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Research Article

Intercorrelation among *MOC1*, *MOC3*, and *TN1* Gene Expressions with the Architecture of Five Rice Genotypes

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ABSTRACT

Tillering is an important rice characteristic that determines the architecture of the rice plant and affects yields. *MONOCULM 1* protein encoded by the *MOC1* gene interacts with *MOC3* protein to influence axillary meristem formation and promote tillering. *TILLER NUMBER 1* protein encoded by the *TN1* gene to inhibit rice tillering. This study aimed to analyze the expression of tillering regulatory genes *MOC1, MOC3,* and *TN1* in five rice genotypes based on their morphological characteristics. RNA was isolated at the pre tillering and tillering stages. Gene expression was analyzed using RT-PCR. The results showed that Hawara Bunar and Landeo rice produced fewer tillers (3-5) than IR64, Towuti, and Tukad Petanu (7-9). Although the number of tillers was lower, the grain weight produced by the Hawara Bunar rice cultivar was higher than that of the other four rice cultivars. The formation of a few tillers in Hawara Bunar and Landeo rice was influenced by low expression of the tiller regulatory genes *MOC1* and *MOC3* and by high expression of the *TN1* gene, which inhibits tiller formation. These findings reveal a novel relationship between the expression of *MOC1, MOC3,* and *TN1* genes and tiller formation, highlighting Hawara Bunar as a promising breeding line for rice with ideal plant architecture.

1. Introduction

Rice (*Oryza sativa* L.) is of staple food consumed by more than half of the world's population in 100 countries, and 90% of the world's rice is produced in Asian countries (Mohidem *et al.* 2022). As one of the rice-producing countries, Indonesia strives to increase rice production. However, data from the Indonesian Central Statistics Agency shows that 2023's rice production decreased by 2.05% from the 2022 rice production (BPS 2023).

Tillering is an essential characteristic that can determine the architecture of cereal plants, such as rice, affecting the panicle formation and yield (Takai 2024). In some members of Poaceae, such as rice, the axillary meristem is a vegetative structure that forms branches from the leaf axils and tillers from the lower parts of leaves. The formation of tillers occurs through two stages of development: initiation of axillary meristem development and growth of axillary shoots into tillers. The formed tillers will then produce panicles and rice grains until they finally produce yields (Yuan *et al.* 2024).

Several genes regulate rice tillering, which determines rice architecture. *MONOCULM 1 (MOC1)* gene, located on rice chromosome 6 (Os6g40780), encodes a transcription factor of the GRAS family gene involved in the formation of axillary meristems and promotes tillering growth. The presence of *moc1* mutants results of a single-stem phenotype and a loss of tiller formation (Li *et al.* 2003). *MOC3* gene (Os04g56780) on rice chromosome 4 is a homologue of the *WUSCHEL*

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(OsWUS) gene in rice, which is essential to promote the axillary meristem formation by expressing the *FON1* gene (Lu *et al.* 2015; Shao *et al.* 2019). Several genes have also been identified as negatively regulating rice tillering. The *TILLER NUMBER 1 (TN1)* gene is located on rice chromosome 1 (Os01g42460) and interacts with the TIF1 gene, activating the expression of the *D14* gene and inhibiting the growth of rice tillers. The *tn1* mutant increases the number of tillers, and the overexpression of *TN1* causes a decrease in the number of tillers (Zhang *et al.* 2023). Although these regulatory mechanisms have been well characterized in model rice varieties, the expression profiles of *MOC1, MOC3,* and *TN1* genes in Indonesian local rice cultivars remain poorly understood. Considering the unique genetic diversity of Indonesian rice, investigating these genes could reveal distinct regulatory patterns of tillering specific to local varieties.

The potential of the gene candidates involved in tiller formation needs to be further analyzed, especially in local rice cultivars. Hawara bunar is one of the local rice cultivars (cv.) with a habitus height of around 150 cm, and is tolerant of aluminum and drought stress (Fendiyanto *et al.* 2019; Miftahudin *et al.* 2020; Satrio *et al.* 2021). The Hawara Bunar rice cultivar's ability to withstand aluminum stress is influenced by an aluminum stress tolerance gene known as the *B11* gene (Miftahudin *et al.* 2007; Wahyuningtyas *et al.* 2016; Siska *et al.* 2017). Landeo rice cultivar is a local rice cultivar with morphological characteristics similar to those of the rice cv. Hawara Bunar, with a habitus height of around 123 cm. Both cultivars have few productive tillers. The Towuti rice cultivar, with a short height of around 115-120 cm, and the Tukad Petanu rice cultivar, with a plant height of around 90-100 cm, have similar morphological characteristics to the IR64 rice cultivar and produce a greater number of productive tillers than the Hawara Bunar rice cultivar (Sujitno *et al.* 2011; Ladja and Widiarta 2012; Lestari and Ubaidillah 2022). The current information of the expression profiles of the tiller-number-regulating genes can be used effectively to determine their effects on axillary meristems and productive tiller formation. This study aimed to analyze the expression profile of rice tiller-regulating genes *MOC1, MOC3,* and *TN1* in five local Indonesian rice genotypes: Hawara Bunar, IR64, Landeo, Towuti, and Tukad Petanu to provide new insights into the molecular regulation of tiller development. In addition, we also analyzed the relationship between the expression pattern of the three genes and several morphological characters of rice.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Rice seeds from Hawara Bunar, IR64, Landeo, Towuti, and Tukad Petanu cvs. were obtained from the collection of the Plant Physiology and Genetics laboratory of the Department of Biology, Bogor Agricultural University. Rice seeds were planted in pots and grown in a greenhouse following the lowland rice cultivation technique. Rice plants were regularly irrigated and fertilized with Urea, NPK, and KCl based on the recommended rates for lowland rice provided by the Indonesian Ministry of Agriculture (Regulation No. 40/Permentan/OT.140/4/2007). The recommended field application rates were subsequently converted to pot-based doses according to pot volume and planting density.

2.2. Morphological Observation

Six replications were used for each rice cultivar, and morphological traits were observed weekly from two weeks after planting until harvest. The observed traits included plant height, number of tillers, number of productive tillers, number of nodes, panicle length, grain weight per panicle, grain weight per plant, number of filled and empty grains, and the weight of 100 grains.

2.3. Total RNA Isolation and cDNA Synthesis

Young leaf samples were taken from two stages of plant development: the pre tillering phase (30 DAP) and the tillering phase (50 DAP). For each treatment, three biological replicates were prepared, and total RNA was isolated using GENEzol™ reagent (Geneaid, Taiwan). The quality of the RNA was analyzed through electrophoresis using 1.5% agarose, and the concentration and purity of total RNA were analyzed using a MaestroNano Spectrophotometer (Maestrogen, Taiwan) at 260 and 280 nm. One microgram of total RNA was used for cDNA synthesis with the RevertAid First Strand cDNA Synthesis Kit (Thermo Fisher Scientific, USA) following the manufacturer's instructions using Oligo (dT)18. The concentration and purity of the cDNA were measured and analyzed using the same method as RNA analysis.

2.4. Gene Expression Analysis

Gene expression was analyzed by quantitative real-time PCR (qRT-PCR) using the SensiFAST SYBR Lo-ROX Kit (Meridian Bioscience, USA) on a QuantStudio 5 Real-Time PCR System (Applied Biosystems, USA). Each sample was analyzed with three biological replicates and two technical replicates. Primers sequences for the target genes (*MOC1, MOC3,* and *TN1*) and the housekeeping gene (ACT) are listed in Table 1. The qRT-PCR program was set as follows: pre-denaturation at 95°C for 30 sec, followed by 60 cycles of denaturation at 95°C for 10 sec, annealing at 60°C for 30 sec, and extension at 72°C for 30 sec. Gene expression levels were quantified using the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen 2001).

2.5. Data Analysis

Statistical data analysis was performed using One-Way ANOVA in R software version 4.4.1 (Fendiyanto *et al.* 2019). Data showing significant differences were further tested using Tukey's HSD test of $p \leq 0.05$. Pearson correlation analysis between gene expression and morphological characters was also conducted in R software at a significance level of 5%.

3. Results

3.1. Morphological Characteristics of Five Rice Genotypes

Morphological characters of five rice genotypes were observed from the vegetative phase to the generative phase. Differences in plant height and number of tillers in the vegetative phase are the main characteristics that distinguish the five rice genotypes (Figure 1A). Hawara Bunar and Landeo rice cultivars (cvs.) are two tall-habit rice genotypes with average heights of 181 and 170.6 cm, respectively. The three other genotypes: IR64, Towuti, and Tukad Petanu rice cultivars (cvs.) have shorter habitus with an average of 118 cm, 100 cm, and 98 cm, respectively (Figure 1B). The differences in morphological characters of the vegetative phase are also evident in the number of tillers and the number of productive tillers, where the Hawara Bunar and Landeo rice cvs have fewer tillers, i.e., 3-4. In contrast, Tukad Petanu, Towuti, and IR64 rice cvs have significantly higher numbers of tillers compared to the former cultivars (Figure 1C). Hawara Bunar and Landeo rice cvs. have a tall habit, with approximately 6-7 nodes per plant. On the contrary, IR64, Towuti, and Tukad Petanu rice cvs. have fewer nodes, around 4-5 nodes per plant (Figure 1E).

This study examined the relationship between the tiller number and several reproductive characters, including panicle length, the number of grains, the weight of grains per panicle, the weight of grains per plant, and the weight of 100 grains.

Hawara Bunar rice cv. with a small number of tillers produces longer panicle, higher grain weight per panicle, grain weight per plant, weight of 100 grains, and filled grains or total compared to the other cultivars (Figure 2). Interestingly, the grain weight per plant of the Hawara Bunar rice cv. (small number of tillers) was almost the same as the weight of Towuti rice cv. (large number of tillers) (Figure 2E). A significant difference was observed in Tukad Petanu rice cv., which had the highest number of tillers among the other cultivars. Tukad Petanu rice cv. produces more panicles, but the panicles are relatively short. The size of the panicle affects the quantity of grain produced, with smaller grain size, lighter grain weight, and more empty grain than other cultivars.

3.2. Quality and Quantity of Total RNA

Total RNA was isolated at two stages of seedling development: pre-tillering and tillering. The good quality of total RNA from rice leaves is indicated by the presence of 18S and 5.8S rRNA bands and mRNA in the agarose gel electrophoresis (Figure 3). In addition to

Table 1. The primer pairs for gene expression analysis of *MOC1, MOC3, TN1,* and *ACT* genes in five rice genotypes

Target gene	Locus	Oligonucleotide sequence (5' to 3')	Tm (°C)	Product size (bp)
MOC1	Os06g40780	F: ACTGGCCTCGAGTTTCACCC	59.7	114
		R: CATGGCCTTCACCCACTTCA	57.7	
MOC3	Os04g56780	F: GGTGAGCATGAGCAGTAGTAGG	57.0	150
		R: TGCTACCTCCAACACCATTACG	56.9	
TN1	Os01g42460	F: TTCAGCCATTCCCTTTCCC	55.1	100
		R: TTTGGACACACTCTCCTCTTTC	54.5	
ACT	Os03g50885	F: CCTTCAACACCCCTGCTATGTACG	59.4	156
		R: GACGAAGGATAGCATGGGGGAGAG	60.0	

Tm: melting temperature; bp: base pair

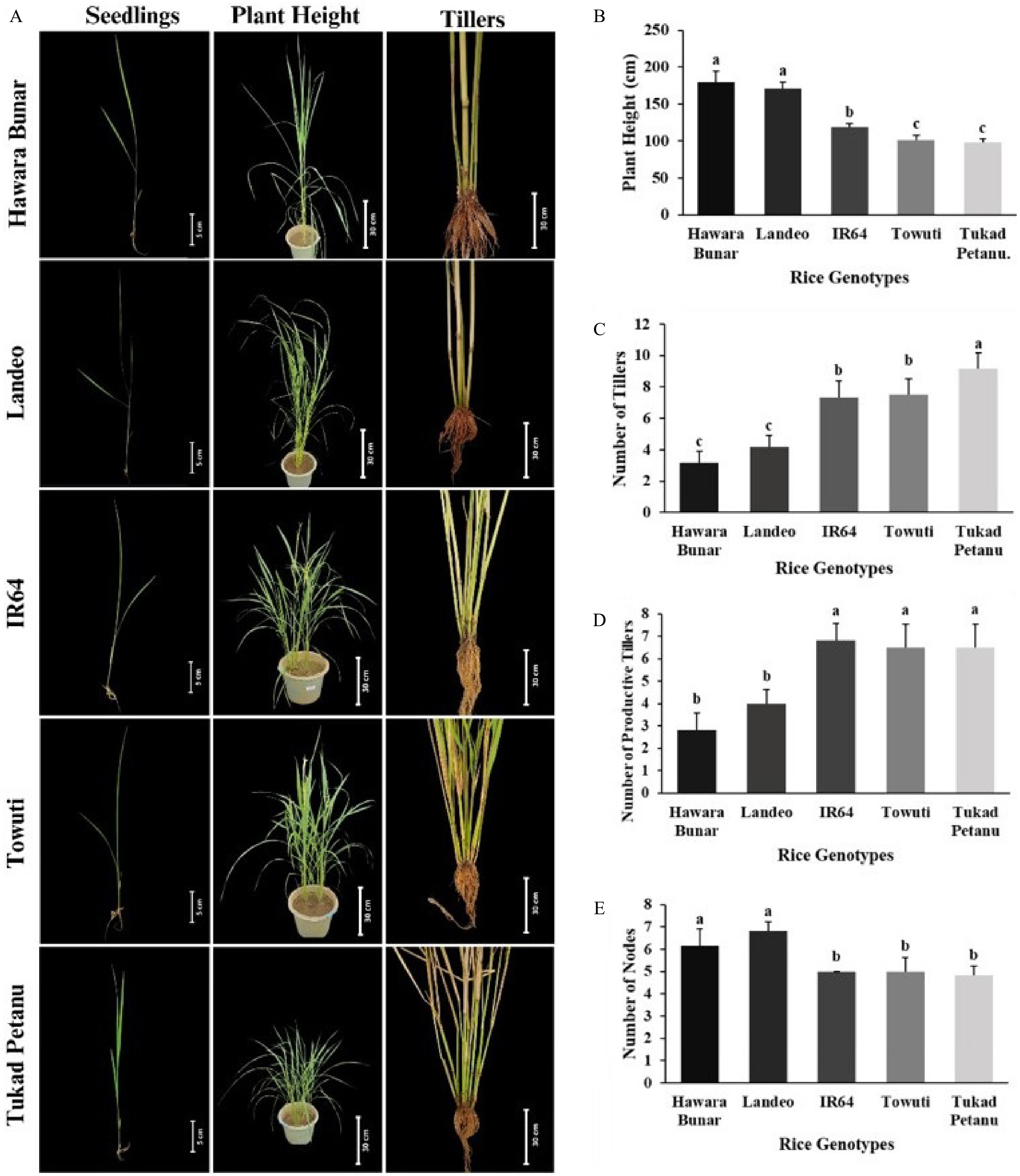


Figure 1. Morphological differences of five rice genotypes. (A) Morphological characters of the vegetative phase, seedlings scale bar = 5 cm, plant height and tiller scale bar = 30 cm, (B) plant height, (C) number of tillers, (D) number of productive tillers, (E) number of nodes. Error bars indicate standard deviation (n = 6 biological replicates)

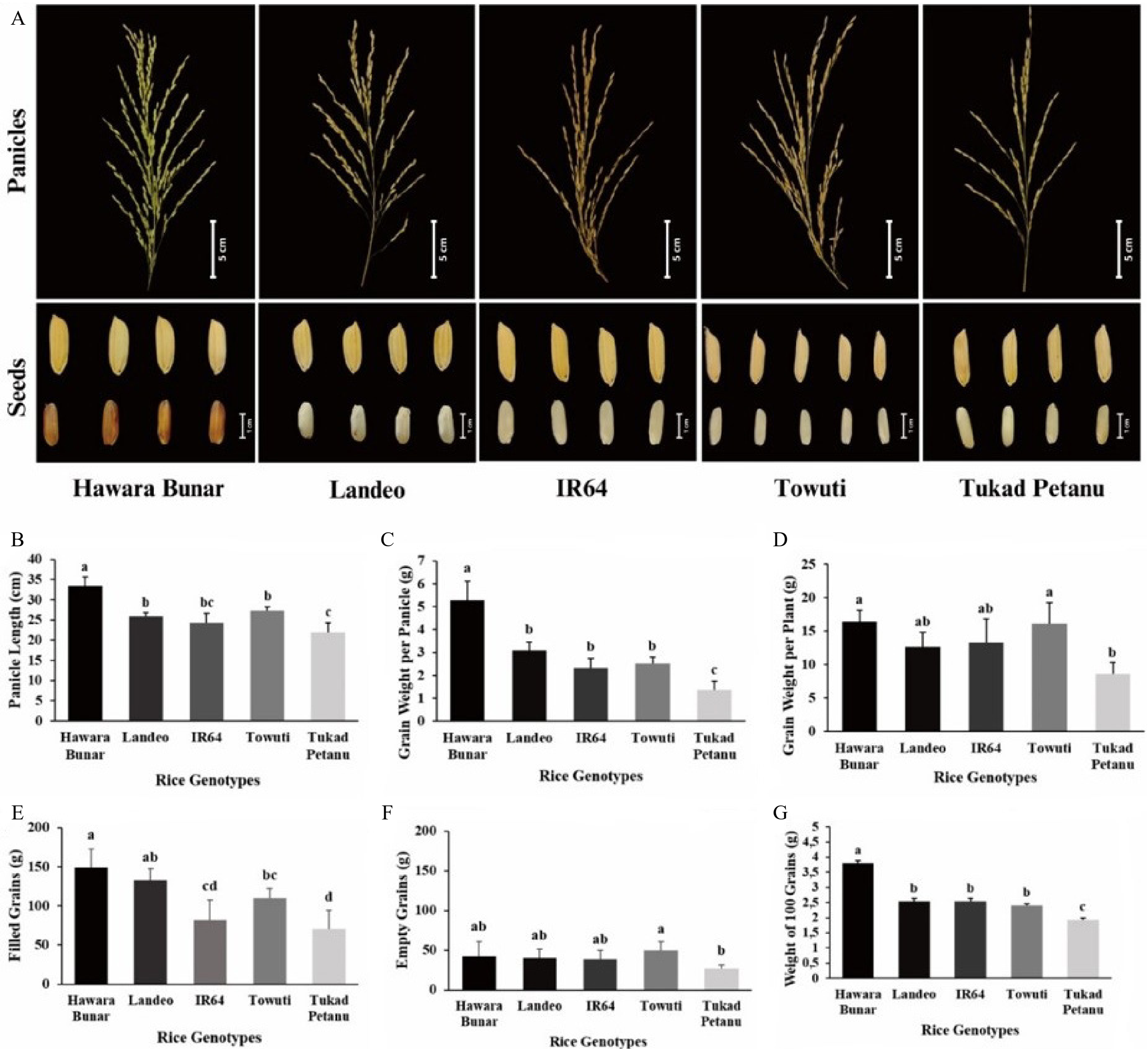


Figure 2. Rice panicles and grain characteristics of five rice genotypes. (A) Rice panicles and grain; panicle scale bar = 5 cm and seed scale bar = 1 cm, (B) panicle length, (C) grain weight per panicle (g), (D) grain weight per plant (g), (E) filled grains, (F) empty grains, (G) weight of 100 grains. Error bar indicates standard deviation (n = 6 biological replicates)

quality, the RNA also showed a high concentration and moderate to high purity, as indicated by the A260/230 and A260/280 absorbance ratios (Table 2).

The results of total RNA isolation showed a high concentration ranging from 446–1687 ng/µL, with an A260/A280 ratio of 1.6-2.3. The RNA was then used to synthesize complementary DNA (cDNA) using the reverse transcriptase enzyme. The results showed that the concentration of the synthesized cDNA ranged from 1599 to 2027 ng/µL, a sufficient amount of cDNA for further analysis. In addition, the cDNA produced had an A260/280 absorbance ratio of 1.8, indicating pure RNA and cDNA (Alshaibani *et al.* 2020).

3.3. Relative of Gene Expression

To ensure the success of cDNA synthesis, qualitative analysis of cDNA was performed through PCR using ACT and the target gene primers (Figure 4A). PCR results showed that all primers used in this study successfully amplified the cDNA template from the pre-tillering stage. The ACT at 156 bp, the *MOC1, MOC3,* and *TN1* genes, with a size of 114, 150, and

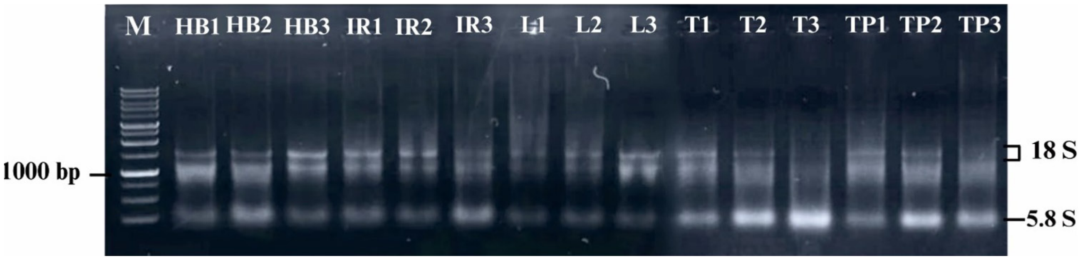


Figure 3. Electrophoregram of total RNA extracted from five rice genotypes: Hawara Bunar (HB), IR64 (IR), Landeo (L), Towuti (T), and Tukad Petanu (TP). Lanes 1–3 represent three biological replicates for each genotype. M: 100 bp; 18S and 5.8S indicate ribosomal RNA bands

Table 2. Concentration and purity of total RNA isolation results of five rice genotypes

Sample	Pre tillering			Tillering		
	Concentration (ng/µL)	A260/A230	A260/A280	Concentration (ng/µL)	A260/A230	A260/A280
HB1	1597.5	1.8	1.8	506.5	1.1	1.8
HB2	1025.5	1.2	1.6	539.5	1.1	1.7
HB3	1685.5	2.0	2.0	474.5	0.8	1.8
IR1	537.0	1.0	1.9	1494.5	1.7	1.7
IR2	821.5	0.8	2.1	1520.0	1.7	1.7
IR3	446.0	1.2	2.3	830.5	1.0	1.8
L1	1303.0	1.6	2.1	1562.0	1.8	1.9
L2	1523.5	1.7	2.1	1136.0	1.3	1.8
L3	970.0	1.3	1.6	816.5	1.0	1.7
T1	623.5	1.7	1.7	1574.0	1.8	2.0
T2	635.5	0.8	1.9	895.5	1.0	1.6
T3	490.5	0.8	2.1	1098.0	1.2	1.9
TP1	1687.0	1.9	2.1	857.5	1.2	1.8
TP2	766.5	0.9	2.0	933.5	1.2	2.0
TP3	1612.0	1.9	1.8	858.0	1.3	1.8

HB: Hawara Bunar, L: Landeo, IR: IR64, T: Towuti, TP: Tukad Petanu

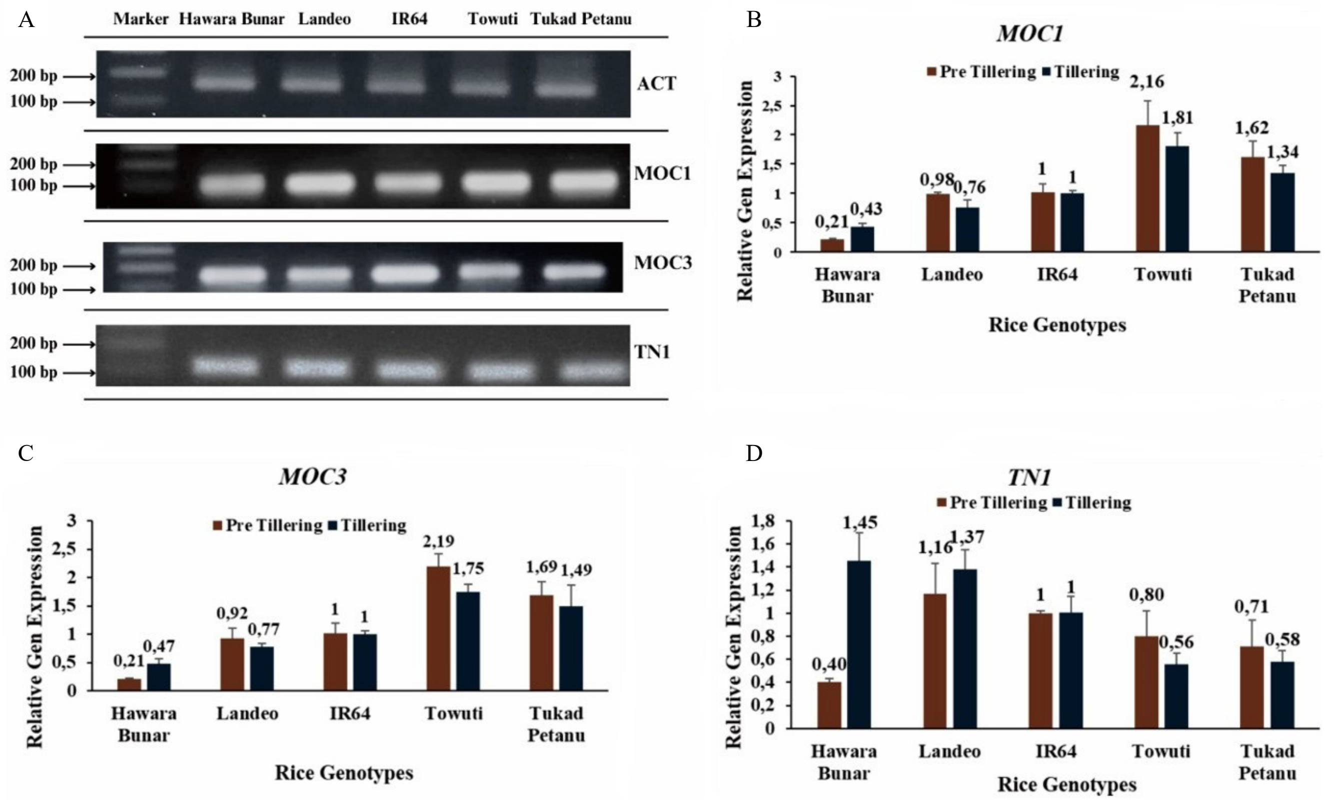


Figure 4. Results of qualitative PCR cDNA and quantitative (qRT-PCR) expression analysis of *MOC1, MOC3,* and *TN1* genes in five rice genotypes. (A) PCR cDNA, (B) relative gene expression of *MOC1*, (C) relative gene expression of *MOC3*, (D) relative gene expression of *TN1*. Error bars indicate standard deviation (n = 3 biological replicates)

156 bp, respectively. These results indicate that cDNA can serve as a template for gene expression analysis by RT-PCR.

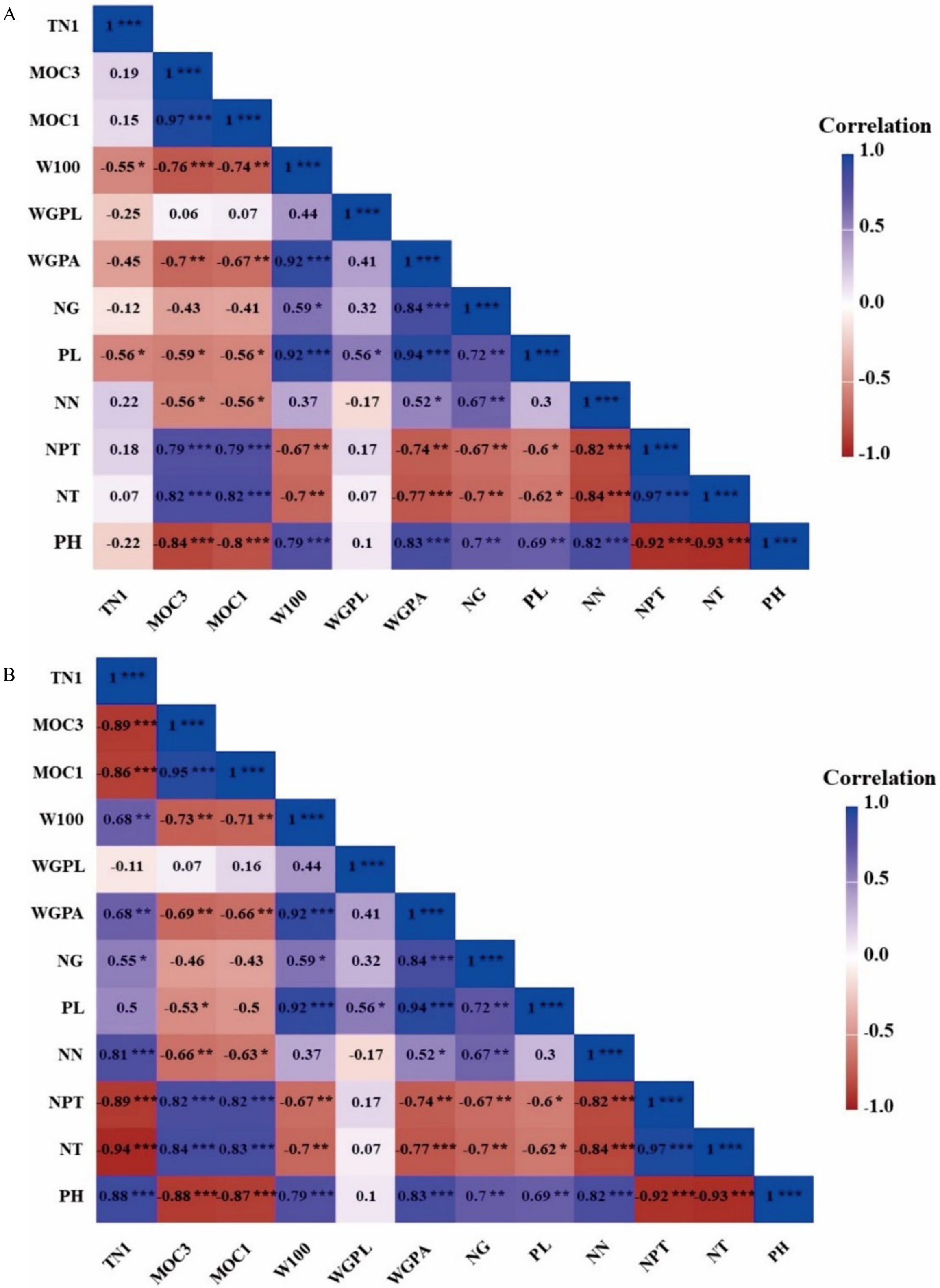
Among the five rice cultivars used, the relative gene expression of *MOC1* and *MOC3* was higher in the Towuti and Tukad Petanu cultivars, especially in the pre tillering phase, where the relative expression of the *MOC1* gene in the Towuti and Tukad Petanu rice cvs. was 2.16 and 1.62 times higher than the expression in the IR64 rice cultivar (control plant), respectively, while the relative gene expression values of *MOC3* in both cultivars were 2.19 and 1.69 times higher than the control plant. The Hawara Bunar and Landeo rice cvs. had lower *MOC1* and *MOC3* gene expression, where expression of the *MOC1* gene in Hawara Bunar and Landeo rice cvs. was 0.21 and 0.98 times lower than in control plants, respectively. In contrast, the relative gene expression values of *MOC3* in both rice cvs. were 0.21 and 0.92 times lower than that of control plants. The relative gene expression values of *MOC1* and *MOC3* decreased in the tillering phase. A different gene expression pattern was observed for the *TN1* gene, with higher expression in Hawara Bunar and Landeo rice cvs, especially in the tillering phase. The *TN1* gene expression values in Hawara Bunar and Landeo rice cvs. were 1.45 and 1.37 times higher than those of control plants. In contrast, Towuti and Tukad Petanu cvs. had relative gene expression values that were 0.56 and 0.58 times lower than those of control plants.

3.4. Correlation between Gene Expression and Morphological Character

Figures 5A and B show a correlation between multiple morphological characters. Several morphological characters show significant positive correlations with other morphological parameters, such as plant height and the number of nodes, panicle length, number of grains, weight of grains per panicle, and weight of 100 grains. In addition, panicle length is also positively correlated with the number of grains, weight of grains per panicle, weight of grains per plant, and weight of 100 grains. Positive correlations were also observed between morphological parameters and gene expression, with the *MOC1* and *MOC3* genes positively correlated with the number of tillers, especially in the pre-tillering phase, with respective correlation coefficients of 0.82. A significant positive correlation was also observed between the correlation of *MOC1* and *MOC3* genes and the number of productive tillers, with respective correlation coefficients of 0.79 (Figure 5A). Several morphological characters showed significant negative correlations with each other, including plant height, which negatively correlated with the number of tillers and the number of productive tillers in both the pre-tillering and tillering phases. In addition, significant negative correlations were observed between the *MOC1* and *MOC3* genes and plant height. The correlation of *TN1* was observed in the tillering phase, where the *TN1* gene was negatively correlated with the number of tillers and the number of productive tillers, with correlation coefficient values of -0.89 and -0.94, respectively. In terms of the gene correlation with the *MOC1* and *MOC3* genes, it shows a negative correlation with the values of -0.86 and -0.89, respectively (Figure 5B).

4. Discussion

Morphological characteristics are one of the determining factors for the ideal architecture of rice plants. Figure 1 shows rice plants with a taller habitus produce fewer tillers. Rice plants with a smaller number of tillers will produce fewer panicles, which will affect the number of grains. On the other hand, rice with a shorter habitus produces more tillers with more grains, but smaller panicles and fewer filled grains. Rice plants that are too tall have weak stems and often fall over due to the wind and rain, making the plants more prone to damage and pests (Yang *et al.* 2006; Liu *et al.* 2017) and diseases such as fungal infection, which will reduce the grain quality, harvest efficiency, and yield (Hashem *et al.* 2016; Wu *et al.* 2022; Zhang *et al.* 2025). The results of this study also showed that the character of plant height is inversely proportional to the number of tillers. Similar research results were also reported by Prabhu *et al.* (2024), which showed a negative correlation between plant height and tiller number of 150 selected rice plant accessions planted in various seasons. This negative correlation is influenced by the genetic factors, plant hormonal regulation, and environmental factors (Miao *et al.* 2024), and environmental factors (Hairmansis *et al.* 2023). Gibberellin (GA) influences increases in shoot height and suppresses tiller number by triggering degradation of the *SLR1* gene. The *SLR1* gene encodes a DELLA protein that can inhibit GA-mediated stem elongation. The *SLR1* gene is also involved in tiller formation by protecting the *MOC1* protein, a protein controlling tiller formation, from degradation (Ikeda *et al.* 2001; Liao *et al.* 2019). In addition, a protein encoded by the



A

	TN1	MOC3	MOC1	W100	WGPL	WGPA	NG	PL	NN	NPT	NT	PH
TN1	1 ***											
MOC3	0.19	1 ***										
MOC1	0.15	0.97 ***	1 ***									
W100	-0.55 *	-0.76 ***	-0.74 **	1 ***								
WGPL	-0.25	0.06	0.07	0.44	1 ***							
WGPA	-0.45	-0.7 **	-0.67 **	0.92 ***	0.41	1 ***						
NG	-0.12	-0.43	-0.41	0.59 *	0.32	0.84 ***	1 ***					
PL	-0.56 *	-0.59 *	-0.56 *	0.92 ***	0.56 *	0.94 ***	0.72 **	1 ***				
NN	0.22	-0.56 *	-0.56 *	0.37	-0.17	0.52 *	0.67 **	0.3	1 ***			
NPT	0.18	0.79 ***	0.79 ***	-0.67 **	0.17	-0.74 **	-0.67 **	-0.6 *	-0.82 ***	1 ***		
NT	0.07	0.82 ***	0.82 ***	-0.7 **	0.07	-0.77 ***	-0.7 **	-0.62 *	-0.84 ***	0.97 ***	1 ***	
PH	-0.22	-0.84 ***	-0.8 ***	0.79 ***	0.1	0.83 ***	0.7 **	0.69 **	0.82 ***	-0.92 ***	-0.93 ***	1 ***

B

	TN1	MOC3	MOC1	W100	WGPL	WGPA	NG	PL	NN	NPT	NT	PH
TN1	1 ***											
MOC3	-0.89 ***	1 ***										
MOC1	-0.86 ***	0.95 ***	1 ***									
W100	0.68 **	-0.73 **	-0.71 **	1 ***								
WGPL	-0.11	0.07	0.16	0.44	1 ***							
WGPA	0.68 **	-0.69 **	-0.66 **	0.92 ***	0.41	1 ***						
NG	0.55 *	-0.46	-0.43	0.59 *	0.32	0.84 ***	1 ***					
PL	0.5	-0.53 *	-0.5	0.92 ***	0.56 *	0.94 ***	0.72 **	1 ***				
NN	0.81 ***	-0.66 **	-0.63 *	0.37	-0.17	0.52 *	0.67 **	0.3	1 ***			
NPT	-0.89 ***	0.82 ***	0.82 ***	-0.67 **	0.17	-0.74 **	-0.67 **	-0.6 *	-0.82 ***	1 ***		
NT	-0.94 ***	0.84 ***	0.83 ***	-0.7 **	0.07	-0.77 ***	-0.7 **	-0.62 *	-0.84 ***	0.97 ***	1 ***	
PH	0.88 ***	-0.88 ***	-0.87 ***	0.79 ***	0.1	0.83 ***	0.7 **	0.69 **	0.82 ***	-0.92 ***	-0.93 ***	1 ***

Figure 5. The results of the Pearson correlation analysis of morphological characters and gene expression of *MOC1, MOC3,* and *TN1.* (A) Pearson correlation of pre-tillering phase, (B) pearson correlation of tillering phase. The asterisk (*) indicates a significant correlation. *p-value <0.05, **p-value <0.01, and ***p-value <0.001. PH: Plant height, NT: number of tillers, NPT: number of productive tillers, NN: number of nodes, PL: panicle length, NG: number of grains, WGPA: weight of grains per panicle, WGPL: weight of grains per plant, W100: weight of 100 grains

TAD1/TE gene plays a role in regulating plant height and controlling the number of rice tillers by interacting with the *MOC1* protein and triggering its degradation (Lin *et al.* 2012; Xu *et al.* 2012; Lin *et al.* 2020). In addition, this research showed a positive correlation between plant height and the number of nodes, where the higher the rice habitus, the greater the number of nodes produced.

Figure 2 shows that the rice shoot architecture during the vegetative phase correlates with panicle and grain characteristics produced at the reproductive stage. The results showed that the number of tillers is one of the rice architectural components that affect rice's growth and yield (Artadana and Supaibulwatana 2023). According to Fukushima (2019), rice is classified as a panicle-weight type architecture with a larger Shoot Apical Meristem (SAM). A plant with a larger SAM size produces more main shoots and fewer tillers. As a result, fewer panicles were produced, with the larger size of the spikelet and panicle. Panicle length affects grain filling, which may, in turn, affect grain weight, which determines panicle weight. Rice cultivars with heavier panicles produce better yield (Heng *et al.* 2018; Jin-long *et al.* 2020). The three factors that may determine the rice yield are the number of panicles, the number of grains per panicle, and the weight of the grain (Li *et al.* 2021). Therefore, the ideal rice architecture is a target of the current rice breeding program through the development of semi-dwarf rice varieties (Lan *et al.* 2023).

Figure 4B and C show that the expression levels of *MOC1* and *MOC3* genes were higher in Towuti and Tukad Petanu rice cultivars, which produced a greater number of tillers compared with Hawara Bunar and Landeo cultivars. In contrast, higher expression of the *TN1* gene in Hawara Bunar and Landeo resulted in fewer tillers. *MOC1* is a key gene that regulates the growth and development of rice tillers. Mutations that disrupt *MOC1* function lead to impaired tiller formation due to loss of its activity (Li *et al.* 2003). According to Shao *et al.* (2019), the *MOC3* gene interacts directly with *MOC1*, functioning as a *MOC3* coactivator that binds to the *FON1* gene promoter to activate its expression. Therefore, *MOC1* and *MOC3* genes contribute not only to the initiation of axillary shoots but also to the elongation of tiller shoots, which collectively shape rice tiller architecture. Furthermore, research conducted by Fan *et al.* (2024) found that *DWARF* and *LESS TILLER ON CHROMOSOME 3 (DLT3)* bind *MOC3* and recruit *MOC1*, which will later form a *DLT3-MOC3-MOC1* complex to regulate tillering. This complex maintains the expression of *MOC1, MOC3,* and *FON1,* then activates the *FON1* promoter to regulate tillering development. The *MOC1* and *MOC3* genes encode nuclear transcription factors. The *MOC1* and *MOC3* genes are highly expressed during the pre-tillering phase and then decline during tillering. Li *et al.* (2003) compared the expression levels of *MOC1* in various tissues, including epidermal cells in leaf axils, axillary meristems, shoot apical meristem (SAM), leaf axillary primordia, and young leaves, which showed that the highest *MOC1* expression was found in the axillary meristem in tillering shoots and was not detected in the apical meristem. Similar results were also reported by Shao *et al.* (2019), who found the highest *MOC3* expression in young panicles and tillers. *MOC3* expression was also found in the elongation of tillers phase. Still, the expression level was lower, consistent with the results of previous studies showing that the *MOC1* and *MOC3* genes are expressed in the axillary meristem and involved in the initiation of tiller growth. The expression of the *MOC1* and *MOC3* genes was low in the Hawara Bunar and Landeo rice cultivars, which is assumed to be influenced by the high expression of the *TAD1* gene. The *TAD1* gene increases plant height and reduces the number of tillers. The relative expression of the *TAD1* gene in the Hawara Bunar rice cv. in the pre tillering phase was 6.2 times higher and increased in the tillering phase by 19.2 times higher than in the IR64 rice cultivar (Sindiya *et al.* 2024).

Figure 4D shows that the *TN1* gene is highly expressed during the tillering phase in the Hawara Bunar and Landeo rice cultivars. The *TN1* gene functions as a negative regulator of tiller development, and its high expression has been associated with reduced tiller number Zhang *et al.* (2023). Also reported that *TN1* is predominantly expressed in tillers and shoot bases, supporting its role in controlling tiller initiation. In agreement with these studies (Dong *et al.* 2023; Yang *et al.* 2024). Our results suggest that the high expression of *TN1* in Hawara Bunar and Landeo restricts tiller initiation. In contrast, lower expression in Towuti and Tukad Petanu promotes axillary bud growth and increases tiller number. These findings emphasize the regulatory importance of *TN1* in shaping rice tiller architecture.

The correlation matrix in Figure 5 illustrates the relationships between various morphological parameters and the expression of *MOC1, MOC3,* and *TN1* genes during the pre-tillering and tillering phases. The increased expression of *MOC1* and *MOC3* was positively associated with the number of tillers, suggesting a role in promoting tiller formation. In contrast, high *TN1* expression showed a negative correlation, indicating a suppressive effect on tiller development. Similar observations were reported by Thuy *et al.* (2023), who found that plant height was negatively correlated with the total and productive tiller numbers. Overall, these findings highlight the coordinated regulation between gene expression and morphological traits that determine rice tiller architecture.

In conclusion, tillers are one of the architectural characteristics that affect the growth and yield of rice. Of the five rice genotypes used, the local Hawara Bunar rice cultivar has potential for development; although it has a low number of tillers, it can produce better harvest quality. The Hawara Bunar rice cultivar has a low number of tillers, which is influenced by the low expression of genes that trigger tiller formation (*MOC1* and *MOC3*) and the high expression of the gene that inhibits tiller formation (*TN1*). The results of this study can serve as a reference for further research on developing the local rice cultivar, Hawara Bunar, to create an ideal rice cultivar in terms of architecture.

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