factor influencing grain yield and consumer preference (Nayak *et al.*, 2022). GWAS identified five candidate SNPs associated with brown rice length on Chr03, Chr07, Chr08, and Chr11, corroborating the findings of Ponce *et al.* (2020). One candidate SNP on chr07 has a significant association with brown rice length. This SNP exhibited three major allele types, requiring further validation to confirm its role in grain length determination. These findings align with earlier work by Ponce *et al.* (2020), who identified grain length-associated SNPs on similar chromosome locations. The presence of multiple SNPs suggests a complex genetic architecture for grain width, which is an essential factor for grain quality and milling yield. Rice shape is a vital quality trait in rice breeding (Zhou *et al.*, 2019; Sultana *et al.*, 2022). Therefore, GWAS for grain shape traits of 469 indica accessions, as carried out by Feng *et al.* (2016), identified 47 SNPs. In this study, eight candidate SNPs succeeded in their detection across the five chromosomes.

In 31 rice landraces, the most common allele pattern was evident, and excluding heterozygous SNPs improved classification accuracy. The concentration of SNPs on chr12 aligns with findings by Ponce *et al.* (2020), which highlighted its importance in grain shape determination. The results provided valuable insights into the brown rice width and shape, which are crucial for breeding programs to meet market demands. Three candidate SNPs located on chr03 proceeded to identification within the candidate gene *LOC_Os03g29520*. These SNPs expressed an association with three QTLs: gw3.1 (grain weight), qGL-3 (grain length), and qLWR-3 (grain length-to-width ratio). Additionally, these SNPs showed close linkage to the *Os03g0407400* gene, which influences the grain size traits (Mansueto *et al.*, 2016).

CONCLUSIONS

This study analyzed 11 agronomic traits in 65 rice (*O. sativa* L.) landraces using GWAS and identified 681 significant SNPs across the 12 chromosomes. Strong associations emerged for nine key traits, and the plant height revealed the highest number of candidate SNPs. Brown rice grain width and the grain length-to-width ratio shared the most overlapping SNPs, indicating potential pleiotropic effects. Several genes contained multiple SNPs linked to different traits, highlighting key genomic regions influencing rice plants morphology and grain traits. The promising results enhanced the understanding of genetic diversity and provided valuable markers for future rice breeding programs.

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