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GENETIC VARIABILITY, TRAIT CORRELATION, AND PATH ANALYSIS OF GRAIN YIELD AND QUALITY-RELATED TRAITS IN IMPROVED SOUTHERN THAI RICE

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SUMMARY

Genetic variability and trait relationships were evaluated in 15 improved cultivars of Southern Thai indigenous rice (*Oryza sativa* L.). The study focused on grain yield and quality-related traits to reinforce rice breeding initiatives. Significant genetic variability was evident among the rice genotypes, with substantial genotypic and phenotypic coefficients of variation for the number of tillers and the number of ears, along with high heritability estimates for these traits. These indicate a robust genetic control and suitability for selection. Path coefficient analysis identified the number of tillers and the number of ears as primary contributors to seed weight per panicle. Protein content exhibited a complex relationship, receiving negative influences from seed weight per panicle and the number of seeds, suggesting their importance for improvement in grain yield. Correlation analysis revealed a considerable positive association between the number of tillers and the number of ears; however, a negative correlation between seed weight per panicle and protein content indicates a challenge in simultaneously improving both traits in rice. Principal component analysis confirmed seed weight per panicle and protein content were the primary drivers of the variability. The results will enable breeders to optimize grain yield and quality and develop high-yielding and nutritious rice cultivars for sustainable production.

Keywords: Rice (*O. sativa* L.), improved cultivars, genetic variability, path analysis, correlation, yield-related traits, seed-quality traits

Key findings: In rice (*O. sativa* L.), grain yield sustained direct influences from effective tillers and panicle weight, while significant variability in seed quality traits offers scope for further improvement. Promising genotypes, such as V14 with high protein, V10 (high lipid), and V15 with high amylose content, were successful in their identification as ideal candidates for targeted rice breeding programs.

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INTRODUCTION

Rice (*Oryza sativa* L.) plays a key role in global food security as a primary food source for over half of the world's population. Its widespread cultivation and consumption are a sign of its importance to diets, agricultural livelihoods, and human nutrition (Zeigler and Barclay, 2008). As expectations of the world population reaching over 9.7 billion by 2050 and climate change uncertainties escalate, a dire need to develop high-yielding rice cultivars with improved nutritional values that could endure diverse and harsh climatic conditions is crucial (Chauhan *et al.*, 2017; Shi *et al.*, 2023). Achieving these goals requires a good understanding of the genetic potential and variability of rice genotypes and their trait associations, as these factors provide the base for targeted breeding programs aimed at improving grain yield and quality.

In the research carried out for identifying potential genotypes and improving yield-related traits, the exploration of genetic variability and trait association is a critical endeavor in rice. Previous studies reported the evaluated rice genotypes exhibited remarkable genetic variability, which directly influences their physicochemical properties and yield potential (Sameera *et al.*, 2015). By dissecting the relationship among the important traits, identifying the vital relationship can be successful in producing high-yielding rice cultivars through breeding programs that can flourish in various environments. Consequently, this will develop sustainable agriculture and enhance global food security efforts (Chozin *et al.*, 2017; Yadav *et al.*, 2024).

In these efforts, the study of genetic variation is a critical component of crop improvement for selecting and combining desirable traits in a complex form to enhance rice crop performance (Yadav *et al.*, 2024). In rice, the agronomic traits, such as the number of productive tillers, the number of ears, and seed weight per panicle, have direct associations with the grain yield potential.

Meanwhile, seed quality traits, such as protein and amylose content and gel consistency, influence nutritional values, cooking quality, and consumer preference in rice (Dhanwani *et al.*, 2013; Shi *et al.*, 2013). However, the complex relationship among various traits frequently poses issues for breeders, since increasing one trait may inadvertently affect another due to the genetic trait correlation in rice (Nagaraju *et al.*, 2023).

In addressing these challenges, researchers use various statistical approaches, such as correlation and path analysis, to study the relationship between rice traits, measure their strengths and directions, and explore the direct and indirect effects on grain yield and quality traits (Garson, 2013). These biometrical analyses play a crucial role in determining important characteristics and comprehending the genetic framework of complex characters. As an example, in rice the tiller and ear counts appeared as positively correlated with grain yield traits, whereas seed quality parameters, such as amylose level and gelatinization temperature, were also essential to cooking and eating quality, affecting consumer choice (Li *et al.*, 2019).

Although several studies have had reports on the genetic variability and trait associations in rice, most have focused on yield components or quality traits in isolation, with limited integration of both trait groups within improved indigenous germplasms. In addition, Southern Thai indigenous rice cultivars are yet to be explored despite their adaptation to local agroclimatic conditions and their potential for improving grain nutritional quality. The following study addressed this gap by simultaneously assessing agronomic and seed quality traits using correlation, path coefficient, and principal component analysis for identifying key characteristics that control the trade-off between yield and quality. Although outcomes came from regionally adapted cultivars, the identified trait relationships and selection principles are broadly applicable to rice breeding programs targeting yield and nutritional improvement across diverse rice-growing environments.

MATERIALS AND METHODS

Breeding material and experimental design

The following study, carried out at the Rajamangala University of Technology Srivijaya, Thungyai Campus, Thailand (8°21'02.4"N, 99°25'06.4"E), used 15 improved indigenous rice cultivars (V1–V15). The seedbed, raised at 5–10 cm and puddled, has a cultivar sown separately. Thirty-day-old nursery seedlings, transplanted (one per hill) into 1 m × 1 m plots, had a randomized complete block design layout with three replications, maintaining 20- and 15-cm row and plant spacings, respectively. Standard fertilizer doses and agronomic practices succeeded in their equal applications to all rice experimental field plots.

Data collection and analysis

In each rice genotype and replication, three plants entailed random selection for recording data on various parameters. The recorded observations were on agronomic traits, such as plant height, the number of ears, the number of total tillers, ear length, the number of branches, seeds per ear, 100-seed weight, seed weight per panicle, and seed weight per plant. Additionally, recording 11 rice qualitative traits included protein, carbohydrate, ash, lipid, seed length, seed moisture, seed gel consistency, and seed shape. These underwent analysis in the laboratory according to the method of Wisetkomolmat *et al.*, 2022. The use of the R software (version 4.2.1) conducted the analysis of variance (ANOVA) according to the agricolae package (De-Mendiburu, 2023). Moreover, correlation and path coefficient analyses, as well as estimation of various genetic parameters, including genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), broad-sense heritability (H_b^2), and genetic gain, were performed (Khomphet, 2025). The correlation coefficient and principal component analysis, when performed, utilized the psych and ggbiplot packages (Revelle, 2024; Vu *et al.*, 2024).

RESULTS AND DISCUSSION

Analysis of variance and genetic variability

The presented study assessed the 15 rice genotypes for their genetic variability, heritability, and trait relationships across nine agronomic traits and 11 seed quality traits. Significant genetic variability was evident among the rice genotypes, providing a broad scope for further selection. High heritability estimates for traits like plant height and seed weight revealed considerable genetic control and confirmed them to be more responsive to breeding efforts (Visscher *et al.*, 2008). Trait correlations, such as plant height and seed weight, offered insights for balanced selection in the rice genotypes.

Agronomic traits

The analysis of variance showed significant differences among the genotypes for various traits, highlighting substantial genetic variability in rice cultivars (Table 1). Traits like the number of ears, the number of tillers, and 100-seed weight exhibited highly significant variations, with high treatment mean squares and low error mean squares. The results suggested these traits gained considerable influence from the rice genotypic factors.

The genetic variability analysis further revealed that traits, such as the number of ears, the number of tillers, and seed weight per plant, had the highest genotypic (GCV) and phenotypic (PCV) coefficients of variation (Table 1). For instance, the number of ears had a GCV of 27.68% and PCV of 34.06%, while the number of tillers showed the GCV of 32.68% and PCV of 38.45%. These high GCV and PCV values revealed these traits were highly variable and can respond well to intensive selection. Additionally, the high heritability values were notable for the traits of the number of ears (66.03%), the number of tillers (72.24%), and seed weight per plant (48.53%), also confirming their genetic potential.

Table 1. Analysis of variance and genetic variability on observed traits of improved cultivars of Southern Thai indigenous rice.

Traits	Trait MS	Error MS	GCV	PCV	H _b ²	GA	GAM
NoE	210.93**	32.17	27.680:H	34.063:H	66.035:H	12.969:M	46.336:H
HT	353.34*	164.53	6.330:L	10.501:M	36.334:M	10.707:M	7.860:L
NoT	435.65**	49.41	32.676:H	38.445:H	72.239:H	19.865:M	57.211:H
LtE	21.70**	6.93	8.783:L	13.856:M	40.182:M	2.872:L	11.469:M
NoB	6.17**	1.34	12.641:M	17.050:M	54.970:M	1.941:L	19.307:M
NoS	1,530.09*	890.95	13.668:M	28.225:H	23.449:L	15.590:M	13.634:M
WS100	0.10*	0.06	8.386:L	17.821:M	22.142:L	0.118:L	8.129:L
WSE	0.48*	0.42	12.584:M	36.987:H	11.575:L	0.150:L	8.819:L
WSP	1,111.59**	298.04	35.092:H	50.373:H	48.532:M	23.744:H	50.360:H
PT	2.47*	1.03	6.654:L	12.002:M	30.739:M	0.783:L	7.560:L
LI	0.14*	0.08	9.559:L	22.799:H	17.580:L	0.117:L	8.257:L
CB	3.97*	2.11	1.016:L	2.173:L	21.859:L	0.749:L	0.978:L
ASH	0.08*	0.04	9.943:L	21.587:H	21.216:L	0.104:L	9.435:L
HuS	1.68**	0.41	6.149:L	8.590:L	51.243:M	0.963:L	9.068:L
LS	0.02 ^{ns}	0.03	1.038:L	2.666:L	15.355:L	0.048:L	0.843:L
WS	0.01*	0.003	1.4161:L	3.411:L	17.237:L	0.024:L	1.211:L
TS	0.001*	0.001	0.837:L	2.015:L	17.249:L	0.012:L	0.716:L
Sh	0.008*	0.008	0.560:L	3.109:L	3.245:L	0.006:L	0.208:L
Gel	253.10*	259.09	2.495:L	26.081:H	-0.916:L	-0.303:L	-0.492:L
Amy	2.45*	1.62	4.179:L	10.190:M	16.821:L	0.469:L	3.531:L

^{ns}not significant, **, ** significant at $p < 0.05$ and $p < 0.01$, respectively. High: H, Moderate: M, Low: L. NoE: Number of ears, HT: Plant height, NoT: Number of tillers, LtE: Ear length, NoB: Number of branches, NoS: Number of seeds/panicle, WS100: 100-seed weight, WSE: Seed weight/panicle, WSP: Seed weight/plant, PT: Protein content, LI: Lipid content, CB: Carbohydrate content, ASH: Ash content, HuS: Seed moisture content, LS: Seed length, WS: Seed width, TS: Seed thickness, Sh: Seed shape, Gel: Gel consistency, and Amy: Amylose content.

Genetic influence is the source of phenotypic variability in traits, such as the number of ears, the number of tillers, and 100-seed weight, as confirmed by significant rice genotypic differences and the highest heritability and genetic gain for these traits. The considerable genetic control and high heritability of the traits of number of ears and number of tillers make them ideal targets for breeding. Path analysis further revealed the number of ears and the number of tillers have substantial direct effects on seed weight per plant, underscoring their importance in determining grain yield in rice. These results align with previous findings that also highlighted the positive role of tiller number and effective tillers in enhancing rice grain yield (Kacharabhai, 2015; Tripathi *et al.*, 2018).

Seed quality traits

The study also highlighted the importance of seed quality traits in determining nutritional values, cooking quality, and marketability of the rice produce. Protein content, being a key indicator of nutritional value, ranged from 9.22% to 12.43% among the rice genotypes, and the genotype V14 exhibited the highest protein content (12.43%), approving it as a promising candidate genotype for improving dietary quality (Figure 1). Lipid content (LI), which influences the energy content and storage stability, varied from 1.20% to 1.99% among the rice genotypes, and the genotype V10 showed the highest lipid content (1.99%). The highest variability (CV = 20.11%) suggested the potential for enhancing energy density, though higher lipid content could also affect the shelf life and texture. Similarly, the amylose content ranged from 11.94% to 15.29%; V15 showed the highest, producing firmer cooked rice.

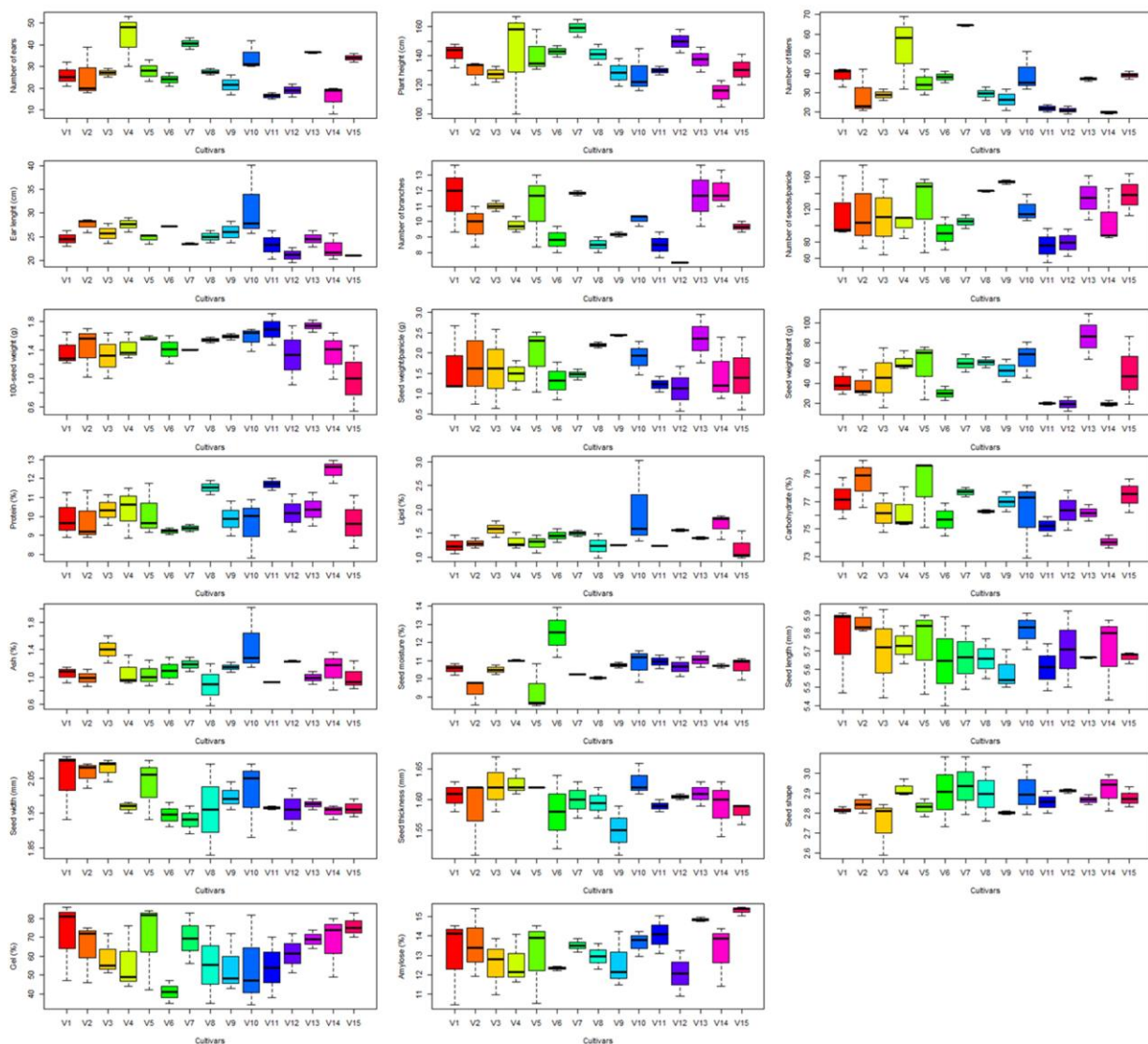


Figure 1. Box plots on agronomic traits of Thai indigenous rice cultivars (V1-V15), showing variability across traits. Boxes indicate the interquartile range, central lines represent medians, whiskers show minimum and maximum values, and colors denote different cultivars.

Rice seed dimensions, including length, width, and thickness, expressed low variability, and the genotypes V2, V3, and V4 revealed the longest, widest, and thickest grains, respectively. However, seed weight per panicle displayed the highest variability (CV = 38.16%), highlighting the differences in grain filling efficiency. Seed shape, determined by the length-to-width ratio, ranged from 2.75 to 2.94 among the rice genotypes, and the genotype V7 provided the highest ratio (2.94),

confirming it as an ideal genotype for markets favoring elongated rice grains (Figure 1). Gelatinization temperature (Gel) and gel consistency also varied, and genotype V15 requires longer cooking times and produces firmer cooked rice, suitable for specific culinary uses.

The nutritional value of rice, cooking quality, and marketability depend on seed quality characteristics, such as protein content, amylose content, and seed size (Saha *et al.*,

2019). The results enunciated with substantial differences occurred in these characteristics, which provide the possibility of selective breeding. The rice cultivars V14, V10, and V15 were high-yielding and observed with the highest protein, amylose content, and desirable seed size genotypes with the potential to breed in the future (Wimalasekera, 2015).

Path analysis

Path analysis was performed to determine the direct and indirect impacts of different traits on seed weight per plant and protein content, which were identified as the key factors affecting rice grain yield and quality. The path analysis revealed the number of ears had the highest direct effect on single panicle weight (0.849), indicating that an increased number of effective tillers directly contributes to higher single panicle weight, a key component of yield (Table 2). These results align with the considerable positive correlation between the number of effective tillers and single panicle weight observed in the presented study. Research by Akinwale *et al.* (2011) supported this, who highlighted the importance of the number of effective tillers in enhancing yield potential. Chuchert *et al.* (2018) reported the highest direct effects on yield refer to the number of spikelets per panicle and the number of panicles per plant. The direct effect of the number of tillers on single panicle weight was negative (-0.295), suggesting that while increasing the number of tillers may not directly improve single panicle weight, it could still play a positive role through indirect pathways. Additionally, single panicle weight itself showed a significant direct effect (1,111.59**), emphasizing its importance as a yield-determining trait. The rice traits of plant height and the number of branches have a minor influence on single panicle weight indirectly through their effects on plant architecture and resource allocation. The value of residual effect (1-R²) in the single panicle weight was 2.80%, which revealed these traits explain maximal variation in single panicle weight, with a low impact of environmental factors.

For protein content, the direct effects of the number of effective tillers (-0.047) and single panicle weight (-0.009) were significantly negative and relatively small in magnitude compared with their effects on the single panicle weight (Table 3). These results suggested these traits have some influence on protein content, and their impact was not very evident on single panicle weight. Indirect effects on protein content resulted from traits, such as taller plants and the number of effective tillers, indicating that improving these traits could indirectly enhance the protein content. For example, taller plants and those with more tillers might allocate more resources to seed development, thereby improving protein content. The residual effect value for the protein content in the path analysis model was 3.40%, indicating the comprising traits explain a big portion of the variability in protein content. According to Mahesh *et al.* (2022), the complexity of protein content as a trait was underscored by its dependence on the combination of genetic, environmental, and physiological factors. Kumar *et al.* (2018) emphasized that protein content and other seed quality parameters received influences from complex interactions between a plant's genetic makeup and environmental factors. This means that soil quality, climate, and farming practices may have a substantial impact on the rice grain's protein levels. Singh *et al.* (2019) pointed out that efforts to improve yield-related traits, such as the number of tillers and seed weight, can sometimes lead to a reduction in seed quality traits like protein content. This emphasizes the delicate balance that breeders must achieve between increasing output and retaining nutritional values.

Principal component analysis

The principal component analysis (PCA) biplot showed the first two principal components capture a high amount of total variance (Figure 2). Dim 1 (23%) appeared closely correlated with agronomic characteristics, including plant height and the number of tillers, while Dim 2 (17.1%), with associated seed quality traits, included 100-seed weight and protein content,

Table 2. Path analysis on seed weight per plant of improved cultivars of Southern Thai indigenous rice.

Traits	NoE	HT	NoT	LtE	NoB	NoS	WS100	WSE	PT	LI	CB	ASH	HuS	LS	WS	TS	Sh	Gel	Amy	R
NoE	0.849	0.051	-0.257	-0.014	0.009	0.013	-0.060	-0.012	-0.002	0.000	0.007	0.010	0.004	0.021	-0.010	-0.013	-0.006	0.003	0.018	0.80**
HT	0.348	0.124	-0.162	-0.001	-0.002	-0.054	-0.034	-0.040	-0.003	0.001	0.014	0.004	-0.002	-0.025	0.049	-0.004	-0.035	-0.004	-0.024	0.21
NoT	0.739	0.068	-0.295	-0.014	0.014	-0.013	-0.057	-0.026	-0.003	0.000	0.009	0.009	0.009	0.014	0.016	-0.011	-0.031	0.002	0.010	0.56*
LtE	0.187	0.002	-0.062	-0.066	0.004	0.026	0.064	0.040	-0.003	0.000	0.011	0.001	0.010	0.058	-0.059	-0.002	0.013	0.000	-0.003	0.36
NoB	0.144	-0.005	-0.080	-0.005	0.052	0.042	0.017	0.028	0.000	-0.001	0.006	0.010	-0.019	-0.010	-0.014	-0.003	0.025	0.003	-0.001	0.36
NoS	0.034	-0.021	0.012	-0.005	0.007	0.320	0.131	0.217	0.000	0.000	0.002	-0.009	-0.009	-0.008	-0.004	0.009	0.010	0.003	0.010	0.65**
WS100	-0.153	-0.012	0.050	-0.013	0.003	0.125	0.335	0.165	0.001	-0.001	-0.005	-0.001	-0.004	-0.033	0.030	-0.001	-0.010	-0.004	-0.013	0.31
WSE	-0.042	-0.021	0.032	-0.011	0.006	0.295	0.235	0.236	0.001	0.000	0.000	-0.004	-0.008	-0.014	0.002	0.007	0.006	0.001	0.001	0.70**
PT	-0.212	-0.046	0.097	0.025	-0.003	0.010	0.044	0.017	0.008	-0.001	-0.036	-0.005	0.000	-0.029	0.010	-0.005	0.015	-0.001	0.003	-0.32
LI	0.008	-0.012	0.009	0.004	0.004	-0.016	0.034	0.009	0.001	-0.006	-0.022	0.108	0.006	-0.016	0.069	-0.011	-0.069	-0.006	-0.023	-0.02
CB	0.127	0.037	-0.053	-0.015	0.006	0.016	-0.034	0.000	-0.006	0.003	0.048	-0.034	-0.049	0.053	-0.049	0.001	0.010	0.004	0.005	-0.35
ASH	0.068	0.004	-0.021	-0.001	0.004	-0.022	-0.003	-0.007	0.000	-0.006	-0.013	0.126	-0.003	-0.021	0.047	-0.014	-0.040	-0.008	-0.032	0.02
HuS	0.034	-0.002	-0.029	-0.007	-0.011	-0.032	-0.013	-0.021	0.000	0.000	-0.027	-0.004	0.088	-0.047	0.039	0.013	-0.002	-0.002	0.004	-0.15
LS	0.085	-0.015	-0.021	-0.018	-0.003	-0.013	-0.054	-0.017	-0.001	0.001	0.012	-0.013	-0.020	0.206	-0.095	-0.025	-0.073	0.010	0.043	0.05
WS	0.042	-0.031	0.024	-0.020	0.004	0.006	-0.050	-0.002	0.000	0.002	0.012	-0.030	-0.018	0.099	-0.197	-0.001	0.135	0.009	0.025	0.05
TS	0.212	0.010	-0.062	-0.003	0.003	-0.058	0.003	-0.033	0.001	-0.001	0.000	0.033	-0.022	0.099	-0.002	-0.052	-0.083	-0.001	0.007	0.33
Sh	0.025	0.021	-0.044	0.004	-0.006	-0.016	0.017	-0.007	-0.001	-0.002	-0.002	0.024	0.001	0.072	0.128	-0.021	-0.208	-0.002	0.008	-0.01
Gel	0.144	-0.024	-0.035	0.000	0.009	0.045	-0.067	0.007	0.000	0.002	0.010	-0.052	-0.008	0.103	-0.097	0.002	0.025	0.019	0.057	0.20
Amy	0.195	-0.037	-0.035	0.003	-0.001	0.042	-0.054	0.002	0.000	0.002	0.003	-0.050	0.004	0.111	-0.063	-0.005	-0.021	0.014	0.080	0.36

R = Correlation, *** correlation at $p < 0.05$ and 0.01 . Residual effects ($1-R^2$) = 2.80%. Direct (bold and diagonal) and indirect effect path coefficients. NoE: Number of ears, HT: Plant height, NoT: Number of tillers, LtE: Ear length, NoB: Number of branches, NoS: Number of seeds/panicle, WS100: 100-seed weight, WSE: Seed weight/panicle, WSP: Seed weight/plant, PT: Protein content, LI: Lipid content, CB: Carbohydrate content, ASH: Ash content, HuS: Seed moisture content, LS: Seed length, WS: Seed width, TS: Seed thickness, Sh: Seed shape, Gel: Gel consistency, and Amy: Amylose content.

Table 3. Path analysis on protein content of improved cultivars of Southern Thai indigenous rice.

Traits	NoE	HT	NoT	LtE	NoB	NoS	WS100	WSE	WSP	LI	CB	ASH	HuS	LS	WS	TS	Sh	Gel	Amy	R
NoE	-0.047	-0.004	0.077	0.003	-0.004	-0.058	0.133	-0.095	-0.006	-0.003	-0.211	-0.015	-0.033	0.134	-0.090	0.007	-0.049	-0.013	0.026	-0.49
HT	-0.019	-0.010	0.048	0.000	0.001	0.246	0.074	-0.322	-0.001	0.034	-0.423	-0.006	0.017	-0.161	0.448	0.002	-0.279	0.015	-0.034	-0.47
NoT	-0.041	-0.006	0.088	0.003	-0.006	0.058	0.125	-0.209	-0.004	0.010	-0.254	-0.013	-0.083	0.094	0.144	0.006	-0.246	-0.009	0.013	-0.56**
LtE	-0.010	0.000	0.018	0.013	-0.002	-0.116	-0.140	0.322	-0.002	0.020	-0.324	-0.002	-0.091	0.376	-0.538	0.001	0.099	0.000	-0.004	-0.34
NoB	-0.008	0.000	0.024	0.001	-0.022	-0.188	-0.037	0.228	-0.002	-0.027	-0.169	-0.015	0.174	-0.067	-0.126	0.001	0.197	-0.013	-0.001	0.01
NoS	-0.002	0.002	-0.004	0.001	-0.003	-1.449	-0.287	1.745	-0.006	0.017	-0.070	0.013	0.083	-0.054	-0.036	-0.005	0.082	-0.011	0.015	-0.12
WS100	0.009	0.001	-0.015	0.003	-0.001	-0.565	-0.736	1.327	-0.004	-0.034	0.141	0.002	0.033	-0.215	0.269	0.000	-0.082	0.016	-0.018	0.22
WSE	0.002	0.002	-0.010	0.002	-0.003	-1.333	-0.515	1.896	-0.007	-0.014	0.000	0.006	0.074	-0.094	0.018	-0.004	0.049	-0.002	0.001	-0.02
WSP	-0.029	-0.002	0.039	0.003	-0.004	-1.014	-0.339	1.365	-0.009	-0.024	-0.099	-0.011	0.017	-0.013	-0.018	0.001	0.016	-0.011	0.021	-0.32
LI	0.000	0.001	-0.003	-0.001	-0.002	0.072	-0.074	0.076	-0.001	-0.339	0.648	-0.158	-0.058	-0.107	0.628	0.006	-0.542	0.026	-0.032	-0.04
CB	-0.007	-0.003	0.016	0.003	-0.003	-0.072	0.074	0.000	-0.001	0.156	-1.409	0.050	0.463	0.349	-0.448	0.000	0.082	-0.016	0.007	-0.65**
ASH	-0.004	0.000	0.006	0.000	-0.002	0.101	0.007	-0.057	-0.001	-0.292	0.380	-0.184	0.025	-0.134	0.431	0.007	-0.312	0.032	-0.045	-0.33
HuS	-0.002	0.000	0.009	0.001	0.005	0.145	0.029	-0.171	0.000	-0.024	0.789	0.006	-0.828	-0.309	0.359	-0.007	-0.016	0.007	0.006	-0.13
LS	-0.005	0.001	0.006	0.004	0.001	0.058	0.118	-0.133	0.000	0.027	-0.366	0.018	0.190	1.342	-0.861	0.013	-0.575	-0.039	0.060	-0.22
WS	-0.002	0.003	-0.007	0.004	-0.002	-0.029	0.110	-0.019	0.000	0.119	-0.352	0.044	0.166	0.644	-1.794	0.000	1.068	-0.038	0.036	-0.17
TS	-0.012	-0.001	0.018	0.001	-0.001	0.261	-0.007	-0.265	0.000	-0.075	0.014	-0.048	0.207	0.644	-0.018	0.026	-0.657	0.003	0.010	-0.01
Sh	-0.001	-0.002	0.013	-0.001	0.003	0.072	-0.037	-0.057	0.000	-0.112	0.070	-0.035	-0.008	0.470	1.166	0.011	-1.643	0.009	0.011	0.05
Gel	-0.008	0.002	0.011	0.000	-0.004	-0.203	0.147	0.057	-0.001	0.112	-0.282	0.075	0.074	0.671	-0.879	-0.001	0.197	-0.078	0.079	0.03
Amy	-0.011	0.003	0.011	-0.001	0.000	-0.188	0.118	0.019	-0.002	0.098	-0.085	0.074	-0.041	0.725	-0.574	0.002	-0.164	-0.055	0.112	0.03

R = Correlation, *** correlation at $p < 0.05$ and 0.01 . Residual effects ($1-R^2$) = 3.40%. Direct (bold and diagonal) and indirect effect path coefficients. NoE: Number of ears, HT: Plant height, NoT: Number of tillers, LtE: Ear length, NoB: Number of branches, NoS: Number of seeds/panicle, WS100: 100-seed weight, WSE: Seed weight/panicle, WSP: Seed weight/plant, PT: Protein content, LI: Lipid content, CB: Carbohydrate content, ASH: Ash content, HuS: Seed moisture content, LS: Seed length, WS: Seed width, TS: Seed thickness, Sh: Seed shape, Gel: Gel consistency, and Amy: Amylose content.

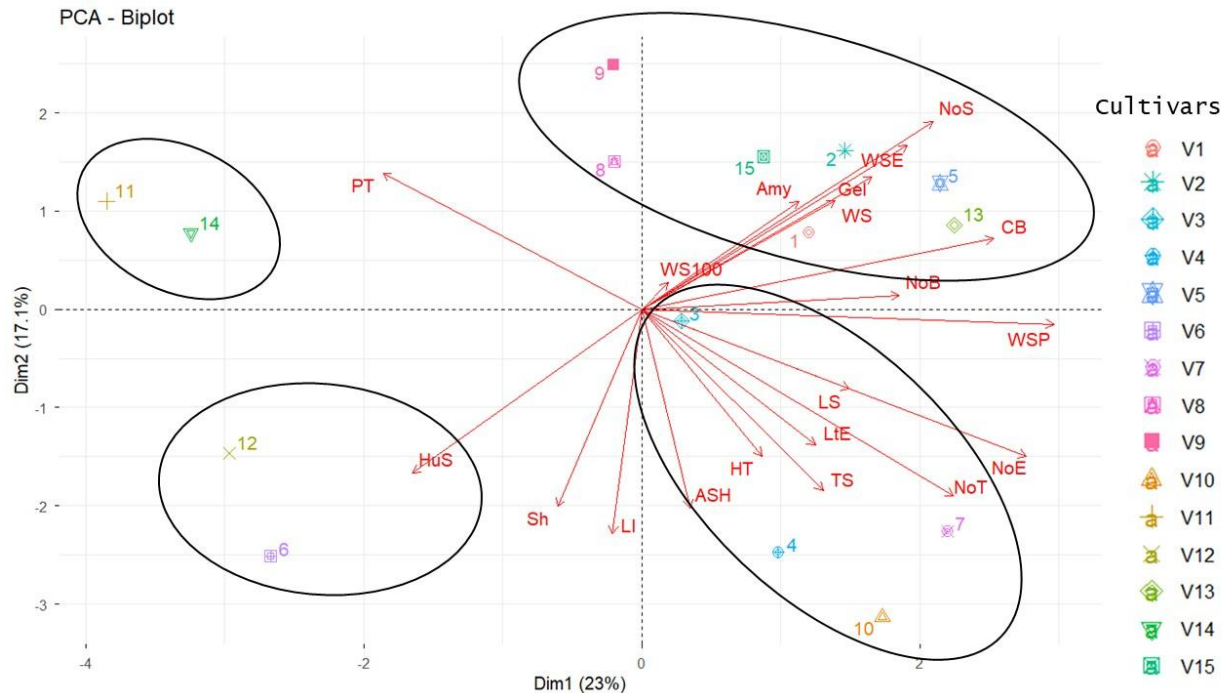


Figure 2. Principal component analysis on observed traits of Thai indigenous rice. NoE: Number of ears, HT: Plant height, NoT: Number of tillers, LtE: Ear length, NoB: Number of branches, NoS: Number of seeds/panicle, WS100: 100-seed weight, WSE: Seed weight/panicle, WSP: Seed weight/plant, PT: Protein content, LI: Lipid content, CB: Carbohydrate content, ASH: Ash content, HuS: Seed moisture content, LS: Seed length, WS: Seed width, TS: Seed thickness, Sh: Seed shape, Gel: Gel consistency, and Amy: Amylose content.

providing an obvious separation that enhanced the understanding of trait interrelationships. In accordance with their positions, it was possible to identify Group 1 (high agronomic performance genotypes, such as V1, V2, and V3) aligned with taller plants and the number of tillers; Group 2 (seed quality focus: V4, V5, V6) that corresponds to the contribution of both trait categories; and Group 3 (balanced traits: V7, V8, V9), which can be described as moderate contributors. The correlation coefficient of the number of effective tillers and the number of tillers was very positive, and the number of effective tillers might increase with breeding of a high number of tillers, thus increasing grain yield. However, the traits of single panicle weight and protein content showed a positive correlation, and breeding to enhance them might lead to an increase in grain yield and quality. Small values of residual effects in path analysis revealed the

environment had a low impact on considered traits. These results were different from the findings of Sadimantara *et al.* (2021), who observed that environmental variability has a significant impact on tiller-related traits, and they recommended that future analyses must consider the site-specific features. Tiwari *et al.* (2022) observed that the optimality of protein content and single panicle weight depends upon the genotype-by-environment interactions (GEI), thus necessitating integration of site-specific data into future studies.

CONCLUSIONS

The study highlighted the importance of improving agronomic and seed quality traits through breeding to improve the grain yield and nutritional quality in rice. The number of

effective tillers and single panicle weight significantly influenced grain yield. Similarly, promising genotypes identified in this study (V14, V10, and V15) require further evaluation in multi-location and multi-season evaluation trials to assess the stability of their yield potential and nutritional consistency. They should also undergo genotype × environment interactions before further potential incorporation into formal rice breeding programs. Moreover, multi-trait selection obtained considerable support from significant correlation among the number of tillers, the number of effective tillers, single panicle weight, and protein content. The residual effect values were low, which could indicate the low impact of additional environmental effects on the study results. These insights can help the breeders to produce rice genotypes with enhanced grain yield, nutrition, and market attractiveness to ensure global food security.

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