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PHYSIOLOGICAL AND MOLECULAR COMPARATIVE ANALYSIS OF TWO CONTRASTING RICE VARIETIES UNDER JASMONIC ACID TREATMENT

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SUMMARY

Rice is one of the most important crops but its productivity is severely threatened by both biotic and abiotic stresses. Jasmonic acid and its derivatives (referred to JA) are the lipid-based plant hormones that were commonly known as regulators of plant growth, development and defense responses. In this study, we compare the physiological and molecular responses of two rice accessions, G38 (Nep_nuong) and G11 (Tam-tron) to JA treatment. G38 plants under JA treatment experienced a reduction in shoot length, root weight, shoot weight and total plant weight which suggested its sensitiveness to JA, whereas G11 plants showed a less reduction in these traits. The expression levels of 12 JA-related genes were investigated in order to better understand how the JA biosynthesis and responses differ in these two contrasting rice accessions. A significantly higher expression level of a set of genes related to JA biosynthesis, signaling and response in G11 compare to G38 was observed. Furthermore, the inorganic phosphorus starvation (Pi) response was also examined in the two varieties G11 and G38. In low Pi condition (40 µM), G11 plants showed more roots, longer root length and shoot length, higher weight compared to the G38 plants which suggest that G11 did not suffer much effect of Pi deficiency. This study highlights the differences in JA growth response in 2 contrasting rice genotypes and also suggests the link between JA developmental response and the tolerance to the Pi starvation condition in rice.

Keywords: *abiotic stress, Jasmonic acid (JA), JA–responsive genes, Phosphorus starvation, Rice (Oryza sativa* L.)

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most abundant food crops around the world, especially in Asia. Nowadays, the demand on rice increase significantly due to the rising of the world population. Along with the escalation in rice requirement, rice production is being forced to cope with numerous obstacles, for example, climate change, reduction of cultivable land and natural disasters. This challenge impulses an urge solution for creating new varieties of rice which can withstand harsh condition and also maintain high productivity.

Jasmonic acid, its derivatives and conjugates (referred to JAs), are known to be important regulators of plant responses to wounding, insects, herbivores and environmental stresses. In interaction with other hormones pathways, JAs are involved in various aspects from plant growth and development regulation to the adaptation to environmental stimuli (Devoto, Turner, 2005; Goossens *et al*., 2016). JA was also known as hormone involving in the

response of plants to phosphate starvation condition. In *Arabidopsis*, Pi starvation enhanced synthesis of JA and JA-isoleucine, and therefore led to the expression JA-related genes (Khan *et al*., 2016). In 2019, under Pi starvation, four candidate genes involving in the JA signaling pathway, including three *Jasmonate-zim-domain* (*JAZ*) genes and one *Coronatine insensitive 1* (*COI1*) gene were also induced in the sensitive rice accessions (Zhang *et al*., 2019). The JA-signaling pathway is regulated by the key model COI1-JAZs-MYC2 (Chini *et al.*, 2009). CORONATINE INSENSITIVE 1 (COI1) is an F-BOX E3 LIGASE protein which only interacts with JA-Ile. JASMONATE ZIM DOMAIN protein (JAZ) is a repressor of MYC2 transcription factor of JA-signaling. JA-Ile binds to COI1 and JAZ protein thus leads to JAZ degradation. MYC2 would not be repressed anymore; it is active to conduct the transcription process (Chini *et al.*, 2007; Thines *et al*., 2007). Lying downstream in the JA-signaling pathway, Pathogenesis-Related (PR) genes are regulated by MYC2 and response to cold signals with the pathogen in plants (Seo *et al.*, 2010).

The whole scenario however is not that clear in rice. Since this research tends to focus on JA and its effect on the molecular and morphological characterization of contrasted rice varieties in Vietnamese rice collection, we want to evaluate firstly expression of JA biosynthesis related genes under JA treatment. The expression of JA-related genes would be analyzed and associated with the phenotyping results of root to understand the differences in the physiological aspect and molecular aspect between two contrasted rice varieties. The thorough knowledge of the JA pathway involved in plant resistance and development will assist breeders in selecting cultivars possessing an improved stress tolerance capacity in the future.

MATERIALS AND METHODS

Plant materials

The seeds of G11 or Tam_tron (Hai Duong) and G38 or Nep_nuong (Ha Giang) were provided by Plant Resource Center, Hanoi, Vietnam. Both of two varieties are traditional landraces, G11 represent for *Indica* group and G38 represents for *Japonica* group. These accessions were selected according to the contrasted results of JA response presenting in (To *et al*., 2019).

Primers used in this study

A total of 12 JA biomarkers including 3 markers related to the JA biosynthesis, 3 markers related to the JA signaling pathway, 6 markers related to the JA defense response were used in this study in order to investigate the difference between two contrasting rice varieties. Actin was used as housekeeping gene. The primer list of these 13 genes was summarized in Table 1.

Seed germination and growth plants

Seeds of each variety were selected based on their typical and consistent size, shape and color, without symptoms neither damaged embryos nor contamination. The seeds were kept in the drying chamber at 45°C for 3 days to break the seed dormancy.

Sterilization process was conducted as 2 minutes shaking in ethanol 70% then soaked in Javel water (NaClO 3.8%) including 2 drops of Tween 20% (China). After 25 minutes, discard the liquid and rinse the seeds with sterilized distilled water at least 7 times to remove the Javel water. The tubes were incubated at 28°C for overnight to maximize the water absorption. In the next day, the rice grains were transferred to the petri dishes containing 6g/L Agar. The petri dishes were incubated at 28°C for 2 days in the dark for germination. Qualified germinated seeds were transferred into glass test tubes of half Murashige and Skoog medium (MS/2) at pH= 5.8, containing 2.7 g/L Phytagel (Sigma Aldrich) with or without 5 µM of JA (TCI-Japan) for JA stress phenotype experiments. For low Pi experiment, the qualified germinated seeds were grown in glass test tubes of half Murashige and Skoog medium (MS/2) at pH= 5.8, containing 2.7g/L Phytagel (Sigma Aldrich) with full phosphate (625 µM) or low phosphate (40 µM) content by modifying the amount of KH_2PO_4. The tubes were left in a growth chamber (DAIHAN Scientific, Thermo Stable GC-450) under a 12 h daily light cycle at a humidity of 80%. The light intensity was 12,000 lux. The temperature was adjusted to 26°C in the dark phase and 28°C during light phases. After 7 days, the glass tubes were taken out to measure phenotype parameters: number of crown root (NCR), root length (RTL), shoot length (SHL), root weight (RTW), shoot weight (SHW), total plant weight (TTW). For qPCR experiments, tissues were taken from at least 4 plants.

RNA extraction and cDNA synthesis

RNA was extracted using Trizol® Reagent (Thermo Scientific) following the manufacturer's protocol. Briefly, the sample was ground in liquid nitrogen using a mortar and pestle, 0.75 mL Trizol was added, and the mixture was incubated for 15 minutes at room temperature. After centrifuging for 10 minutes at 12000 rpm, 4ºC, the aqueous phase was transferred into 2 mL Eppendorf tube, 0.3 mL of chloroform was added; the tube was shaken vigorously for 15 seconds, and then incubated at room temperature for 2 - 3 minutes. The sample was centrifuged for 10 minutes at 12000 rpm, 4ºC; 0.75 mL of the clear upper aqueous layer containing RNA was transferred into a new tube containing 0.75 mL isopropanol (-20ºC) followed by incubation at 4ºC for 1 h. RNA was precipitated by centrifugation at 12000 rpm, 4ºC for 15 min and washed twice with 1mL of 75% Ethanol. Pellet was dried in air for 30 min - 1 h and dissolved in 30 µL of MilliQ water, stored at 4ºC for 15 h. RNA integrity was checked on 1% agarose gel. Potential co-purified genomic DNA was digested using DNAse I (Thermo Scientific) according to the manufacturer's recommendation. Extracted RNA was assessed for quality and quantity using NanoDrop-2000 spectrophotometer (Thermo Scientific) before and after DNAse I treatment.

cDNA was synthesized from 2 µg of total RNA (after DNAse I treatment) with Maxima® First Strand cDNA Synthesis Kit (Thermo Scientific), using Oligo(dT) according to the manufacturer's instruction. The reaction was conducted with the thermal cycle of 15 minutes at 25ºC, followed by 45 minutes at 50ºC and terminated by 5 minutes at 85ºC. cDNA quality was checked by PCR with housekeeping gene (*OsACT*) followed by running the PCR products on the agarose gel.

qPCR (Real-time PCR)

Quantitative PCR reactions were performing in the Mx3005P qPCR system (Agilent Technologies) with GoTaq® qPCR master mix (Promega) followed the manufacturer's instruction. The thermal profile was: 95°C for 2 min, followed by 38 cycles of 95°C for 30s, 56°C for 30s and 72°C for 1 min. Data was interpreted by MxPro ET qPCR software ver 4.10 (Agilent Technology). Gene expression level was normalized to the reference gene (Actin) and calibrated with the J0 condition without JA added. In order to determine the relative gene expression in different conditions, mean Ct values were obtained and fold change values were calculated using the 2-ΔΔCT method (Livak and Schmittgen, 2001).

Statistical analysis

The data represented mean ± SD of three replicates and the differences between the data were examined by Student's *t*-test at $p < 0.05$. Statistical analysis (Student t-test) was conducted using Graphpad Prism 6 (https://www.graphpad.com/).

Table 1. List primer of 13 genes used in this study.

No	Primer name	Sequence (5'-3')	Reference
1	OsHI-LOX	GCATCCCCAACAGCACATC AATAAAGATTTGGGAGTGACATATTGG	Qiu *et al.*, 2007
2	OsAOS2rt	CAATACGTGTACTGGTCGAATGG AAGGTGTCGTACCGGAGGAA	Qiu *et al.*, 2007
3	OsAOCrt	AAGAGGAATCGAGGACAAGATATTTG AAGCCTCTTCTTGTTCGGATCA	Qiu *et al.*, 2007
4	OsJMT	CACGGTCAGTCCAAAGATGA CTCAACCGTTTTGGCAAACT	Qiu *et al.*, 2007
5	OsJAZ5	AATGAGGATGGCAACCGAGG	Qiu *et al.*,

		TCTCTTGGAGAGGAATCGTTGC	2007
6	OsJAZ8	GATGGCGTCGACAAGAACAC TGCATTCATCCTGCCCTTTC	Qiu *et al.*, 2007
7	OsbHLH148	ATCTCCATATCTCCTTGT TTTGTACTCTTCTCTTTCTT	Qiu *et al.*, 2007
8	OsMYC2	CTAGCGAGGAAACCCAATCG CCATCCATCCATCCTAACAC	Qiu *et al.*, 2007
9	OsPR1a	AACTTCGTCGGCCAATCTC CATGCATAAACACGTAGCATAGC	Qiu *et al.*, 2007
10	OsPR3	GTGGTGACCAACATCATCAACG TTGTAGCAGTCCAAGTTGGC	Qiu *et al.*, 2007
11	OsPR4	TGGCTACACGGACTATCCTT ATGGAAGTGAGGGTCACTTA	Qiu *et al.*, 2007
12	OsPR10	ACGCCTAAGATGAAGAGGAATAC CTCAAACGCCACGAGAATTTG	Qiu *et al.*, 2007
13	OsACT	CAGCACATTCCAGCAGAT GGCTTAGCATTCTTGGGT	Qiu *et al.*, 2007

RESULTS

The contrasting effect of JA treatment on two genotypes

The remarkable differences in term of phenotype under 5 µM of JA treatment between the two varieties were selected throughout the study of screening from 156 Vietnamese rice collection against exogenous (To *et al*., 2019). The percentage of reduction of each trait was used to analyze the effect of JA while the two varieties were exposed to 5 µM of JA compare to non-treatment condition. Figure 1 showed clearly the differences in phenotypes between G38 plants and G11 plants. G38 plants reduced the SHL, RTW, SHW and TTW negatively in response to JA treatment compare to medium without JA, whereas G11 plants change their phenotype slightly in the same condition except for the RTL trait. Based on this analysis, the contrasting response in term of JA treatment between G11 and G38 can be confirmed.

Gene expression study of JA-related genes in two contrasting genotypes

Figure 2 and 3 summarized the difference in the genes expression level of 12 JA markers genes between the sensitive variety G38 and from the tolerant variety G11. Changes are more obvious in plant's root than in the leaf might indicate that external JA mostly alters the root's metabolism as its first exposed organ with JA in the medium. Interestingly, there was a significant increase of expression level of some biosynthesis genes group such as *OsHILOX, OsAOS, OsAOC and OsJMT* in the root variety G11 plants compare to that in G38 - a sensitive genotype.

In the pool of examined genes, JASMONATE ZIM-domain *OsJAZ5* and *OsJAZ8* shown to be clearly up-regulated by JA in root: *OsJAZ5* in G11 was up-regulated over 40 times and also in G38, the up-regulation was nearly 20 times; *OsJAZ8* is over 10 folds greater in the presence of JA for G11 and around 13 folds greater for G38. We observed the activation of

OsPR1a and *OsPR10* (around 9 times and 40 times more expressed when plants were treated with JA, respectively) in G11 while it was nearly the same as the control level in the case of G38 variety for each.

Effect of low phosphorus condition (40 µm) on two JA-contrasted-response rice varieties

The percentage of change was used to analyze the effect of low phosphorus condition (40 µM) plants compared to full-phosphorus condition (625 µM) for each trait. Effect of phosphorus starvation in G11 was significantly different compared to that in G38 plants for all 5 traits, especially increase more than 30% in root weight (Figure 4).

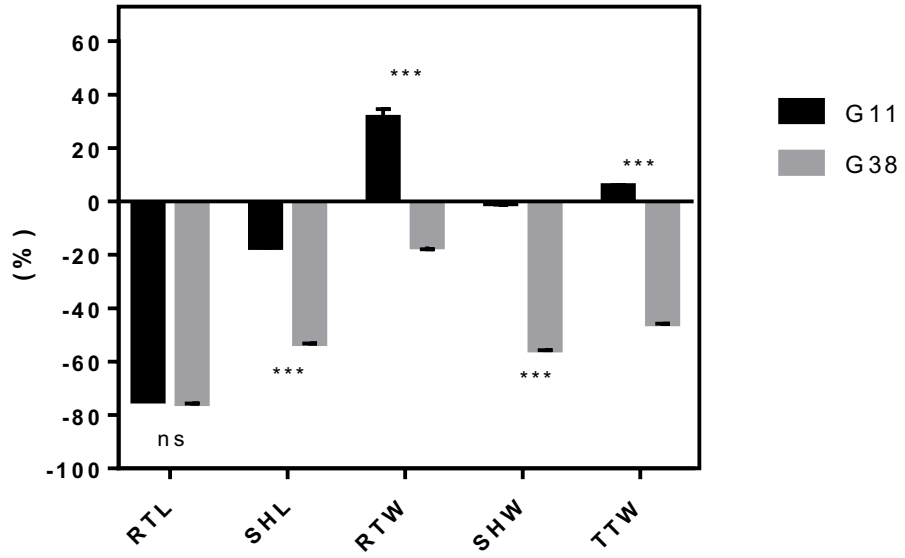

Figure 1. Effect of JA treatment (5 µM) compared to non-treatment condition (0 µM) to 7 day-olds plantlets of G11 and G38. Ratios (%) of variation for 5 traits including root length (RTL), root weight (RTW), shoot length (SHL), shoot weight (SHW) and total weight (TTW) was calculated by an offset of means of the treated trait to means of non-treated trait then dividing by means of the non-treated trait. Presented data are means ± SD from 13 plants grown in the independent glass tube. Statistical significance (*, P < 0.05; **, P < 0.01; and ***, P < 0.001) according to Student's *t*-test.

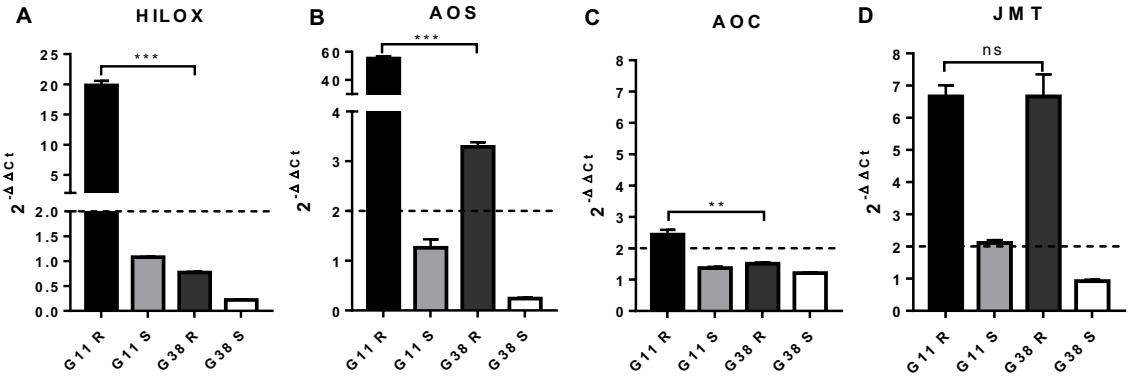

Figure 2. Genes involved in JA biosynthesis are induced after 7 days under 5 µM of JA treatment. The expression level of *HILOX* (A), *AOS* (B), *AOC* (C), and *JMT* (D) measured in root (R) and shoot (S) of G11 and G38. The expression level of interested genes was normalized with Actin level and then calibrated with the expression level of J0 (non JA treatment). A minimum 2-fold change is considered as significant relative quantification within the technical variation. Presented data are means ± SD of three samples obtained from independent plates, with three technical replicates for each sample. Each sample consists of a pool of tissues isolated from 4 plants for shoots and roots. Statistical significance (* for P < 0.05; ** for P < 0.01; and *** for P < 0.001) according to Student's *t*-test.

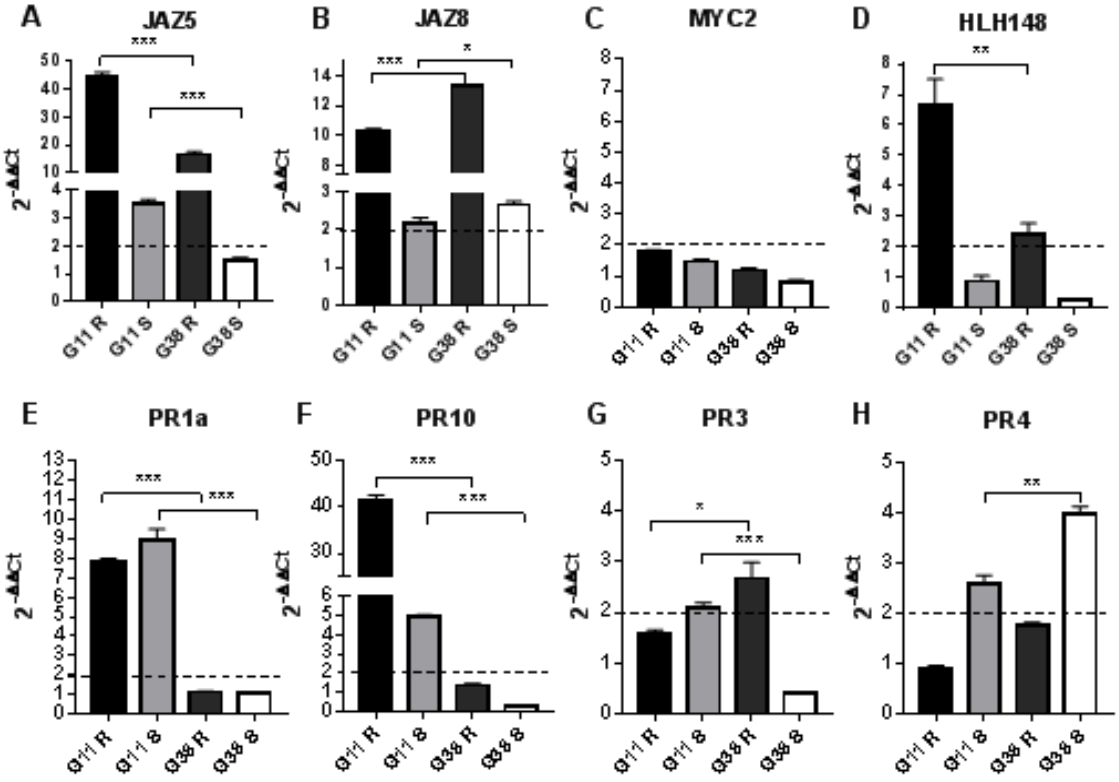

Figure 3. Genes involved in JA signaling (A, B, C, D) and JA response (E, F, G, H) are induced after 7 days under 5 µM of JA treatment. The expression level of *JAZ5* (A), *JAZ8* (B), *MYC2* (C), *HLH148* (D), *PR1a* (E), *PR10* (F), *PR3* (G) and *PR4* (H) measured in root (R) and shoot (S) of G11 and G38. The expression level of interested genes was normalized with Actin level and then calibrated with the expression level of J0 (non JA treatment). A minimum 2-fold change is considered as significant relative quantification due to the technical variation. Presented data are means ± SD of three samples obtained from independent plates, with three technical replicates for each sample. Each sample consists of a pool of tissues isolated from 4 plants for shoots and roots. Statistical significance (*, P < 0.05; **, P < 0.01; and ***, P < 0.001) according to Student's *t*-test.

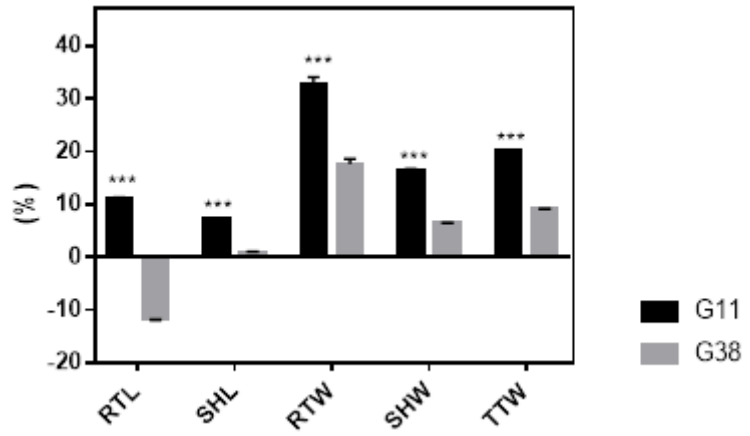

Figure 4. Effect of low Pi condition (40 µM) compared to full phosphate condition (625 µM) to 7 day-old plantlets of G11 and G38. Ratio (%) of variation for 5 traits including root length (RTL), root weight (RTW), shoot length (SHL), shoot weight (SHW) and total weight (TTW) was calculated by the offset of means of the treated trait to means of non-treated trait then dividing by means of the non-treated trait. Presented data is means ± SE from 10 plants grown in the independent test tube. Statistical significant (*, P < 0.05, **, P < 0.01, and ***, P < 0.01) according to Student's *t*-test.

Root hairs play an important role in facilitating phosphorus acquisition when phosphorus availability is low by increasing the absorptive surface area of the root and allowing the root to explore a greater soil volume (Jungk., 2001). This role has been demonstrated in wheat (*Triticum aestivum* L.) and barley cultivars (*Hordeum vulgare* L.) (Singh Gahoonia *et al*., 1997). The increase up to 0.7 mm of root hair length was also seen in tomato (*Lycopersicon esculentum*), rape (*Brassica oleracea*), spinach (*Spinacia oleracea*) when phosphate concentration decreased to 2 µM (Foehse, Jungk, 1983) and in *Arabidopsis thaliana* (Bates, Lynch, 2000); (Song *et al*., 2016). Longer root hairs were also observed in our two selected rice lines in Pi deficiency condition compared to full Pi condition (Figure 5). Moreover, G11 seems to react stronger than G38 by increasing more root hair length than G38. It shows that the genetic variation for root hair length in response to P deficiency also exists.

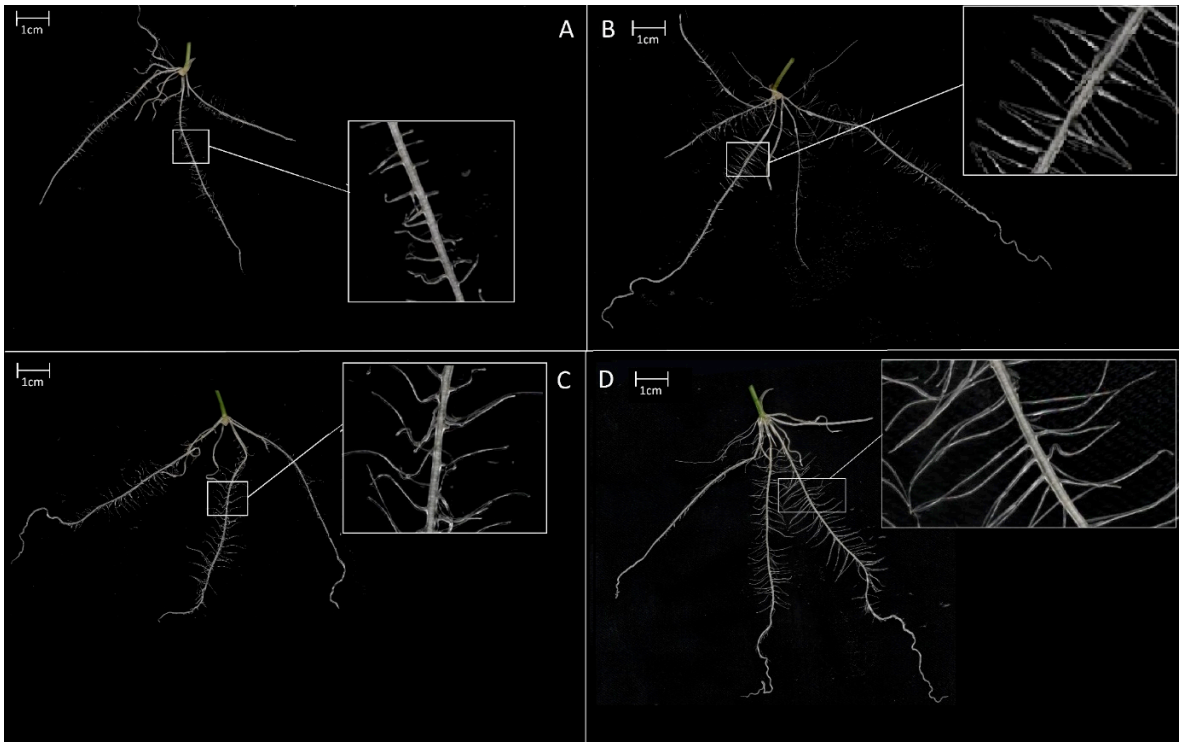

Figure 5. Effects of low Pi condition (40 µM) in root hair of G11 and G38 7-day-old plantlets compare to full phosphorus (625 µM) plants' root hair. Root hair of G38 P0 (A), G38 P* (B), G11 P0 (C), G11 P* (D) were scanned. A section of root was selected and zoomed (5x) from 2cm from the stem base of the primary root. Scale bar = 1cm. P* indicates the Pi starvation medium, P0 indicates the full Pi medium.

DISCUSSION

Abiotic stress is becoming more and more intense in Vietnam, which reduces rice production severely. Therefore, it is necessary to identify the "tolerant variety to stress as well as to understand the mechanism underlying the stress response in rice. In this study, we found that G11 plants can tolerate better in JA treatment condition in term of phenotyping index compare to G38 - a "sensitive" one. Combined physiological and molecular approaches through the JA pathway help us to understand better how these contrasting varieties response differently. The tolerance of G11 plants can be explained through different aspects; the contribution of JA-signaling pathway in term of its defense was investigated in this paper. It is generally accepted that exogenous JAs causes a significant up-regulation of some genes, especially in root part. However, the level of expression of some key

markers in JA biosynthesis and JA transcriptional regulation genes were remarkably different between the two varieties. Figure 6 shows the simplified schema of the JA biosynthesis and response pathway for 12 JA genes markers used in this study. G11 had a higher expression level of some JA-biosynthesis genes and transcriptional regulation genes than G38 under JA treatment.

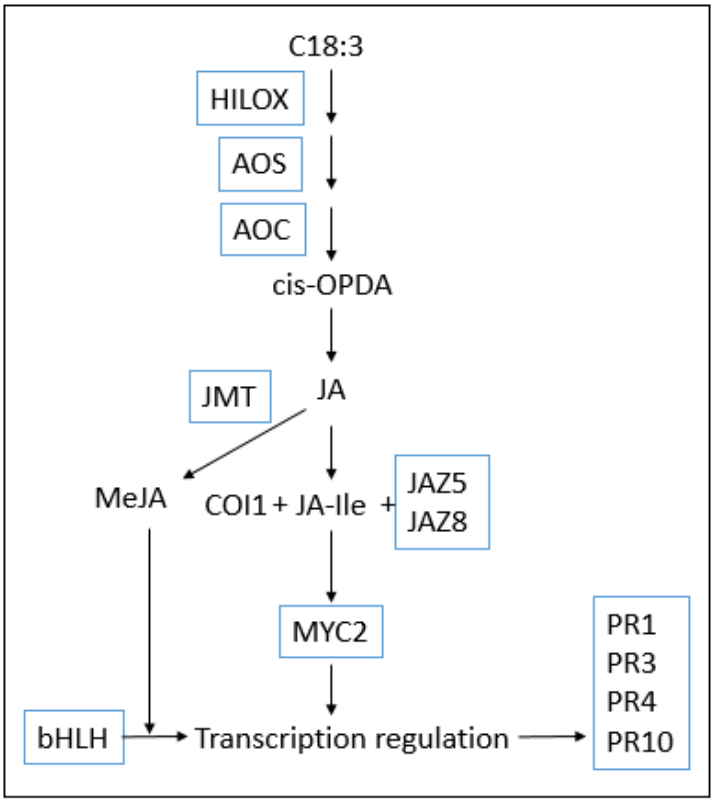

Figure 6. Simplified schema of JA- biosynthesis and signaling pathway. The blue box marked genes studied in this research.

Following the pathway of JA-signaling, the group of JA-biosynthesis players which includes *OsHI-LOX*, *OsAOS* and *OsAOC* are the first set of enzymes that needed to be analyzed and discussed. The involvements of these genes into biosynthesis pathway are simplified and highlight in the following schema (Fig. 6). From that, *OsHI-LOX* is the first gene (involved in JA biosynthesis pathway. The upregulation (20-folds) of *OsHI-LOX* in G11 is significantly higher compared to that of G38. Following up is the dramatic increase of *OsAOS* transcript in G11 (60 times), which is the next key component in the synthesis process of JAs. Subsequently, the expression level of *OsAOC* in G11 is still nearly 2 times higher than that of G38.

In stress condition, after JA has been synthesized, JA was derived in some distinguished branches: the making of hormonally active metabolite JA-Isoleucine (JA-Ile) and the production of a non-active yet very active locally signaling compound, for example: MeJA (Wasternack, Hause, 2013). JA-Ile is one of the active branches of JAs metabolites that can interact with SCF COI1-JAZs co-receptor to promote the transcription of JA-induced genes. This mechanism happened strictly under the control of some OsJAZs protein network family. *OsJAZ5* and *OsJAZ8* were used as representatives of JAZs encoding genes in the gene set markers. The increase in expression of these two genes is one of the most significant features in the

results indicated the binding of JA-Ile to SCF COI1-JAZs complex, which requires multiple JA-dependent physiological responses.

The expression level of *OsPR1a* in G11 was 9 times induced, whereas there was almost no induction in G38. Regards to *OsbHLH148,* a gene which is involved in JA-signaling, the expression level of this gene in G11 is significantly different compare to that in G38. These results give support for the hypothesis of JA is synthesized in larger quantity in G11 compared to G38, which leads to the high expression of some stress-responsive genes such as *OsPR1a* and *OsPR10*, then conferring its tolerance in G11.

The diverse response of Vietnamese rice to Pi starvation has been studied (Mai *et al*., 2018). Here, we also show the different response to Pi starvation of 2 Vietnamese rice accessions which response contrastly to JA. The link between JA pathway and Pi starvation has been investigated in various studies. In 2016, Khan and his colleagues found that phosphorus starvation induces the JA pathway by an accumulation of JA, JA-Ile and other derivatives level in both root and leaves in *Arabidopsis thaliana*. Moreover, the Pi starvation also activates the *AtJAZ10* and *AtVSP2* expression, resulting in the resistance to insect herbivory (Khan *et al.*, 2016).

In 2016, Huang and his colleagues found that the overexpression of *OsPR10* under Pi condition confers to rice and *Arabidopsis* the resistance to pathogen *Xoo* and *Xoc* (Huang *et al*., 2016). In this study, we also found that the genes *OsPR10* is more than 40 times up-regulates in G11 than in G38 in root tissues and 5 times in shoot tissues. Consistence to the phenotype effect, these results obtained suggest a strong involvement of JA signaling pathway and regulation pathway in order to deal with the Pi starvation response in rice.

CONCLUSION

The obtained results above demonstrated that shoot growth of G11 accession is less inhibited by exogenous JA treatment and even “stimulated” by phosphorus starvation than G38 plant. Pi deficiency has a negative impact to G38 root length by inhibiting its growth while positively affected G11 root length suggesting that G11 did not suffer much effect of Pi stress, which was the similar effect with JA treatment. This study highlights the differences in JA growth response in 2 contrasting rice genotypes. Also, it suggests the link between JA developmental response and the tolerance to the Pi starvation condition in rice.

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PHÂN TÍCH SO SÁNH VỀ BIỂU HIỆN SINH LÝ VÀ PHÂN TỬ CỦA HAI GIỐNG LÚA CÓ KIỂU HÌNH TƯƠNG PHẢN VỚI ĐÁP ỨNG JASMONIC ACID

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TÓM TẮT

Lúa là một trong những cây lương thực quan trọng nhất, tuy nhiên năng suất của cây lúa đang bị đe dọa nghiêm trọng bởi các điều kiện bất lợi sinh học và phi sinh học. Axit jasmonic (JA) và dẫn xuất của nó là một loại hooc môn thực vật được sử dụng rất phổ biến như một chất điều hòa sinh trưởng, phát triển và phản ứng bảo vệ của cây. Trong nghiên cứu này, chúng tôi so sánh các phản ứng về mức độ sinh lí và phân tử của hai giống lúa G38 (Nếp nương) và G11 (Tám tròn) trong phản ứng với JA. Khi xử lý với JA, giống lúa G38 bị giảm chiều dài thân, khối lượng rễ, khối lượng thân và khối lượng cả cây. Kết quả chỉ ra tính nhạy cảm của G38 với JA. Trái lại, giống lúa G11 ít bị ảnh hưởng hơn về tất cả các tính trạng khi bị xử lý với JA. Để hiểu rõ hơn đáp ứng này thông qua con đường sinh tổng hợp JA và các phản ứng khác nhau của hai giống lúa trái ngược, mức độ biểu hiện của 12 gen liên quan đến JA đã được nghiên cứu. Các gen liên quan đến sinh tổng hợp JA biểu hiện cao hơn hẳn ở giống lúa G11 so với giống G38. Ngoài ra, phản ứng của hai giống lúa G11 và G18 với điều kiện môi trường thiếu phốt phát cũng được nghiên cứu. Trong môi trường thiếu phốt phát (40 µM), giống lúa G11 có nhiều rễ hơn, rễ và thân dài hơn, khối lượng thân và rễ cao hơn so với giống G38. Điều này chỉ ra rằng: giống G11 không bị chịu nhiều ảnh hưởng trong điều kiện môi trường thiếu phốt phát. Nghiên cứu này nhấn mạnh sự khác nhau trong phản ứng với JA của hai giống lúa trái ngược, đồng thời cũng chỉ ra mối liên quan giữa phản ứng với JA và chống chịu với điều kiện môi trường thiếu phốt phát ở lúa.

Từ khóa: *stress phi sinh học, Axit Jasmonic (JA), Các gene đáp ứng với JA, thiếu phosphate, lúa (Oryza sativa* L.*)*