



RESEARCH ARTICLE

Exploring the genetic wealth of Vietnamese coloured rice (*Oryza sativa* L.) accessions

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Abstract

Coloured rice genotypes possess superior nutritional traits, meeting an increasing consumer demand for functional foods. This study evaluated 45 Vietnamese coloured rice accessions to characterise their genetic divergence using 45 simple sequence repeats (SSR) markers across 13 phenotypic and biochemical traits. The analysis of variance (ANOVA) results indicated highly significant phenotypic variation among genotypes and substantial genotype-by-environment interactions. Genetic diversity analysis revealed moderate to high polymorphism information content values ranging from 0.08–0.52 and an average of 1.79 alleles per locus. The analysis of molecular variance (AMOVA) results demonstrated that most of the genetic variation (85 %) resided within panels, indicating extensive intra-panel diversity. Furthermore, cluster and principal coordinates analyses (PCoA) identified three distinct genetic groups, reflecting geographical origins and complex genetic backgrounds. Notably, upland and mega rice varieties showed higher differentiation, whereas traditional rice (TR) and mega rice varieties exhibited greater genetic similarity. The study identified key markers, such as RM28561 on chromosome 12, significantly associated with anthocyanin content–43.45 % phenotypic variance explained (PVE) and 10.03 % PVE grain width (GW). Additionally, RM214 located on chromosome 1 explained up to 79 % of the variance for plant height (PH). Other markers associated with panicle length (PL), grain weight and yield per plant (YPP) were also identified, explaining up to 39.68 % of the phenotypic variance. Three promising accessions, Blau Sang, Nep Cam and Nep Do, were recommended for future biofortification breeding programs. These findings provide a valuable foundation for developing high-yielding, nutrient-rich coloured rice varieties using marker-assisted selection.

Keywords: anthocyanin content; molecular markers; QTL; Vietnamese coloured rice

Introduction

White rice is a dietary staple globally, while black, red, purple and brown rice contain natural anthocyanin pigments in the seed coat, pericarp and aleurone layers (1–2). White rice lacks micronutrients, macronutrients and antioxidant concentrations, in contrast, coloured rice derives vibrant colours from natural pigments like anthocyanins and carotenoids, which are potent antioxidants (3). Based on pericarp colour, Vietnamese rice is also classified into four types: white, brown, red and black. In non-flooded soils, upland rice (UP) varieties exhibit distinct characteristics such as aroma, colour and morphology diversity (4). Developing rice genotypes that accumulate nutrients in the endosperm would significantly impact population health. Anthocyanin accumulation results in black and purple pericarps, whereas proanthocyanidins cause red pericarps (5–6). Rice varieties with colour possess higher protein, healthy amino acids, fat, fibre and vitamin E (5, 7, 8). Red rice proanthocyanidins (PAs) and purple rice anthocyanins are linked to health benefits, including lowering the risk of diabetes, obesity, heart disease and cancer (9–12). The six subclasses of flavonoids formed in the biosynthesis process include flavonols, flavones, flavanones and flavan-3-ols (13, 14).

In recent studies, coloured rice varieties exhibit diverse total anthocyanin content (0–493 mg 100 g⁻¹) and genetic diversity (0–0.65) (15–17). The study geographically classified 42 coloured rice accessions from the Philippines using simple sequence repeats (SSR) markers (18). Analysis of a core collection of 307 *japonica* and *indica* accessions identified 20 single nucleotide polymorphisms (SNP) markers for genotype differentiation (3). A 14-bp deletion at exon 6 of the *Rc* gene results in white grains. The *Rd* and *Rc* genes collaboratively regulate red colour intensity (3, 19, 20); *Rd* controls proanthocyanidin levels while *Rc* regulates accumulation. Other pigmentation genes include *Pb*, *Pp*, *Kala1*, *Kala3* and *Kala4* (21–23). For instance, a promoter rearrangement in the *Kala4 bHLH* gene causes ectopic expression, resulting in black rice (24). Phenotypic, biochemical and biophysical markers are cost-effective but less reliable than molecular markers due to environmental influences (25). Molecular markers effectively identify genetic variations in plants, enabling precise descriptions of genetic diversity and contributing to high-quality genotypes for breeding programs (26). Simple sequence repeat markers are commonly used in genetic diversity studies due to their high polymorphism and accuracy (27). To better understand polygenic traits, utilising SSR markers is imperative for assessing genetic associations among diverse cultivated genotypes.

Therefore, this study aimed to determine the genetic diversity and population structure of 45 coloured rice accessions using 45 SSR markers, 7 agronomic traits and 6 biochemical traits. It also sought to identify pigmented genotypes within Vietnamese rice core panels and develop highly polymorphic microsatellites for nutritional and functional rice breeding programs.

Materials and Methods

Plant materials

A total of 45 coloured rice genotypes with white, brown, red and black seed pericarp were representative of breeding lines, uplands and landraces from the College of Agriculture, Can Tho University, Vietnam (Supplementary Table 1). The experiment was conducted in Can Tho, Vietnam (10.03° N, 105.76° E; altitude 0.8 m above sea level), during the 2021 dry season (2021DS). Rice genotypes were germinated in plastic trays before transplanting 14-day-old seedlings to the field with a spacing of 20 x 20 cm. The study followed a randomised complete block design (RCBD) with three replications. Nitrogen (N), phosphorus (P) and potash fertilisers were applied at a rate of 100:40:30 kg ha⁻¹. Standard agronomic practices and plant protection measures were implemented to ensure optimal crop growth.

Data collection

Field observations were recorded for seven agronomic traits: days to maturity (DTM), plant height (PH; cm), panicle length (PL; cm), grain yield per plant (YPP; kg ha⁻¹), thousand-grain weight (TGW; g), grain length (GL; mm) and grain width (GW; mm). Traits were measured following the standard evaluation system (31). For six biochemical grain traits, amylose content (AC) was measured using the biochemical techniques (28, 29). The gelatinisation temperature (GT) trait was assessed using the method followed by a previous study (30). The International Rice Research Institute (IRRI) scale was used to evaluate the AC and GT results (31). Anthocyanin content (AntC) was analysed based on the method from a previous study (32). The analysis of flavonoid content (FlaC), phenolic content (PheC) and (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid)) [ABTS] content was conducted using the sample extraction method (33).

DNA extraction and polymerase chain reaction (PCR) analysis

DNA was extracted from the seedling leaf of each rice accession using the cetyltrimethylammonium bromide (CTAB) method (34). Genotyping of 45 coloured rice accessions was conducted using 45 SSR/SNP markers, as detailed in Supplementary Table 2. Polymerase chain reaction reactions were conducted in a total volume of 20 µL. The reaction mixture consisted of 7.5 µL of GoTaq® Green Master Mix (Promega, USA), which included DNA polymerase, deoxynucleoside triphosphates (dNTPs), magnesium chloride (MgCl₂) and reaction buffer. Additionally, 1 µL of each forward and reverse primer (10 µM concentration) was added, along with 1 µL of template DNA. The remaining volume was adjusted with nuclease-free water to achieve the final 15 µL volume. The PCR protocol included an initial denaturation at 95 °C for 5 min, 35 cycles of 94 °C for 1 min, 50–69 °C for annealing temperature and 72 °C for 1 min, followed by a final extension at 72 °C for 5 min. The PCR products were separated on a 2 % agarose gel at 75 V for 15 min, stained with ethidium bromide (10 mg mL⁻¹) and visualised under UVP GelStudio (Analytik Jena US LLC). The polymorphic bands produced by each primer were recorded, with the presence of a band at a specific

migration position marked as "1" and the absence of a band marked as "0".

Analysis of molecular variance (AMOVA)

Analysis of molecular variance was performed to assess genetic variation within and among panels. This analysis included both indigenous and exotic accessions and was applied to the entire panel as well as a core collection. The model-based panel approach was employed using GenAlex 6.5 software (35).

Analysis of panel genetic diversity and genetic structure

Panel genetic parameters including the polymorphic percentage, allele number (Na), effective number of alleles (Ne), Nei's genetic distance (H) and Shannon's information index (I), were analysed using the GenAlex v 6.5 software. The genetic structure of the panel was analysed using Structure 2.3.4 (<http://pritch.bsd.uchicago.edu/>) and the mixed model and frequency correlation model were used. The ΔK algorithm was used to estimate the theoretical panel number using the online software Structure Harvest (35). Principal component analysis (PCA) was conducted using GenAlex 6.5 software (36). The markers dendrograms were constructed using Jaccard's similarity matrix and Unweighted pair group method with arithmetic mean (UPGMA) (37) and the factextra/R package (38). This was based on the obtained distance matrix and included 1000 bootstrap replicates. The polymorphic information content (PIC) was determined using the formula from a previous study (39).

$$PIC = 1 - \sum_{i=1}^n p_i^2 - \sum_{i=1}^n \sum_{j=i+1}^n 2p_i^2 p_j^2$$

where: p_i is the frequency of the i -th allele; n is the total number of alleles.

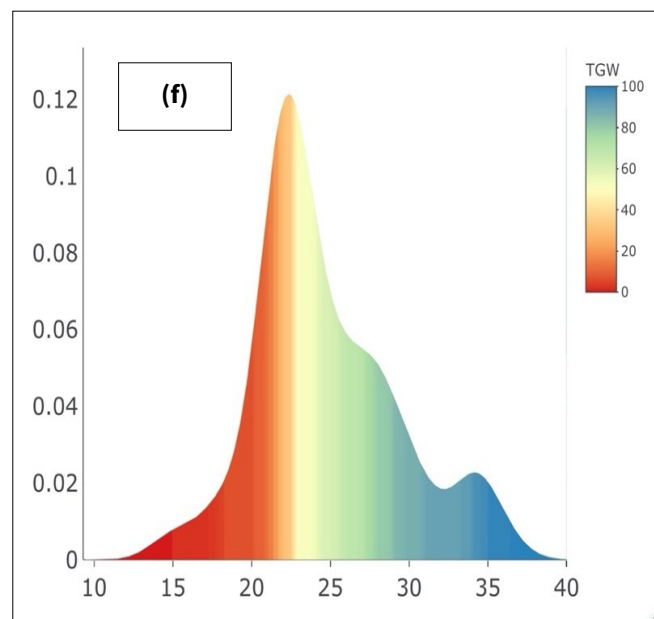
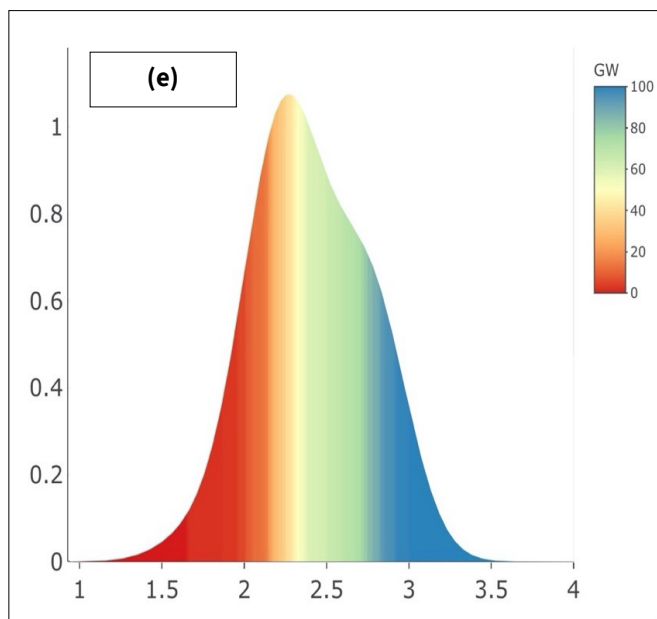
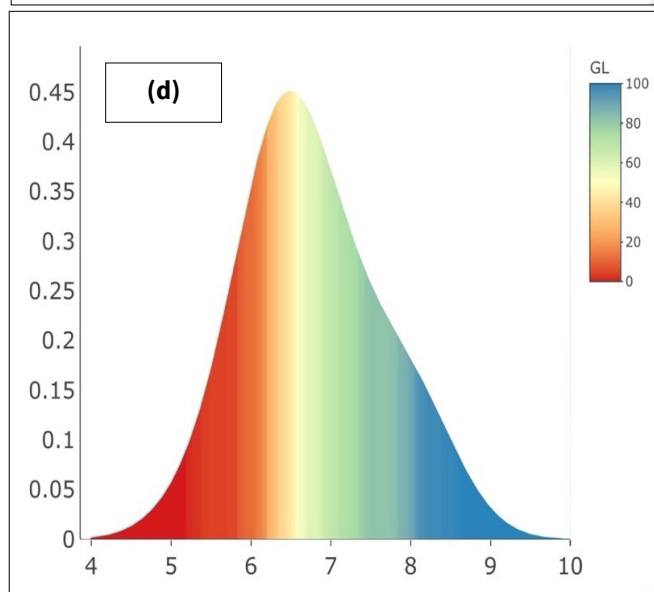
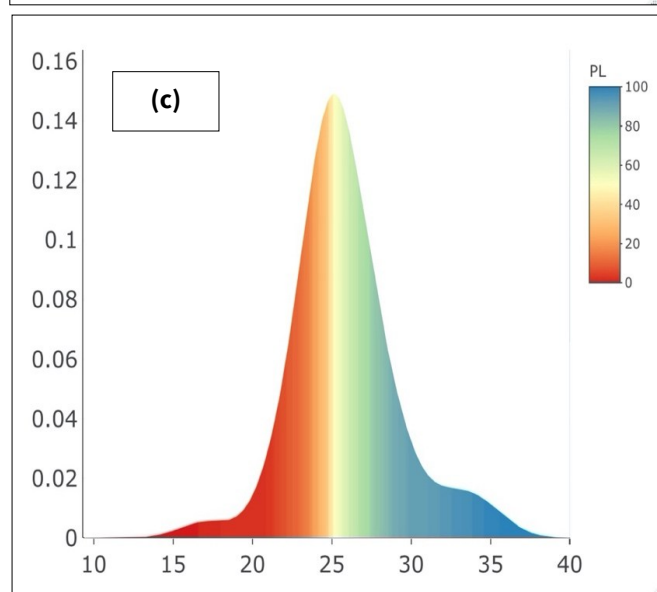
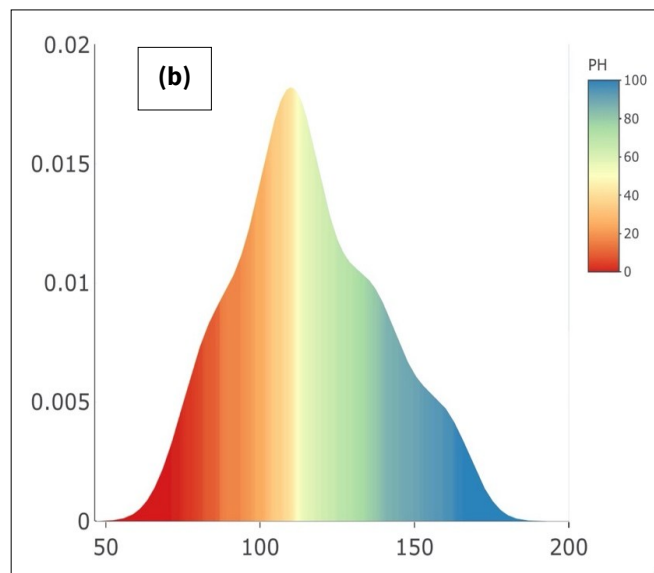
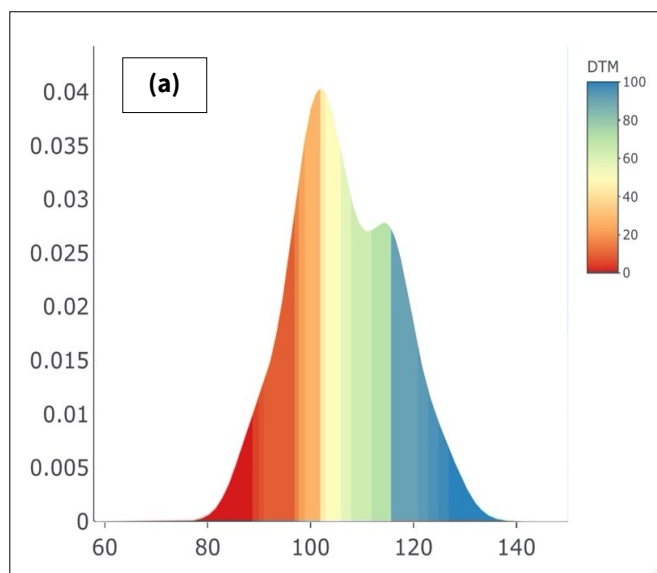
Investigation of the connection between simple sequence repeats markers and all 13 evaluated traits

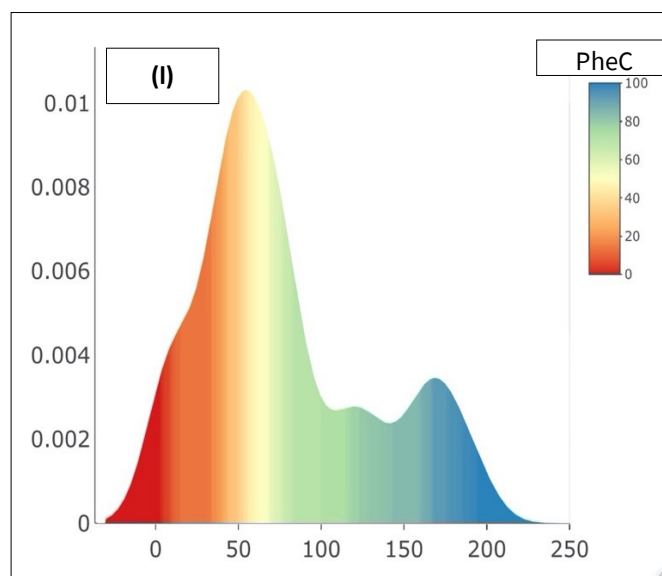
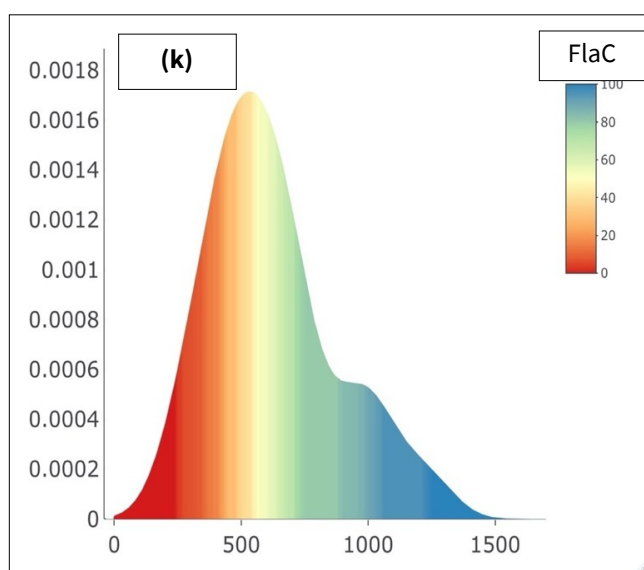
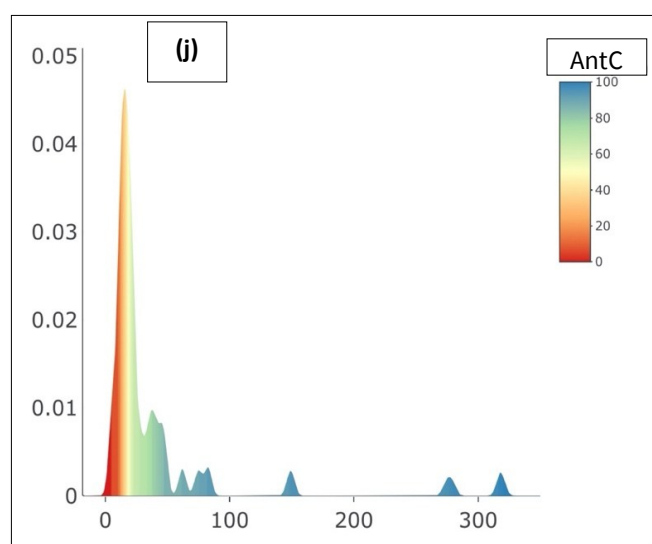
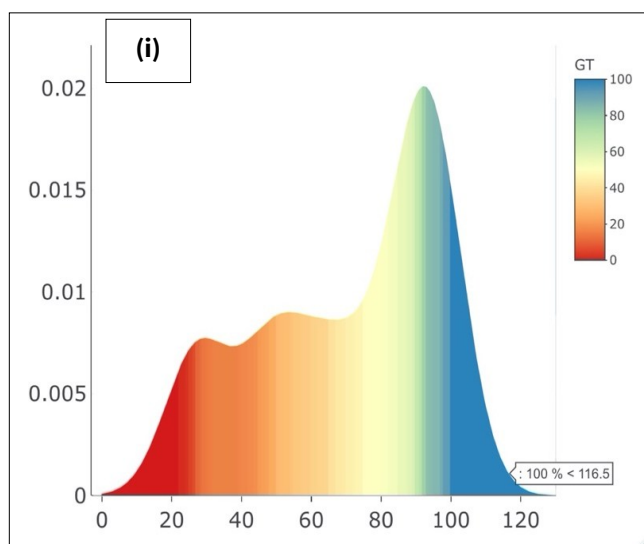
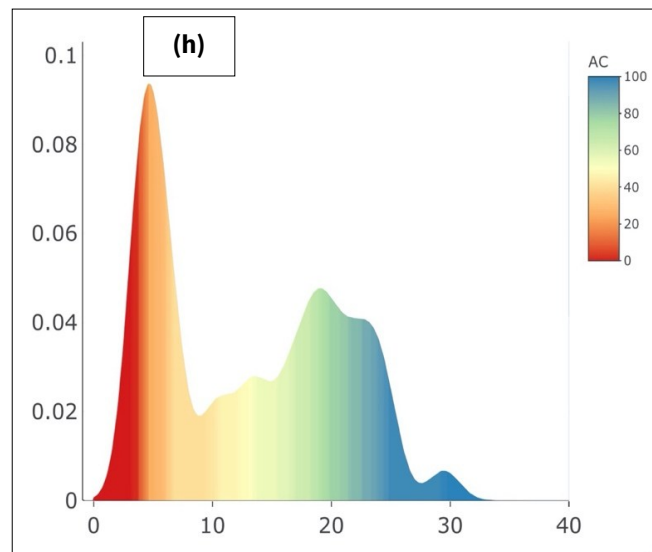
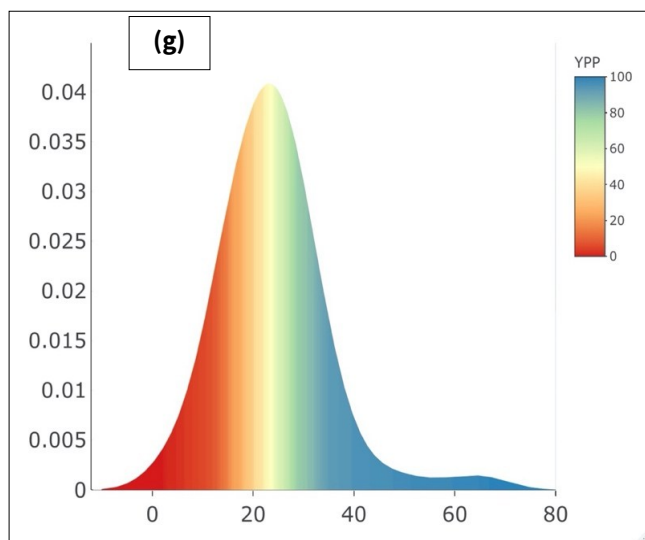
The genetic relatedness between the phenotypic performances of the rice accessions and SSR markers was determined using a mixed linear model (MLM) within the GAPIT/R package (40). Markers significantly associated with traits were identified based on their R^2 values and p values (< 0.05).

Results

Phenotypic analysis

Analysis of variance (ANOVA) for the 13 quantitative traits revealed highly significant differences among genotypes ($p < 0.001$), indicating strong genetic influence on trait expression (Table 1). Normal distributions were observed for PH, PL, YPP, GL, GW and ABTS. In contrast, DTM, TGW, AC, AntC, GT, FlaC and PheC exhibited bimodal or multimodal distributions (Fig. 1), suggesting complex polygenic inheritance. The mean values of agronomic traits were DTM (10.4 days), PH (115.76 cm), PL (25.85 cm), TGW (24.74 g), GL (6.78 mm), GW (2.4 mm) and YPP (23.89 g). For biochemical traits, mean values of AC (13.09 mg kg⁻¹) and GT (70.32 mm) were recorded in Table 1. The mean values of AntC (39.29 mg kg⁻¹), FlaC (623.02 mg kg⁻¹), PheC (77.67 mg kg⁻¹) and ABTS (51.31 mg kg⁻¹). The coefficient of variation (CV) ranged from 0.77–13.88 %, with low CV (< 15 %) were observed across all traits (Table 1), indicating high experimental precision. Furthermore, the significant variations observed were primarily driven by genetic factors rather than random chance.





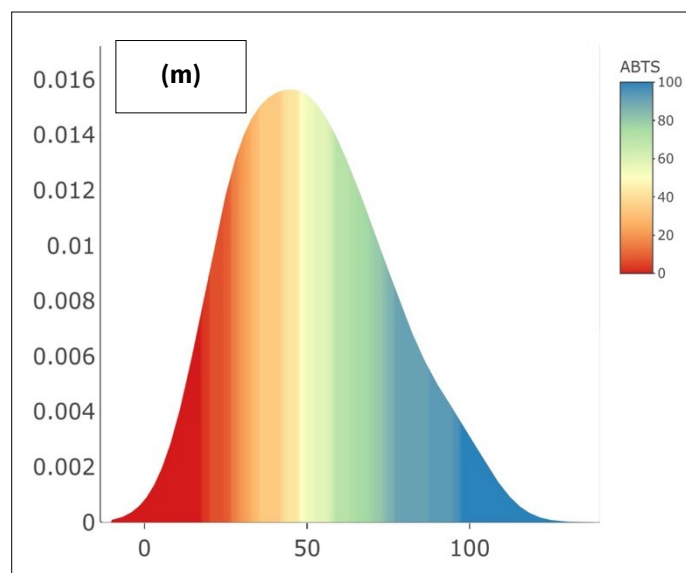


Fig. 1. Heatmap histograms of frequency distribution of 13 evaluated traits. a: days to maturity (DTM); b: plant height (PH); c: panicle length (PL); d: thousand-grain weight (TGW); e: grain length (GL); f: grain width (GW); g: grain yield per plant (YPP); h: amylose content (AC); i: gelatinisation temperature (GT); j: anthocyanin content (AntC); k: flavonoid content (FlaC); l: phenolic content (PheC); m: 2,2'-azino-bis(3-ethylbenzothiazoline 6-sulfonic acid) content (ABTS).

Table 1. Analysis of variance (ANOVA) for the 13 quantitative traits of 45 Vietnamese coloured rice genotypes

No.	Traits	Min	Max	Mean	Genotypes (G)	CV (%)	LSD (5 %)
1	DTM	87.59	127.35	106.4	409.3	***	0.77
2	PH	71.5	166	115.76	69.04	***	4.11
3	PL	16.6	35.7	25.85	26.7	***	3.99
4	GL	5.19	8.61	6.78	362	***	1.03
5	GW	1.65	3.01	2.4	70.59	***	2.57
6	TGW	15	36.5	24.74	163.3	***	2.46
7	YPP	2.49	67.1	23.89	27.37	***	13.88
8	AC	3.23	29.77	13.09	1578	***	2.59
9	GT	22	100	70.32	325	***	3.5
10	AntC	5.3	320.6	39.29	13412	***	2.35
11	FlaC	242	1252	623.02	571.2	***	2.87
12	PheC	3.4	194.3	77.67	2081	***	2.57
13	ABTS	17.3	97.7	51.31	4266	***	1.11

*, **, *** Significant at $p < 0.05$, 0.01 and 0.001; ns: not significant. DTM: days to maturity; PH: plant height; PL: panicle length; TGW: 1000-grain weight; GL: grain length; GW: grain width; YPP: yield per plant; AC: amylose content; GT: gelatinization temperature; AntC: anthocyanin content; FlaC: flavonoid content; PheC: phenolic content; ABTS: 2,2'-azino-bis(3-ethylbenzothiazoline 6-sulfonic acid) content.

Polymorphism of simple sequence repeats markers

The study evaluated 45 coloured rice genotypes, comprising 9 upland, 9 traditional and 27 mega variety lines representing three major rice-growing regions of Vietnam (Supplementary Table 1). To assess genetic relatedness, the study initially utilised 45 SSR markers (Supplementary Table 2), resulting in the generation of polymorphic bands (Supplementary Fig. 1). The PIC of these markers ranged from 0.02–0.93, reflecting varying levels of genetic diversity at each locus (Table 2). The average PIC across all loci was 0.52, indicating moderate genetic variation within the study population.

These results provide a deeper understanding of the extent of genetic diversity, with significant implications for breeding programs and conservation efforts. The loci with higher polymorphism percentages, such as RM16553 (0.93) and RM140 (0.87), demonstrate substantial genetic variability and are highly suitable for further germplasm characterisation. Conversely, there were several markers with lower polymorphism percentages ($< 0.3\%$), including HD1_2, RM127, RM256, RM28561, RM3331, RM3810, RM472, RM541, RM7424, RM8070 and RM8132, which may have more specialised applications in genetic research.

Analysis of molecular variation (AMOVA)

Genetic variation among and within panels of the 45 coloured rice accessions examined by AMOVA was significant ($p < 0.01$) (Table 3). The AMOVA results showed that 15 % of the genetic variation of the coloured rice panels came from inter-panel and 85 % of the genetic variation came from intra-panel. This analysis could provide insights into the distribution of genetic variation in a population and help researchers understand the factors contributing to that variation.

Genetic diversity parameters

The PIC values ranged from 0.08 (RM256 and RM3810) to 0.52 (RM21, RM211, RM253, RM286, RM3288, RM3472, RM3400, RM493, RM6329 and RM7419), with a mean of 0.43 (Table 2). The N_a per SSR locus ranged from 0.67–2 (average 1.79), while the N_e ranged from 1.04–1.92 (average 1.58). Expected heterozygosity (H_e) and unbiased expected heterozygosity (uH_e) averaged 0.33 and 0.34, respectively. Shannon's information index ranged from 0.07–0.67, with an average of 0.48 (Table 2). Among the panels, the mega varieties rice (MR) group consistently exhibited the highest values for all genetic parameters, indicating superior genetic diversity (Table 4). Specifically, the MR panel showed $N_a = 1.96$, $N_e = 1.58$, $H_e = 0.34$,

Table 2. Forty five simple sequence repeats/single nucleotide polymorphisms locus genetic variation of Vietnamese coloured rice panels

Locus	Na	Ne	He	uHe	I	PIC (%)	Percentage of polymorphism
GS3	2.00	1.46	0.29	0.30	0.45	0.44	0.71
HD1_2	2.00	1.23	0.19	0.19	0.33	0.37	0.22
RM11943	2.00	1.45	0.28	0.30	0.44	0.47	0.33
RM1232	1.67	1.51	0.29	0.30	0.41	0.47	0.67
RM127	2.00	1.35	0.24	0.25	0.40	0.42	0.27
RM1354	2.00	1.88	0.47	0.49	0.66	0.45	0.69
RM140	1.67	1.49	0.28	0.29	0.41	0.26	0.87
RM144	2.00	1.79	0.44	0.46	0.63	0.52	0.56
RM16553	1.33	1.27	0.15	0.15	0.21	0.16	0.93
RM19	2.00	1.93	0.48	0.50	0.67	0.45	0.69
RM21	2.00	1.62	0.37	0.38	0.55	0.52	0.49
RM211	2.00	1.75	0.42	0.44	0.61	0.52	0.47
RM212	2.00	1.86	0.46	0.48	0.65	0.44	0.71
RM214	1.67	1.59	0.31	0.32	0.44	0.35	0.8
RM240	2.00	1.85	0.46	0.48	0.65	0.37	0.78
RM24330	2.00	1.92	0.48	0.50	0.67	0.47	0.67
RM246	2.00	1.74	0.42	0.44	0.61	0.52	0.53
RM247	2.00	1.83	0.45	0.47	0.65	0.35	0.8
RM253	1.67	1.46	0.26	0.27	0.39	0.52	0.53
RM256	0.67	1.01	0.01	0.01	0.03	0.08	0.02
RM257	1.67	1.52	0.29	0.30	0.42	0.5	0.6
RM28102	1.67	1.51	0.28	0.30	0.41	0.5	0.6
RM28561	2.00	1.45	0.27	0.28	0.42	0.44	0.29
RM286	1.33	1.51	0.28	0.30	0.41	0.52	0.4
RM302	1.67	1.62	0.32	0.33	0.45	0.44	0.71
RM306	1.67	1.53	0.30	0.31	0.42	0.2	0.91
RM3288	2.00	1.74	0.42	0.44	0.61	0.52	0.53
RM333	2.00	1.76	0.43	0.45	0.62	0.51	0.58
RM3331	1.33	1.45	0.27	0.28	0.39	0.48	0.36
RM3400	2.00	1.61	0.34	0.36	0.51	0.52	0.51
RM3412	2.00	1.84	0.45	0.47	0.64	0.44	0.71
RM3472	2.00	1.71	0.41	0.43	0.60	0.52	0.56
RM3810	0.67	1.04	0.04	0.04	0.07	0.08	0.02
RM471	2.00	1.85	0.45	0.47	0.65	0.48	0.64
RM472	2.00	1.32	0.22	0.23	0.37	0.37	0.22
RM474	2.00	1.61	0.37	0.39	0.56	0.5	0.4
RM493	2.00	1.60	0.36	0.37	0.54	0.52	0.47
RM541	2.00	1.38	0.27	0.28	0.43	0.42	0.24
RM6329	2.00	1.66	0.39	0.41	0.58	0.52	0.47
RM72	2.00	1.80	0.44	0.46	0.63	0.51	0.58
RM7210	2.00	1.85	0.46	0.48	0.65	0.37	0.78
RM7419	2.00	1.75	0.41	0.43	0.59	0.52	0.42
RM7424	1.33	1.43	0.26	0.27	0.38	0.47	0.31
RM8070	0.67	1.09	0.07	0.07	0.12	0.26	0.13
RM8132	2.00	1.32	0.22	0.23	0.37	0.37	0.2
Mean	1.79	1.58	0.33	0.34	0.48	0.43	0.52

Na: no. of different alleles; Ne: no. of effective alleles; I: Shannon's information index; He: expected heterozygosity; uHe: unbiased expected heterozygosity; PIC = polymorphism information content (%).

Table 3. Analysis of molecular variance (AMOVA) of Vietnamese coloured rice panels based on 45 simple sequence repeats (SSR) markers.

Source	df	SS	MS	Est. Var.	Percentage of variation (%)
Among panels	2	63.55	31.77	1.73	15 %
Within panels	42	416.22	9.91	9.91	85 %
Total	44	479.77		11.64	100 %

df: degree of freedom; SS: sum of square; MS: mean Square; Est. Var.: estimated variance component.

p value is based on 999 permutations. Significant at $p < 0.001$.

Table 4. Genetic diversity parameters of the three panels of Vietnamese coloured rice

Panels	UP	TR	MR	Grand mean and SE over loci and pops
Na	1.69	1.49	1.96	1.72
Ne	1.55	1.44	1.58	1.53
He	0.31	0.25	0.34	0.30
uHe	0.33	0.26	0.35	0.31
I	0.45	0.37	0.52	0.44
% P	78.18 %	67.27 %	98.18 %	

Na: no. of different alleles; Ne: no. of effective alleles; He: expected heterozygosity; uHe: unbiased expected heterozygosity; I: Shannon's information index; % P: percentage of polymorphic loci; UP: upland rice; TR: traditional rice; MR: mega varieties rice.

uHe = 0.35 and I = 0.52. Additionally, the MR panel reached a percentage of polymorphic loci (% P) of 98.18 %, suggesting a high genetic variability which could facilitate more robust and sustainable breeding strategies.

The Nei's genetic distance and genetic identity between every two panels ranged from 0.11–0.16 and 0.86–0.89, respectively. The maximum genetic distance was observed between UP and traditional rice (TR) (0.16), corresponding to the lowest genetic identity (0.86). Conversely, the UP and MR panels exhibited the minimum genetic distance (0.11) and the highest genetic identity (0.89) (Table 5). Pairwise population PhiPT and LinPhiPT values were key indicators in population genetics for assessing genetic differentiation among groups (Table 6). Comparisons between UP, TR and MR revealed varying degrees of genetic differentiation. Particularly, the PhiPT and LinPhiPT values for UP-TR comparison were 0.11 and 0.12, respectively, indicating moderate genetic differentiation. The UP-MR comparison showed higher differentiation with PhiPT at 0.18 and LinPhiPT at 0.22. Interestingly, the TR-MR comparison yielded values of 0.00 for both indices, showing no significant genetic differentiation between these two groups.

Table 5. Pairwise population unbiased Nei genetic distance and unbiased Nei genetic identity values

Group		Nei D	Nei I
UP	TR	0.16	0.86
UP	MR	0.11	0.89
TR	MR	0.14	0.87

UP: upland rice; TR: traditional rice; MR: mega-varieties rice; Nei D: Nei genetic distance; Nei I: Nei genetic identity.

Table 6. Pairwise population PhiPT and LinPhiPT values and estimates of Nm

Group		PhiPT	LinPhiPT
UP	TR	0.11	0.12
UP	MR	0.18	0.22
TR	MR	0.00	0.00

UP: upland rice; TR: traditional rice; MR: mega varieties rice

Genetic relatedness through cluster analysis and principal coordinate analysis (PCoA).

The STRUCTURE analysis determined the genetic relationships among the studied genotypes, dividing 45 genotypes into three distinct panels with ΔK value of 65 (Fig. 2 and 3). Further sub-clustering within each group confirmed the presence of three distinct genetic backgrounds across the coloured rice panels. Principal coordinate analysis was used to determine the genetic relatedness among the genotypes (Fig. 4). Genotypes were presented in colours corresponding to the clusters observed in unrooted trees. PCo1 accounted for 30.90 % of the total variance, indicating it captured a significant portion of the data variability (Table 7). PCo2 added another 12.32 %, bringing the cumulative variance explained to 43.22 %. Finally, PCo3 contributed an additional 11.32 %, making the total cumulative variance 54.54 %. The high variance captured by PCo1 indicates a strong underlying genetic structure within the dataset. Cluster analysis was carried out to assess genetic distance and the dissimilarity matrix using the UPGMA method. The 45 coloured rice accessions categorised from 3 different panels clustered into three distinct groups (Fig. 5). The three largest clusters (I, II and III) from 11–21 accessions were grouped with a total of 45 accessions from 3 different panels (UP, TR and MR). Cluster I (11 genotypes) was further divided into sub-groups I-1, I-2 and I-3. Cluster II was partitioned into two sub-groups containing 7 and 14 genotypes, while Cluster III comprised 13 genotypes. Although geographical location did not result in significant overall grouping, sub-groups I-1 and I-2 exclusively possessed genetic traits from the TR and MR panels, indicating localised genetic conservation.

Association of simple sequence repeats with the evaluated traits

The MLM approach identified 29 significant marker-trait associations across 13 related traits ($p < 0.05$), distributed on chromosomes 1, 2, 3, 4, 6, 7, 9, 10, 11 and 12 (Table 8). The phenotypic variance explained (PVE) by these QTLs ranged from 5.44–79 %. For agronomic traits, marker RM214 on chromosomes 1, 4 and 7 explained the highest PVE of 79 % for PH, while RM3400 on chromosomes 1, 3, 4 and 12 accounted for 39.68 % of the variance in PL. For grain characteristics, RM247 was significantly associated with both GL and TGW, explaining 23.96 % and 24.53 % of the variance, respectively. Additionally, RM28561 on chromosome 12 was linked to GW (10.03 % of PVE) and

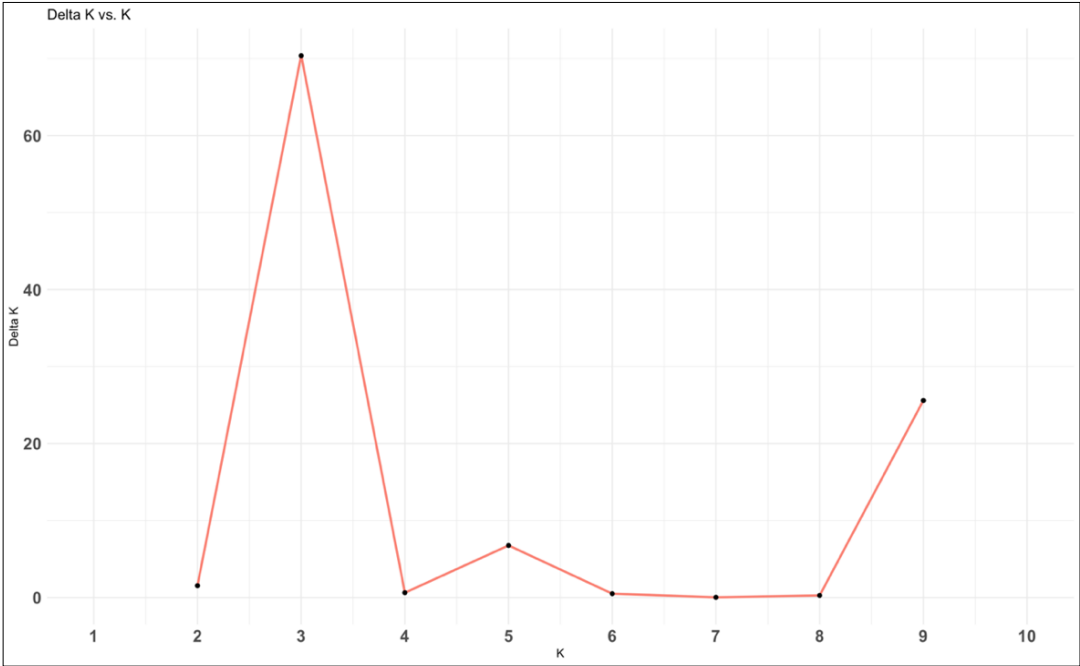


Fig. 2. Estimation of population using LnP (D) derived ΔK from 1–65.

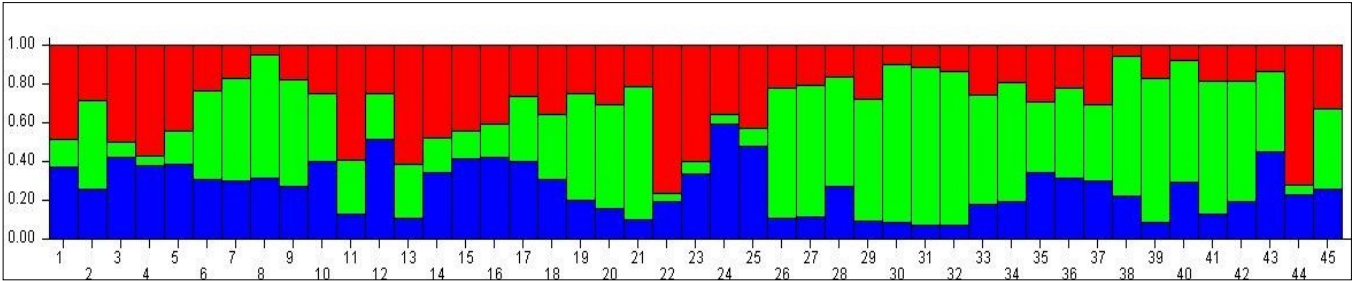


Fig. 3. K = 3, structure analysis in all three Vietnamese coloured rice panels.

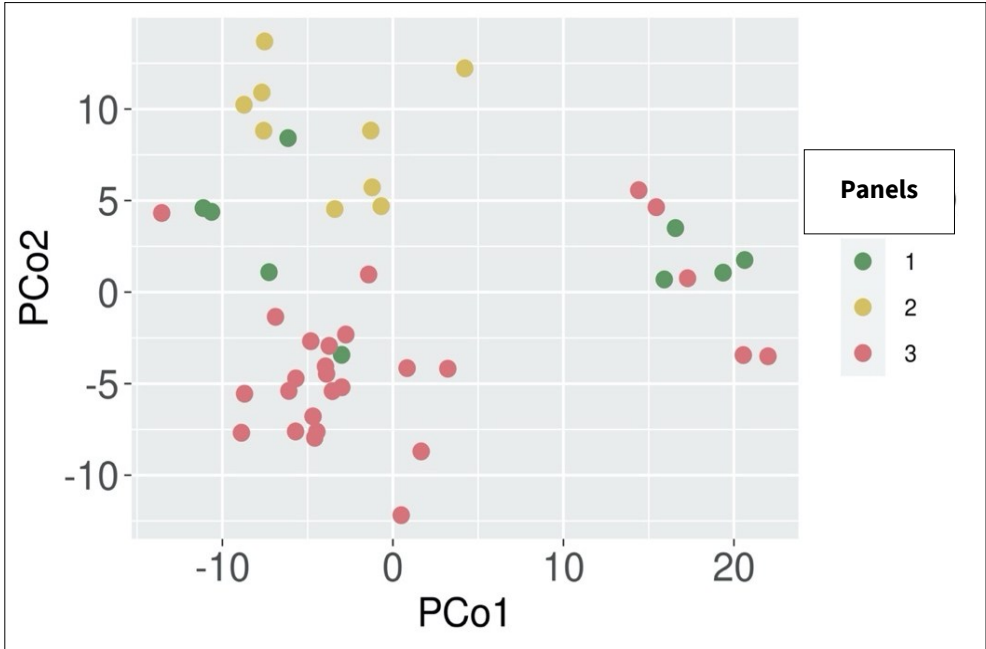


Fig. 4. Principal coordinate analysis of 45 the coloured rice accessions based on the 45 markers. Green circle: upland rice (UP); yellow circle: traditional rice (TR); and red circle: mega-rice (MR).

Table 7. Principal coordinate (PCo) explanation for 3 components of 3 different panels.

Axis	PCo1	PCo2	PCo3
Differentiation explained (%)	30.90	12.32	11.32
Cumulative frequency (%)	30.90	43.22	54.54

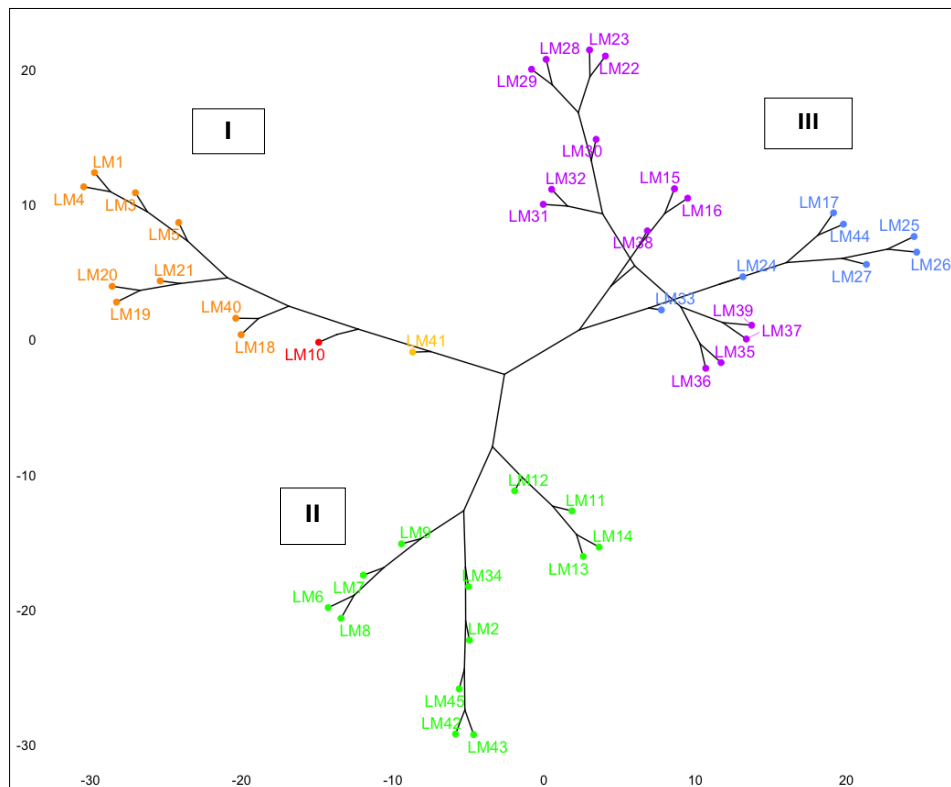


Fig. 5. UPGMA tree constructed for 45 rice genotypes based on 45 trait linked markers.

Table 8. Association of SSR/SNP marker alleles with the rice phenotypic traits using mixed linear model (MLM)

Traits	Markers	Chro.	Position (bp)	p-value	MAF	PVE (%)
DTM	RM257	9	17719660	0.01	0.02	7.77
	RM246	1	27335176	0.04	0.27	26.54
PH	RM302	1	32987234	0.03	0.31	41.79
	RM16553	4	8638862	0.04	0.4	30.74
	RM214	7	12783492	0.03	0.36	79
	RM3412	1	11582975	0.02	0.44	19.11
PL	RM3400	3	17264981	0.04	0.2	39.68
	RM16553	4	8638862	0.04	0.4	18.65
	RM247	12	3185384	0.02	0.22	16.12
GL	RM7419	1	27701259	0.03	0.47	12.32
	RM247	12	3185384	0.04	0.22	23.96
GW	RM541	6	22020833	0.03	0.42	5.44
	RM28561	12	24049993	0.05	0.33	10.03
TGW	RM3412	1	11582975	0.04	0.44	13.38
	RM247	12	3185384	0.05	0.22	24.53
	RM7210	4	28454768	0.05	0.29	11.37
YPP	RM214	7	12783492	0.03	0.36	8.15
	RM257	9	17719660	0.04	0.02	13.26
	RM21	11	24995833	0.02	0.27	18.41
AC	RM19	12	6095833	0.03	0.42	8.3
GT	RM19	12	6095833	0.05	0.42	7.77
AntC	RM11943	1	37851779	0.02	0.29	27.77
	RM28561	12	24049993	0.02	0.33	43.45
FlaC	RM212	1	33053493	0.04	0.33	11.35
	RM127	4	34529722	0.03	0.02	17.05
PheC	RM3400	3	17264981	0.04	0.2	13.66
ABTS	RM306	1	28612500	0.03	0.13	7.66
	RM211	2	4200000	0.03	0.22	16.51
	RM471	4	18824746	0.01	0.44	36.13

DTM: days to maturity; PH: plant height; PL: panicle length; GL: grain length; GW: grain width; TGW: 1000-grain weight; YPP: yield per plant; AC: amylose content; GT: gelatinization temperature; AntC: anthocyanin content; FlaC: flavonoid content; PheC: phenolic content; ABTS: 2,2'-azino-bis(3-ethylbenzothiazoline 6-sulfonic acid) content; MAF: minor allele frequency; PVE: phenotypic variance explained.

AntC, where it explained a substantial 43.45 % of the PV. Other notable associations included RM257 for DTM and YPP and RM19, which influenced both AC and GT. Regarding antioxidant components, RM127 (FlaC), RM3400 (PheC) and RM471 (ABTS) explained 17.05 %, 13.66 % and 36.13 % of the variance, respectively. These findings highlight key molecular markers with high PVE, underscoring their potential for marker-assisted selection in targeted rice breeding programs to enhance nutritional and yield-related traits.

Discussion

Understanding the genetic foundations of the naturally occurring diversity in the nutraceutical properties and health benefits of coloured grain rice across different rice accessions can accelerate functional breeding programs in Vietnamese. Recent studies have highlighted the importance of marker-trait interactions in identifying individual genotypes within closely and distantly related groups, which has been crucial for initiating new breeding programs in crops such as oilseed rape and rice (18, 41–43). Consequently, this study aims to analyse SSR/SNP markers associated with agronomic and health-related traits through marker-trait association analysis, facilitating the development of novel coloured rice varieties with superior agronomic and biochemical attributes.

Phenotypic variation

Genetic diversity is fundamental to successful crop breeding. Complex trait genetics exhibit polygenic and quantitative inheritance, allowing genotype selection within a panel (44). This study found significant variance in all agronomic characteristics and grain biochemical components among the 45 pigmented rice panel, supported by genetic diversity analysis. For example, the significant differences observed in YPP (2.49–67.1 g) and AntC (5.3–320.6 mg kg⁻¹) provides a robust basis for developing functional rice varieties. Days to maturity is a desired characteristics because they contribute to drought escape in the upland region. Overall, the observed phenotypic diversity in the tested panel was confirmed by analysing both traits and molecular variation.

Genetic diversity

This study is the first to use phenotypic and biochemical traits associated with SSR markers to evaluate genetic diversity and panel structure among 45 Vietnamese coloured rice accessions. Recent research has demonstrated that the genetic architecture of various rice accessions can be analysed using model-based and distance-based clustering approaches with SSR data (18, 42, 45–47). The AMOVA results ($p < 1$ %) indicated that 85 % of the total genetic variation resided within panels, while only 15 % existed among panels. Several similar results revealed higher variation within panels when they were compared among panels, in rice (42); in maize (43) and other crops (48). Researchers and breeders can utilise these findings to gain a better understanding of gene flow, evolutionary processes and the genetic composition of coloured rice panels.

Genetic diversity of coloured rice panels

This finding presents genetic diversity metrics for various loci in a panel, with key indices including Na, Ne, He, uHe, I and PIC. Among them, the mean He was identified as 0.33, which was a considerably moderate value. This could suggest that some of coloured rice accessions had a high homozygosity ratio, but lower than that reported in a previous study. Several studies reported a mean He of 0.47 (18) and 0.42 (42), suggesting that some individuals were not

homozygous. Moreover, the average I value of 0.48 indicated moderate genetic diversity in this study, but lower than 0.83 (18). Specific locations, such as RM19, RM240 and RM24330, exhibited high He and I value, reflecting significant localised genetic variability. The average PIC of 0.43 suggests that the 45 markers were highly informative for analysing the genetic structure in Vietnamese coloured rice. This value is superior to PIC ranges reported in similar rice studies (0.24–0.42) (18, 42) and maize (0.31) (43), demonstrating that SSR markers can effectively differentiate between coloured rice genotypes. These results indicated that SSR/SNP markers could effectively differentiate between coloured rice genotypes. Among the loci examined, primers like RM211, RM246 and RM3288 displayed higher PIC values, making them particularly valuable for future genetic research.

Comparing parameters (Na, Ne, He, uHe, I and % P) across groups provided valuable into population history and conservation. The high % P values suggested a greater proportion of polymorphic loci and genetic variation. The MR group consistently showed the highest genetic diversity across all indices, indicating the greatest allelic richness. In contrast, the TR group showed the lowest diversity, while the UP group maintained a moderate level, aligning closer to MR in certain metrics. These findings underscore the strategic importance of prioritising the diverse MR group while preserving rare alleles within the UP and TR groups to enhance the overall genetic pool for future breeding programs.

The pairwise genetic distances indicated that UP and MR are the most genetically similar, with the lowest Nei D (0.11) and highest Nei I (0.89). Conversely, the UP and TR showed the greatest genetic differentiation, with the highest Nei D (0.16) and the lowest Nei I (0.86). TR and MR had intermediate values (Nei D = 0.14, Nei I = 0.87). The PhiPT and LinPhiPT indices showed no to moderate genetic differentiation. Notably, both PhiPT and LinPhiPT values were recorded at 0.00 between (TR-MR), while PhiPT (0.18) and LinPhiPT (0.22), indicated more pronounced divergence. These results reveal complex relationships among the panels, which are further elucidated through PCoA and population structure modeling, providing a comprehensive understanding of the genetic architecture of Vietnamese coloured rice.

Genetic structure and relationship of coloured rice panels

Population structure analysis indicated that the highest Delta K value is observed at K = 3, strongly suggesting that 45 accessions are divided into three distinct genetic clusters. This grouping is essential for understanding the genetic architecture within the population and provides a framework for conservation and targeted breeding. The PCoA further supported this tri-cluster model, with the first three axes (PCo1, PCo2 and PCo3) explaining 30.90 %, 12.32 % and 11.32 % of the total genetic variance, respectively. These PCoA results might indicate a clear underlying structure, effectively differentiating the genotypes based on the genetic backgrounds. Additionally, the UPGMA clustering of 45 coloured rice lines suggested that shared a common genetic ancestry. These results indicated that the study panel consisted of genetically unique individuals, highlighting the significant role of geographical isolation and selection in shaping the diversity of Vietnamese coloured rice.

Relationship between the markers and the used traits

The MLM analysis provided significant insights into the genetic basis of complex traits in Vietnamese coloured rice. Grain yield is influenced by environmental and genetic factors, making it a

complex characteristic (49). In this study, several markers were associated with YPP, including RM7210 (chromosome 4), RM214 (chromosome 7), RM257 (chromosome 9) and RM21 (chromosome 11). Notably, RM21 explained 18.41 % of the PVE ($p = 0.02$), marking it as a promising candidate for yield improvement. The AntC trait is a key determinant of the functional value of coloured rice. The study identified two markers significantly associated with AntC: RM11943 on chromosome 1 and RM28561 on chromosome 12. Specifically, RM28561 accounted for a substantial 43.45 % of the phenotypic variation, providing strong evidence for a major effect locus. These findings complement previous reports (41), which identified *Ra* (chromosome 4) and *Rc* (chromosome 7) as primary loci regulating pericarp colour and nutritional quality. Furthermore, our study expanded the genetic understanding of polyphenols in coloured rice, which primarily consist of flavonoids (50, 51). While previous mapping in white rice identified only RM346 for phenolic content (41), our analysis revealed that RM3400 (chromosome 3) was significantly associated with PheC, explaining 13.66 % of the variance. Additionally, FlaC was linked to RM212 (chromosome 1) and RM127 (chromosome 4), with PVE values of 11.35 % and 17.05 %, respectively.

Furthermore, our study expanded the genetic understanding of polyphenols in coloured rice, which primarily consist of flavonoids (51). While previous mapping in white rice identified only RM346 for phenolic content (41), our analysis revealed that RM3400 (chromosome 3) was significantly associated with PheC, explaining 13.66 % of the variance. Additionally, FlaC was linked to RM212 (chromosome 1) and RM127 (Chromosome 4), with PVE values of 11.35 % and 17.05 %, respectively. By integrating these identified markers into marker-assisted selection (MAS), rice breeders can enhance both yield and antioxidant concentrations. Promising coloured genotypes such as Blau Sang, Nep Cam and Nep Do, which exhibit superior YPP and AntC levels, serve as excellent donor parental lines. Utilising these markers will facilitate the development of high-yielding, nutrient-dense rice varieties that serve to the increasing demand for healthier food products.

Conclusion

This study provides a comprehensive traits of the genetic diversity and population structure of 45 Vietnamese coloured rice accessions. The highly significant phenotypic variation and low coefficients of variation ($CV < 15\%$) underscore the strong genetic control over key agronomic and biochemical traits, particularly those related to nutritional value. The molecular analysis using simple sequence repeats (SSR) markers revealed a moderate-to-high level of polymorphism (mean PIC = 0.52), with most of the genetic variation (85 %) residing within panels by analysis of molecular variance (AMOVA). The high phenotypic variance explained (PVE) of markers such as RM214 for plant height (79 %) and RM28561 for anthocyanin content (AntC) (43.45 %). These specific markers, across with the identified promising accessions Blau Sang, Nep Cam and Nep Do, provide a valuable genetic resource for future biofortification and marker-assisted breeding programs.

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Authors' contributions

HND, CTN and HK carried out the molecular genetic studies, participated in the sequence alignment and drafted the manuscript. PTBT and NLH carried out the biomedical. HND and CTN participated in the sequence alignment. CTN, HND and NLH participated in the design of the study and performed the statistical analysis. HK and NLH conceived the study and participated in its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to make grammar corrections. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

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