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Lodging-related gene expression in upland rice varieties from Pala U Village, Thailand

Laosutthipong, C.*, Seritrakul, P. and NaChiangmai, P.

Faculty of Animal Sciences and Agricultural Technology, Silpakorn University, Phetchaburi IT Campus, Cha-am, Phetchaburi, 76120, Thailand.

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Abstract Native upland rice has been cultivated in Pala U village, Prachuap Khiri Khan Province, Thailand. Gene expression of the five lodging-related genes in the eight varieties of native upland rice, compared with Pathumthani-1 rice were characterized. For lignin biosynthesis genes (*OsPAL* and *Os4CL3*), the level of gene expression in all eight native rice varieties were not significantly difference to Pathumthani-1 rice. Although, the relative fold of *OsPAL* gene expression in R1, R3, and R4 varieties revealed 5.3, 9.0 and 6.1-fold expression, respectively. Another two genes that involved in control strigolactone signaling and effect on culm strength were *OsTB1* and *OsAPO1* gene. The R4 varieties showed 7.3-fold expression in *OsTB1* gene and significantly different from PT ($P < 0.05$). The *OsCESA-9* gene expression level in the R2 and R6 variety had below 0.58 and 0.65-fold of the PT rice. These results suggested that some genes that important in plant cell structure and effect on lodging in rice had trend to highly express in some varieties of native upland rice.

Keywords: Lodging, Gene expression, Upland rice

Introduction

Rice (*Oryza sativa* L.) is the main cereal grain which the most widely consumed as human staple food more than half of the world, especially in Asia and Africa. There are three main types of *Oryza sativa*: indica, japonica, and javanica. In 2021, the rice production volume in Thailand was round 26.1 million tons (USDA, 2021). which most come from lowland rice. For cultivation of upland rice normally is dryland condition, without irrigation and puddling. Thai native upland rice is also cultivated in various area, such North and highland of South (Karladee *et al*., 2012). Ethnic minority farmers (Paganyaw: a sub-group Karen people) in Prachuap Khiri Khan Province, Hua Hin district cultivated upland rice for several purposes such as consumption in their family, using for local wisdom ritual, and ceremonies (Vechpong *et al*.,

* **Corresponding Author:** Laosutthipong C.; **Email:** laosutthipong_c@su.ac.th

2015). The fluctuated environment, insufficiency water support, climate and land pattern, including genetic trait character in each varieties effect on upland rice yield (Saito *et al*., 2018). Low yield productivity also found in North of Thai upland rice (0.9 tons per hectare), which may cause by the genetic heterogeneity in rice population (Karladee *et al*., 2012). Moreover, lacking of lodging resistant character in some rice traits is a main affect in low-yield productivity.

Lodging in rice is a complex phenomenon which causes by various factors. For example, the variety characteristics, over seeding, long seedling age, too shallow arable layer, and unreasonable planting density or fertilization (Hui, 2018). Three types of cereal crop lodging are stem bending, root lodging and stem breakage (Kono, 1995) and exist in both lowland (Islam *et al.*, 2007) and upland rice (Mustikarini, *et al*., 2019; Wenxia *et al*., 2020). Major traits associated with lodging resistant in wheat and rice are culm diameter, cell wall thickness, plant height, and biochemical contents (lignin and cellulose) (Shah *et al.*, 2019). Recently, the improvement of lodging resistant in rice varieties for increased productivity have been reported in several countries: China (Guo *et al.*, 2020; Shah *et al*., 2019), Japan (Okuno *et al*., 2014; Ookawa *et al*., 2010), India (Yadav *et al*., 2017), and Indonesia (Mustikarini *et al.*, 2021). Anyway, the decreasing of plant height as semi-dwarf varieties in rice revealed the increasing of resistance to plant lodging and allows them to produced high yield, there were some limitation in semi-dwarf trait for higher yield production. Several researches proposed the alternative method to rise lodging resistance such as the quality of the culm development which consist of identification of genes involved in culm quality and applied these genes to high-yield rice varieties (Hirano *et al*., 2017).

The association of biochemical components accumulation in plant cell with the lodging resistance has been reported such as concentration of lignin, cellulose, and pectin in plant stem (Kong *et al*., 2013). Since, lignin and cellulose are major composition in plant cell wall and act as key factors to promote culm strength, secondary cell wall strength, and lodging resistance, several studies attempted to characterize the molecular mechanisms of them to understand their biosynthesis. Genetic manipulation for lodging resistance by using molecular mapping of Quantitative Trait Loci (QTL) in rice has been conducted. Yadav *et al.* (2017) used QTL to identify significant positive correlation between lodging related traits (culm length, diameter, and strength) and grain yield under dry direct-seeded rice and found 12 QTLs which were mapped on chromosome 1, 2, 6 and 7. The effective QTL, *STRONG CULM3* (*SCM3*) (encode an allele of the rice *TEOSINTE BRANCHED 1*; *OsTB1*) combined with *SCM2* to be the Near-Isogenic Line-*SCM2*+*SCM3* (NIL-

SCM2+*SCM3*) showed high strength culm and increased spikelet number (Yano *et al.*, 2015). Recently, the genetic relationship between culm strength and yield in rice was conducted by genome-wide association study combined with linkage analysis of 17 lodging resistance trait and revealed 63 loci linking culm strength and yield (Guo *et al*., 2020).

Lignin, a complex phenolic biopolymer, is one of secondary metabolite that polymerized in the secondary cell wall of plant cell for enhancing rigidity, hydrophobic properties and promote minerals transport through the vascular bundle (Schuetz *et al.*, 2014). Lignin biosynthesis consists of three steps: lignin monomer biosynthesis in cytosol, transport to apoplast, and finally polymerization (Liu *et al*., 2018). First enzyme in lignin biosynthesis pathway is phenylalanine ammonia-lyase (PAL) which synthesize cinnamic acid from phenylalanine. This PAL enzyme is expressed from *pal* genes which has been reported that quadruple mutant (*pal1/pal2/pal3/pal4*) in *Arabidopsis thaliana* showed 20-25% lignin content reduction and increased pathogen susceptibility (Huang *et al*., 2010). The 4-coumarate: CoA ligase (4CL) enzyme activate the *p*-coumaroyl-CoA production in phenylpropanoid pathway. The suppression of *Os4CL3* gene expression resulted in significantly effect on the lignin content, rice plant height and other morphologies (Gui *et al*., 2011). Previously, the lignin content and lignin biosynthesis enzymes (PAL, 4CL, CAD and POD) activities revealed the crucial roles in lodging resistance in buckwheat (*Fagopyrum esculentum*) lignin metabolism (Hu *et al.*, 2017). The *OsPAL* and *Os4CL3* genes from native upland rice varieties in Thailand were sequenced and revealed the identity to *O. sativa* japonica and *O. sativa* indica, respectively (Laosutthipong *et al*., 2019). Plant cell wall mechanical strength is not only cause by lignin content, but also cellulose quality and quantity.

Cellulose, a polymer of linear-unbranched β-1,4-glucans chains, is a main composition of primary (30%) and secondary (90%) plant cell wall (Taylor, 2008). In higher plant, cellulose biosynthesis occurs in plasma membrane by utilization of cellulose synthase (CESA) complex, is encoded by a large gene family, and use uridine diphosphate (UDP)-glucose as substrates (Somerville, 2006). Wang, *et al.* characterized *OsCESA/CSL* (cellulose synthase-like) genes superfamily that showed co-expression pattern in various tissue, especially *OsCESA-4*,*-7* and *-9* which strongly co-expressed on primary and secondary of rice cell wall (Wang *et al*., 2010). Moreover, the S1-60 mutant *japonica* rice (caused by point mutation in *OsCESA-9 gene)* showed the decreasing of cellulose content (44.7%) in culm which effect on the mechanical strength, the flaw in thickening of the sclerenchyma cell wall and fragile culm (Wang *et al.*, 2012). Recently, *OsCESA9* conserved-site mutation give rise to boosted rice lodging resistance which affect stability of CESA4/7/9 complexes and cause a

rapid CESA proteasome degradation but slightly affected on plant growth (Li *et al*., 2017). The cellulose biosynthesis gene (*OsCESA4* and *OsCESA9*) of seven native upland rice varieties in Thailand was partial sequenced and found the identity to *O. sativa* japonica and *O. sativa* indica (Laosutthipong *et al*., 2022).

In an attempt to identify the effective lodging resistance QTL gene in mechanisms of culm strength in rice, several studies isolated the gene that control panicle structure, *ABERRANT PANICLE ORGANIZATION1* (*APO1*) (Ookawa *et al*., 2010) and control stigolactone signaling, *TEOSINTE BRANCHED1* (*OsTB1*) (Yano *et al*., 2015). The NIL-*SCM2*+*SCM3* rice had increased spikelet number and culm strength. A novel role of *TB1* transcription factor gene that effect on plant height and stem elongation was reported in wheat (Dixon *et al*., 2020). The *OsTB1* gene encode transcription factors that involve in lateral branching and function as a negative regulator of axillary buds in rice. Transgenic rice overexpressing *OsTB1* exhibited significantly reduced lateral branching, while the *fine culm 1* (*fc1*)-*OsTB1* mutant revealed the enhanced lateral branching (Takeda *et al.*, 2003). The rice *APO1* gene, encoding an F-box-containing protein, involve in suppression of the conversion of rachis branch meristem to spikelet. The *APO1* mutant had overexpress the level of APO1 activity which caused the delay in the program shift to spikelet formation and regulation on the inflorescence (Ikeda-Kawakatsu *et al*., 2009).

Although, lodging problem in rice has been investigated in various causes, prevention, and control, there still did not have the best strategy, yet. Researchers tried to produce the best lodging resistant variety with high production until now. In Thailand, the information about rice lodging study had not enough on solving lodging problem and enhance grain yield, especially native upland rice. The study aimed to investigate five lodging-related genes expression in native upland rice varieties in Thailand compared with Pathumthani-1 strain.

Materials and methods

Rice samples

The Pathum thani-1 rice and eight native rice varieties were *Aung Jerng Yai* (R1), *Nah San* (R2), *Bue Soo Sue La* (R3), *Kao Niew Pala U* (R4), *Bue Ke* (R5), *Dok Payom* (R6), *Bee Kor Bi* (R7), and *Rao Soo Ya* (R8). All native upland rices were gained from the farmers at Pala-U village, Hua Hin district, Prachuap Khiri Khan province, Thailand. Rice seeds were immersed in sterile water 24 hours and then placed on humid box until germination. Seedlings were collected for RNA extraction at 14 days later.

RNA Extraction, cDNA synthesis and realtime PCR

RNA Extraction

The seedling samples (50 mg) were fresh-cut and prepared for total RNA extraction by using the Plant Total RNA Mini Kit (Geneaid Biotech Ltd., Taiwan). The procedure of RNA extraction was started with cutting of rice seedling in small piece and followed by kit protocol. The extracted RNA was measured using a Nanodrop spectrophotometer (OD260/280).

cDNA synthesis and realtime PCR

The iScript™ Reverse Transcription Supermix for RT-qPCR Kit (Bio-Rad Laboratories, USA) was used rice cDNA synthesis from 1 µg of total RNA. The reverse transcription reaction consists of iScript RT Supermix, Nuclease-free water, and RNA template. After incubation of the reaction mix in thermal cycler, the cDNA was analyzed by realtime PCR.

This research used three primer sets which involved in lignin biosynthesis, strigolactone signaling and cellulose biosynthesis (Table 1).

Table 1. List of primers used in this study

Function	Gene	Forward primer (5'→3')	Reverse primer (5'→3')	Product size (bp)
Lignin biosynthesis	*Os4CL3*	CGCAAGCACAACATCACCAT	TACCGTAACCCTGTCCGAGG	193
	OsPAL	CGAACCGCTTCGTGTATCTTC	GGATGGAATCGAGTAGCAATAC	203
Strigolactone signaling (Yano *et al.*, 2015)	*OsTB1*	TCATCCATCCACACACGAAC	ATGCGATGACCAAACCAAAG	207
	OsAPO1	GGAGAACGTATGGAGCAAGG	CTGAGACGGCTCTTCTCGAC	135
Cellulose biosynthesis	*OsCESA-9*	GCGGAAGGGTGGATCATGAA	CTTCTTGTGGTGCTGGAAGC	180
Actin	*OsAct*	CAGCCACACTGTCCCCATCTA	AGCAAGGTCGAGACGAAGGA	86

Gene expression analysis utilized realtime PCR. The reaction was prepared by follow the iTaq Universal SYBR® Green Supermix kit (Bio-Rad Laboratories, USA), that consist of iTaq Universal SYBR® Green Supermix (antibody-mediated hot-start iTaq DNA polymerase, $MgCl_2$, dNTPs, SYBR® Green I dye, enhancer, stabilizers and blend of passive reference dyes), 0.8 µM of each primer, Nuclease-free water and 100 ng of cDNA template. The thermal

cycling protocol was set up in the qTower^3 (Analytik Jena GmbH+Co. KG 2022, Germany) with the polymerase activation and DNA denaturation at 95 °C (30 sec), followed by amplification steps: 35 cycles of denaturation at 95 °C (5 sec), annealing/extension and plate read at 60 °C (30 sec), finally melting curve analysis extension. Finally, data analysis was performed according to the instrument instructions and software.

Data and statistical analysis

The quantitative realtime PCR result was collected on qTower^3 software such cycle threshold (CT) value data. The housekeeping *OsActin* gene was used as the internal reference gene. The relative expression levels of *Os4CL3, OsPAL, OsTB1, OsAPO1, and OsCESA-9* were analysed using the $2^{-\Delta\Delta CT}$ method (Livak and Schmittgen, 2001). All qPCR amplifications data were conducted in three replicates. The means and standard deviation of the $2^{-\Delta\Delta CT}$ data were calculated and drawn with MS office 365 Excel. Statistically significant differences (* represents $P < 0.05$) were determined by analyses of variance based on Student's *t*-tests.

Results

Characteristics of native upland rice seedlings

A five-day-old seedling of the eight native rice varieties were R1, R2, R3, R4, R5, R6, R7, R8 and Pathum thani-1 rice (Figure 1A-I). Morphology of all plants was observed every day during germination stage. Emergence of radicle and primary leaf in first week revealed the different characters in each seedling variety. Primary root growth and lateral root formation in variety R2, and R6 showed a high complicated root and longer-in length. Pathum thani-1 seedling (Figure 1I) had the tallest and uniform growth.

Lignin biosynthesis gene expression

The expression level of *OsPAL* and *Os4CL3* genes that involved in lignin biosynthesis in rice was examined by quantitative RT-PCR. The level of *OsPAL* expression was found to have highest expression levels in R3 rice 9.0-fold expression and others, R1 and R4 varieties were 5.3 and 6.1-fold expression, respectively (Figure 2A). The levels of *Os4CL3* gene expression in all eight native upland rice varieties were not significantly different from the Pathum thani-1 rice (Figure 2B).

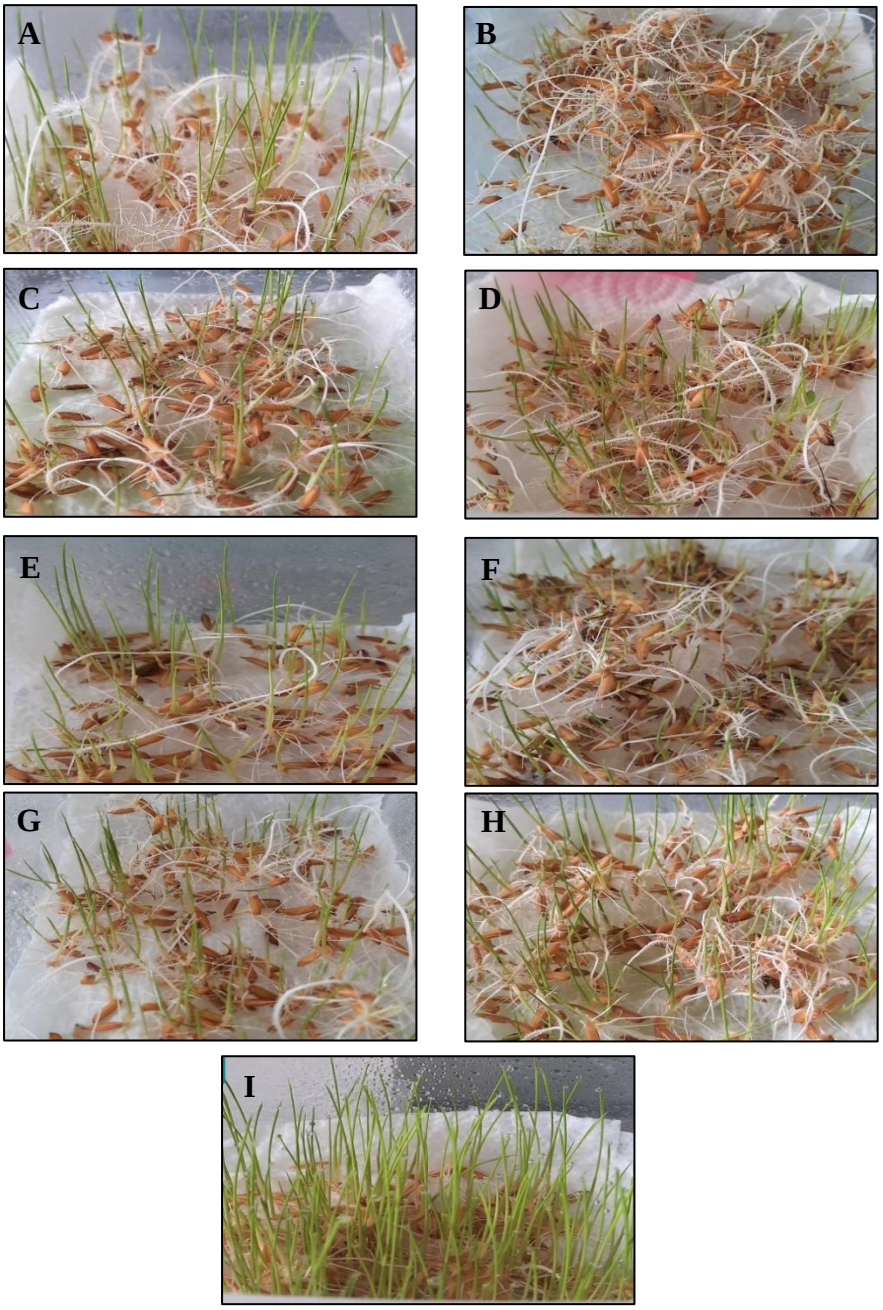
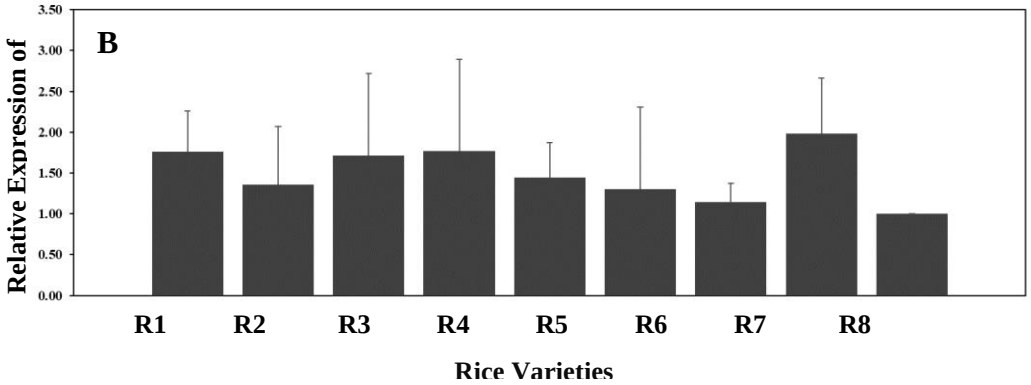


Figure 1. Characteristics of native upland rice seedlings
A five-day-old seedling of the eight native rice varieties were A: Aung Jerng Yai (R1), B: Nah San (R2), C: Bue Soo Sue La (R3), D: Kao Niew Pala U (R4), E: Bue Ke (R5), F: Dok Payom (R6), G: Bee Kor Bi (R7), H: Rao Soo Ya (R8) and I: Pathum thani-1 rice



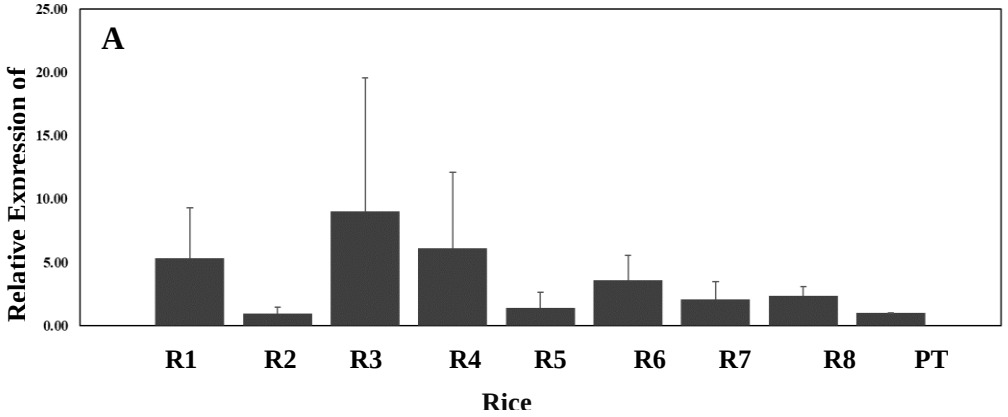


Figure 2. Lignin biosynthesis gene expression

Relative expression level of *OsPAL* (A) and *Os4CL3* (B) gene from the eight native rice varieties were Aung Jerng Yai (R1), Nah San (R2), Bue Soo Sue La (R3), Kao Niew Pala U (R4), Bue Ke (R5), Dok Payom (R6), Bee Kor Bi (R7), Rao Soo Ya (R8) and Pathum thani-1 (PT) rice. The rice *actin* gene was used as an internal reference for normalization. The results were means +SD of independent triplicates data

Strigolactone signaling gene expression

For the culm strength-related gene expression, the *OsTB1* and *OsAPO1* were investigated in seedling stage of the eight native upland rice varieties, comparing with Pathum thani-1 rice (low land and high yield variety). The relative expression level of *OsTB1* (Figure 3A) of R4 revealed the highest 7.3-

fold expression and significantly different from PT ($P < 0.05$). The *OsAPO1* gene expression of all upland rice were not differently expressed from PT rice (Figure 3B).

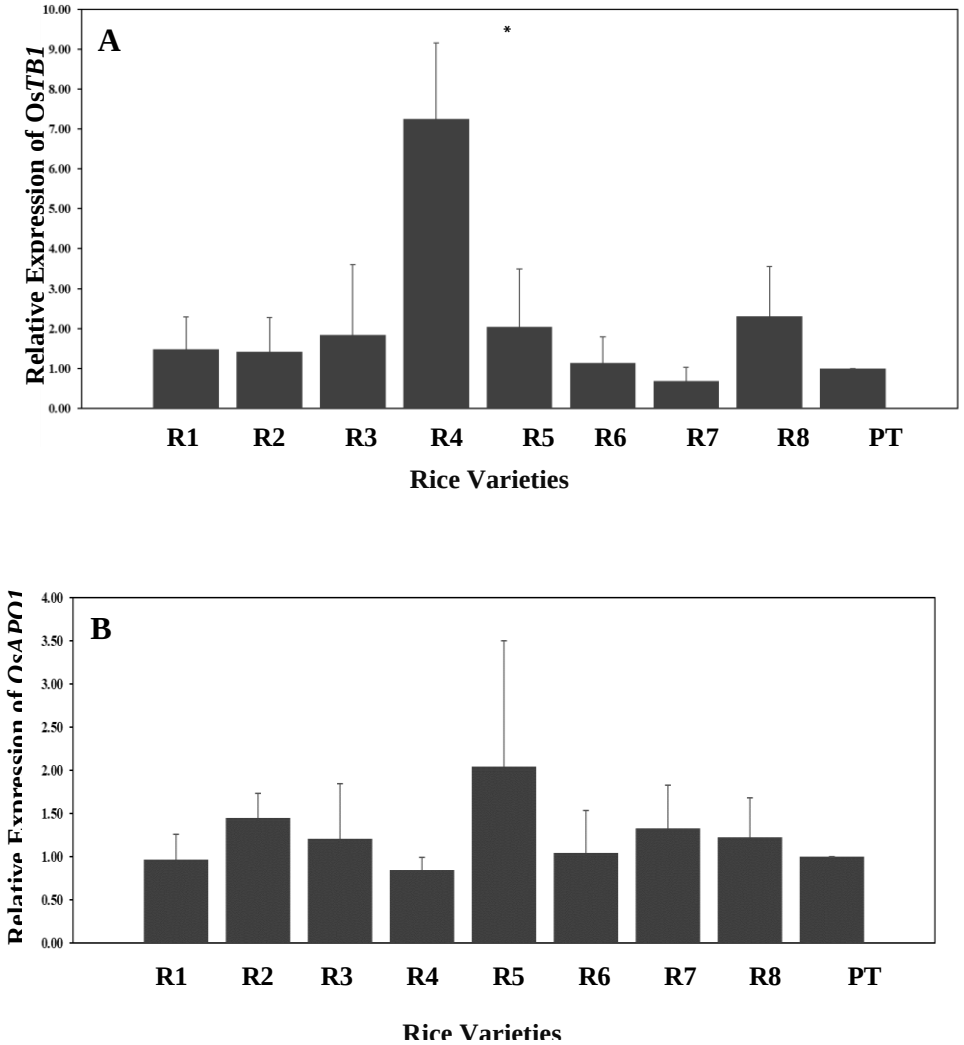


Figure 3. Strigolactone signaling gene expression

Relative expression level of *OsTB1* (A) and *OsAPO1* (B) gene from the eight native rice varieties were Aung Jerng Yai (R1), Nah San (R2), Bue Soo Sue La (R3), Kao Niew Pala U (R4), Bue Ke (R5), Dok Payom (R6), Bee Kor Bi (R7), Rao Soo Ya (R8) and Pathum thani-1 (PT) rice. The rice *actin* gene was used as an internal reference for normalization. The results were means +SD of independent triplicates data. Asterisk indicates significantly different from PT at *, $P < 0.05$

Cellulose biosynthesis gene expression

Result of the *OsCESA-9* expression level in most of native rice samples were not differently from PT rice. The R2 and R6 variety revealed the expression level of *OsCESA9* gene below 0.58 and 0.65-fold of the PT rice expression level (Figure 4).

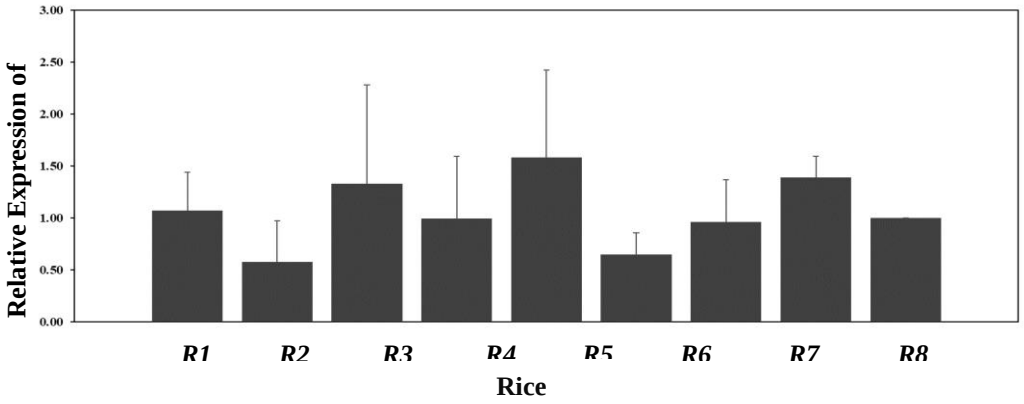


Figure 4. Cellulose biosynthesis gene expression
Relative expression level of *OsCESA9* gene from the eight native rice varieties were Aung Jerng Yai (R1), Nah San (R2), Bue Soo Sue La (R3), Kao Niew Pala U (R4), Bue Ke (R5), Dok Payom (R6), Bee Kor Bi (R7), Rao Soo Ya (R8) and Pathum thani-1 (PT) rice. The rice *actin* gene was used as an internal reference for normalization. The results were means +SD of independent triplicates data

Discussion

Lodging factors in crop production have been classified in morphological and anatomical traits together with the chemical component of stem, especially in rice and wheat. The novel high-throughput phenotyping approach to understand the relationship between genotype-to-phenotype of plant lodging has been proposed to accelerate the plant breeding program (Shah *et al.*, 2019). Several studies aimed to improve rice lodging by engineering the lodging resistance variety which can against lodging and high gain yields (Hirano *et al*., 2017; Ookawa *et al*., 2010). Previously, molecular mapping QTLs combined with phenotypic characteristics in rice demonstrated the lodging resistance trait and candidate genes (Yadav *et al.*, 2017). Since, the lodging is caused by a multifactor, so the improvement of lodging resistance in genetic approach was done.

Phenylalanine ammonia-lyase (PAL) acts in the primary step in the phenylpropanoid pathway of lignin biosynthesis. In Arabidopsis, *PAL* has 4 genes (*PAL1, PAL2, PAL3* and *PAL4*) that encodes PAL(Raes *et al*., 2003) and the expression level of PAL genes were differently found plant tissue and stage (Mizutani *et al*., 1997). Lignin deposition and phenotypic changing (plant growth reduction, altered leaf shape, flower morphology and pigmentation) were reported in tobacco *PAL* gene downregulation (Elkind *et al*., 1990). This study, *OsPAL* gene expression level in R3, R4, and R1variety were 9.0, 6.1 and 5.3-fold expression to PT rice, indicated that the character of *OsPAL* gene expression in each native upland rice varieties which may be grown in different planting plot and soil composition. Previously researches revealed some heavy metal (aluminum, cadmium, copper, and zinc) can induce the expression of lignin synthesis enzymes (PAL and 4CL) and also increase lignin content in plants (Lin *et al*., 2005; Mao *et al*., 2004; Van De Mortel *et al.*, 2006; Yang *et al.*, 2007). In case of the levels of *Os4CL3* gene expression in all eight native upland rice varieties were not significantly different from the Pathum thani-1 rice, these may result from the stage of plant sampling and *4CL* gene-types. Because of *4CLs* gene has five types for 4CLs enzymes activity, which were reported that the magnitude of *4CLs* transcript expression showed different in tissue and rice growth development. The *4CL3* transcript was detected at highest level in all tissue and the course of growth (Gui *et al*., 2011).

Previous study, the overexpression of *OsTB1* transgenic rice showed significantly decreased the lateral branching, while *OsTB1* mutant exhibited enhanced lateral branching (Takeda *et al*., 2003). Our result revealed the relative expression level of *OsTB1* of R4 variety had the 7.3-fold expression and significantly different from PT ($P < 0.05$) in seedling stage, it might or might not be affect on lateral branching of plant. The effect of *Strong culm2* (*SCM2*)/*APO1* gene on culm strength did not differ and its expression level was the same in all organ between Habataki and Koshihikari rice variety, except in the inflorescence meristem which showed a two-fold expression increasing (Ikeda-Kawakatsu *et al*., 2009). In this study, the *OsAPO1* gene expression of all upland rice were not differently expressed from PT seedling.

The *OsCESA9* mutant (*S1-60* and *Osfc16*) and a semi-dominant mutant (*Sdbc1*) rice had lower cellulose content and secondary cell wall thickness compared with wild type, especially enhanced lodging resistance (Li *et al*., 2017; Wang *et al*., 2012; Ye *et al*., 2021). In this study, the *OsCESA-9* expression level of six native upland rice samples were not differently from PT rice, whereas the R2 and R6 variety had the expression level of *OsCESA9* gene below 0.58 and 0.65-fold of the PT. If the defective of *OsCESA9* gene can cause the cellulose content and enhance lodging resistance, the lower *OsCESA9*

gene expression level in both native upland rices may have chance to resist lodging.

In conclusion, this study investigated the five lodging-related genes expression using quantitative RT-PCR in the eight native upland rice varieties at Pala U village, Prachuap Khiri Khun province, Thailand. Our research demonstrated the level of gene expression in seedling stage comparing with Pathum thani-1 variety, which is widely cultivated in irrigated areas of Thailand. Although, all gene expression level results in this study cannot clearly solved lodging problem in native upland rice, more research should be further done. The reason of the lodging problem in rice come from the complex factors that is needed more strategy to study and understand. Anyway, our finding seemed to be the one of jigsaw puzzle of native upland rice research in Thailand.

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