

# Effect of phosphorus deficiency on allelopathic activity of lowland *indica* rice

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Received 29 Mar 2022, Accepted 12 Oct 2022

Available online 5 Dec 2022

**ABSTRACT:** Allelopathy is a phenomenon in which plants exude biochemicals that inhibit the growth of nearby plants. Allelopathic activity and biochemical production are induced by environmental stresses. This study investigated the effect of phosphorus (P) deficiency on growth and allelopathic activities in two landrace rice cultivars of southern Thailand, Nang loy and Niaw look pueng. Rice seedlings were hydroponically grown for 14 days in Yoshida Solution with normal (HP) and low (LP) P concentrations. Growth and phosphate (Pi) contents in rice seedlings were determined to evaluate the difference in internal P status between plants grown under the HP and LP conditions. Water extracts were prepared from shoots and roots of rice seedlings to test allelopathic activity against lettuce seedlings. The results showed that rice seedlings responded to P deficiency by reducing shoot and root Pi content and increasing leaf greenness. Changes in seedling growth were scarcely detected in the young rice seedlings. In a germination assay, water extracts of P-deficient seedlings from both rice cultivars lowered germination indices and inhibited lettuce seedling growth. Furthermore, shoot extracts of the same rice cultivar more strongly inhibited the development of lettuce seedlings than root extracts. The greater allelopathic activity of the shoot extracts might be a result of their higher phenolic contents, which could be induced by P deficiency. Therefore, an allelopathic trait of rice seedlings is an early response to P deficiency prior to growth inhibition under the low P condition.

**KEYWORDS:** phosphorus deficiency, allelopathy, rice, phenolics

## INTRODUCTION

Allelopathy is a phenomenon in which plants release biochemicals that affect the growth of other nearby plants. The released biochemicals are called allelochemicals. The effects of allelopathy can be dilemmatic to receiver plants depending on concentrations and types of allelochemicals and microbial alterations of biochemicals in the soil. Allelochemicals are capable of stimulating the germination and growth of other plants or inhibiting the germination and growth of receiver plants [1, 2].

Rice exudes many allelochemicals into soil. These allelochemicals include phenolic acids (such as *p*-hydroxybenzoic acid, *p*-coumaric acid, ferulic acid, syringic acid, and vanillic acid) and other secondary metabolites (such as flavone, resorcinol, hydroxamic acid, momilactone A, and momilactone B) [3–5]. The major constituents of allelochemicals are phenolic acids, which are less phytotoxic than momilactone A and momilactone B [5, 6]. The production of momilactones is highly conserved in the *Oryza* genus. The only other terrestrial plants reported to produce momilactones are *Echinochloa crus-galli* and the bryophyte *Calohypnum plumiforme* [7].

The production of allelochemicals by plants is altered by environmental stresses. In a recent report,

allelochemicals released by *Solidago canadensis* under drought stress, mimicked by polyethylene glycol-6000, inhibited the seed germination and seedling growth performance of lettuce [8]. A number of recent and earlier works have demonstrated that rice also elevates its allelopathic potential in response to environmental stress. Biotic stress induced by the inoculation of the blast fungus *Magnaporthe oryzae* and abiotic oxidative stress from zinc treatment activated the rice genes *diterpene synthase OsCPS4* and *diterpene synthase OsKSL4*, which are involved in the biosynthesis of allelopathic momilactones [9, 10]. Moreover, the generation of momilactones A and B was positively correlated with drought tolerant rice cultivars [11]. In an earlier work, the increased exudation of momilactone B by rice seedlings treated with jasmonic acid, the key signaling molecule involved with stress responses, increased the inhibition of the growth of *Echinochloa crus-galli* [12]. Furthermore, after UV exposure, the transcription of *OsKSL4* and the production of momilactone under the jasmonate-dependent pathway were shown to be up-regulated [13].

Nutrient deficiency is another environmental stress that increases the allelopathic potential and momilactone production in rice. A study of rice under hydroponic cultivation with Hoagland's solution found that allelopathic intensity was directly correlated with

the macro- and micronutrient contents of the solution [14]. Moreover, there is evidence indicating that nitrogen deficiency enhances rice allelopathy [15], and RNA sequencing analysis revealed that *OsCPS4* and the momilactone biosynthetic genes *CYP99A2* and *CYP99A3* were up-regulated in P-deficient roots of rice [16]. Plants also accumulated higher amounts of low molecular weight allelopathic phenolics, such as *p*-coumaric acid and ferulic acid, in response to P deficiency [17, 18]. Additionally, the phenolic compound nicotinic acid was strongly exuded from plant roots under P deficiency and improved soil P solubilization [19, 20]. Therefore, P deficiency is an abiotic stress that is almost certainly involved with the biosynthesis and accumulation of allelochemicals in rice. However, the direct effect of P deficiency on rice allelopathy has not been clarified.

In rice cultivation, rice is planted at high density, introducing nutrient competition among the rice plants and the need for fertilizers to optimize their growth [21]. Meanwhile, weeds in rice paddies intensify the nutrient competition [22]. Among the essential nutrients, P is a major limiting factor in rice paddy soil because most P is unavailable for plant uptake; and some rice paddies are themselves considered to be P-deficient [23, 24]. When rice is faced with strong intra- and interspecific P competitions, the effect on allelopathy of stress from low P availability remains unknown. The allelopathic traits in aboveground and belowground rice in response to P deficiency are also poorly understood. In this study, we investigated the effect of P deficiency on the different basal allelopathic activities produced by rice seedlings of the Thai *indica* landraces, Nang loy and Niaw look pueng.

## MATERIALS AND METHODS

### Rice growth in hydroponics

Seeds of the lowland *indica* rice cultivars Nang loy and Niaw look pueng were germinated in darkness for 5–7 days until the seedlings were 1–2 cm in length. The seedlings were transferred to grow hydroponically in Yoshida Solution [25] having normal P concentration (HP: 10 mg/ml) and low P concentration (LP: 0.5 mg/ml). Rice plants were grown in micropipette tip boxes (500 ml in volume) with roots submerged in the solution. There were 30 plants per box and five biological replicates (five boxes per treatment). The solution was changed every two days. After growing for 14 days, three rice plants per box were examined for growth. Shoot and root lengths were measured, leaves were counted, leaf greenness was measured with a chlorophyll meter (SPAD-502 plus, Hangzhou Mindful Technology, Japan) on the second leaf from the top, fresh shoots and roots were weighed, and shoots and roots dried at 60 °C for 24 h were weighed.

### Rice phosphate quantification

An assay reagent was prepared by dissolving 5 g  $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$  with 50 ml of 10 N  $\text{H}_2\text{SO}_4$ , giving a 10% ammonium molybdate stock solution. The 10% stock solution was further diluted with distilled water at a ratio of 1:10 to obtain a 1% ammonium molybdate stock solution. Fifty grams of  $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$  was dissolved in 1 l of the 1% stock solution for the preparation of ferrous sulfate-ammonium molybdate assay reagent [26].

Determination of Pi levels in rice was achieved by cutting 10 mg of rice leaf, or 0.5 mg of rice root, into small pieces. The sample was placed into a 1.5 ml microcentrifuge tube. A total of 400  $\mu\text{l}$  of 3%  $\text{HClO}_4$  was added, and the tube was submerged in liquid nitrogen for 5 min, then stored at 4 °C for 3 h. After that, the tube was centrifuged at 15,000 rpm for 5 min. The supernatant was collected, and 120  $\mu\text{l}$  were mixed with 80  $\mu\text{l}$  of assay reagent and left to incubate for 10 min at room temperature. Spectrophotometric absorbance was measured at 720 nm. The result was compared with 0.01 M  $\text{KH}_2\text{PO}_4$  standard solution.

### Assay of rice allelopathy

Water extracts of rice shoot and root at 5% (w/v) were prepared by first air-drying rice plants indoors for 24 h at room temperature. After that, shoots and roots were cut into small pieces (about 1 cm in length). A total of 0.25 g of rice shoot was submerged in 5 ml of distilled water, or 0.1 g of rice root was submerged in 2 ml of distilled water. Samples were left submerged at room temperature for 24 h. On the following day, the contents were filtered with cheesecloth, and the water extracts were used directly in allelopathic assays.

For the allelopathic assay, 20 lettuce seeds were placed on a single layer filter paper (Whatman No. 1, GE Healthcare, UK) in a 3.5 cm diameter Petri dish. A total of 0.7 ml of rice shoot or root water extract was poured into the Petri dish. Distilled water was used as the control. The Petri dish was closed, wrapped with parafilm, and left at room temperature for three days. After that, germination percentage was measured, and 10 lettuce seedlings per Petri dish were randomly selected for root length measurement. The 10 seedlings were dried at 60 °C for 24 h, and the dry weight was recorded. Two technical replicates (two Petri dishes) were used for one biological replicate.

Germination index (GI) was calculated by the following formula [27]:  $\text{GI} = (\text{germination percentage of treatment} \times \text{average root length of treatment}) / (\text{germination percentage of control} \times \text{average root length of control}) \times 100$ .

Inhibition percentage of growth is calculated using the following formula:  $\text{Inhibition percentage (\%)} = (\text{dry weight of control} - \text{dry weight of treatment}) / (\text{dry weight of control}) \times 100$ .

### Quantification of total phenolic and flavonoid contents in rice seedlings

Rice extracts were prepared by crushing 200 mg of rice shoot or root in liquid nitrogen in a mortar. The obtained powder was placed in a 1.5 ml microcentrifuge tube, and 800  $\mu$ l of 85% MeOH were added yielding a 25% (w/v) extract.

To measure the total phenolic content, 10  $\mu$ l of extract were mixed with 200  $\mu$ l of 10% Folin-Ciocalteu phenol reagent, and 1 ml of 10%  $\text{Na}_2\text{CO}_3$  was added. The reaction proceeded at room temperature for 10 min before absorbance was measured at 735 nm and compared with the absorbance of gallic acid standards.

To measure the total flavonoid content, 20  $\mu$ l of the extract were mixed with 80  $\mu$ l of distilled water in a 96-well plate. The diluted extract was incubated with 6  $\mu$ l of 5% (w/v)  $\text{NaNO}_2$  for 5 min at room temperature, then with 6  $\mu$ l of 10% (w/v)  $\text{AlCl}_3$  for 5 min at room temperature. Following the incubation, 40  $\mu$ l of 4% (w/v) NaOH were added, and the total volume was adjusted to 200  $\mu$ l before absorbance was measured at 510 nm. The result was compared with quercetin standards.

### Data analysis

Data were visualized by the ggplot2 package [28] in the R software version 4.0.5 [29]. Significant differences among the means of the treatments were analyzed by one-way ANOVA followed by LSD using the agricolae package [30] in R.

## RESULTS

### Effects of P deficiency on growth and Pi content of rice

To induce P deficiency, the Nang loy and Niaw look pueng seedlings were grown for 14 days in normal P (HP) and low P (LP) hydroponic solutions in the greenhouse. The LP treatment did not change the shoot growth of rice seedlings in either cultivar (Fig. 1A), but reduced root growth was detected in the Niaw look pueng rice seedlings (Fig. 1B). Moreover, no change in the root to shoot ratio of either cultivar was observed among the two P treatments (Fig. 1C). To verify the P deficiency of the rice seedlings, shoot and root Pi contents were quantified. The results showed that shoot and root Pi contents of both cultivars were significantly reduced in the LP treatment (Fig. 1D-E), whereas the leaf greenness of both cultivars was significantly higher in the LP treatment (Fig. 1F). Therefore, due to the lower accumulation of Pi in shoots and roots and the higher SPAD leaf greenness, the rice seedlings of both cultivars could be considered P-deficient.

### Effects of P deficiency on allelopathic activity of rice

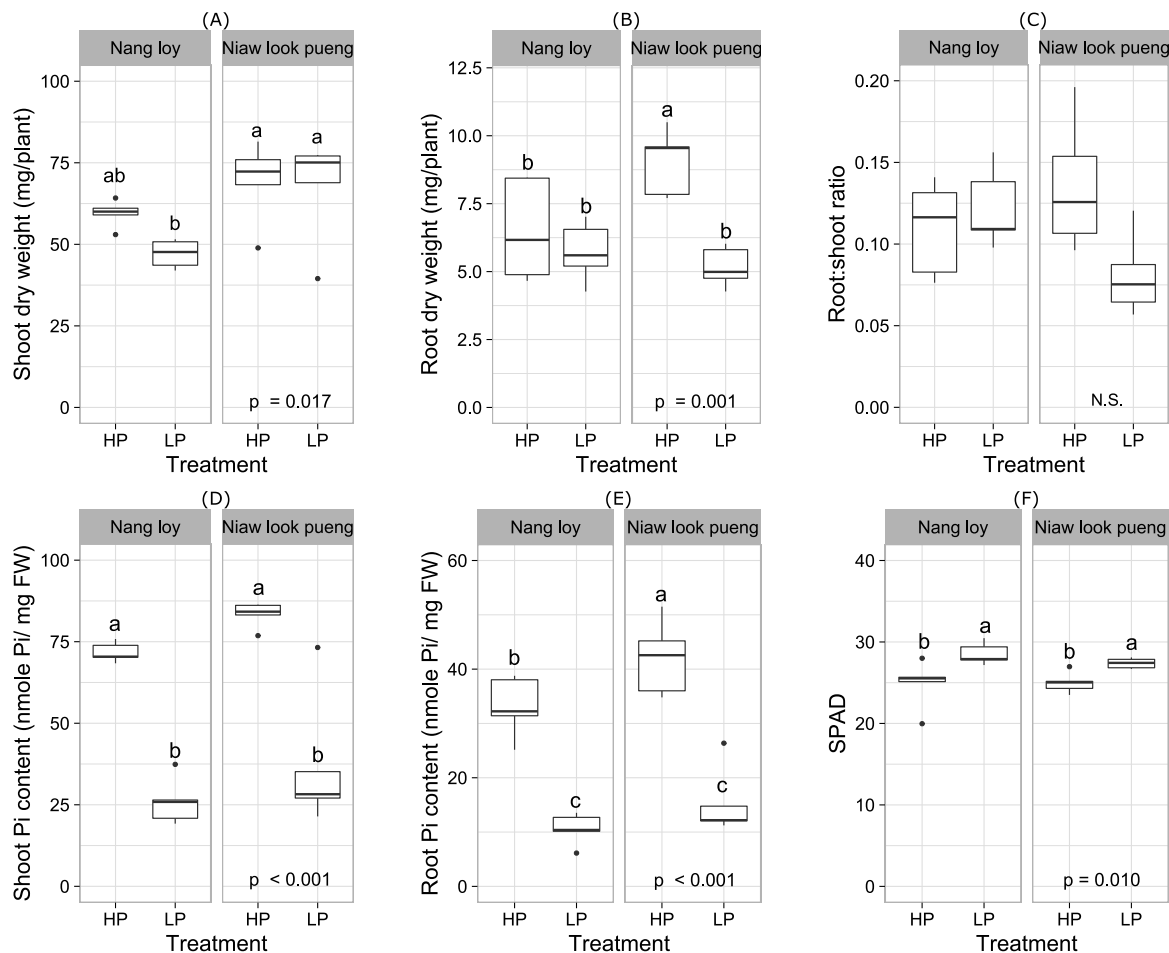
To test the allelopathic activity of both rice cultivars, shoot and root water extracts of both cultivars were applied to lettuce seeds. Lettuce seeds receiving shoot extract of both cultivars grown in the LP condition showed markedly lower germination and growth than seeds in the other six treatments and control (Fig. 2A). The germination indices were overall lower for lettuce seedlings that received extracts of the plants grown in the LP condition, with the exception of the shoot extract of the Nang loy cultivar. Germination indices were higher for lettuce seedlings that received extracts of the Niaw look pueng cultivar than the Nang loy cultivar, indicating greater allelopathic activity and germination suppression by the Nang loy cultivar. The germination indices also showed that germination and root growth of the lettuce seedlings was inhibited more by shoot extracts of both cultivars grown in the LP condition than root extracts of both cultivars grown in the LP condition (Fig. 2B). The growth of the lettuce seedlings (Fig. 2C) was inhibited more by the extracts of the cultivars grown in the LP condition than extracts of the same cultivars grown in the HP condition, with the exception of the root extract of Niaw look pueng. Overall, the shoot extracts exhibited greater inhibition of lettuce seedling growth than root extracts. LP treatment thus significantly heightened the allelopathic activity of both cultivars.

### Effects of P deficiency on total phenolic and flavonoid contents of rice

We hypothesized that P deficiency changes the accumulation of metabolites in rice seedlings. Therefore, total phenolic and flavonoid contents were measured in two-week old rice shoots and roots. The results showed that total phenolic contents in the shoots were significantly higher than the roots (Fig. 3A). The accumulation of phenolic contents in P-deficient rice seedlings tended to be higher but the increased accumulation of phenolic content due to P deficiency was significant only in shoots of the Nang loy cultivar (Fig. 3A). However, differences in total flavonoid contents of the rice seedlings were not detected between rice tissues, cultivars, and P treatments (Fig. 3B). In conclusion, we demonstrated that when the rice seedlings confront P deficiency, phenolic accumulation is higher in shoots than roots.

## DISCUSSION

P deficiency only slightly inhibited the growth of rice and did not alter the root to shoot ratio in two-week old rice seedlings (Fig. 1A-C). However, the soluble Pi contents of shoots and roots of the rice seedlings were reduced (Fig. 1D-E). In a recent work, the inhibition of rice biomass by low P availability was not detected in three-week old rice seedlings, while leaf

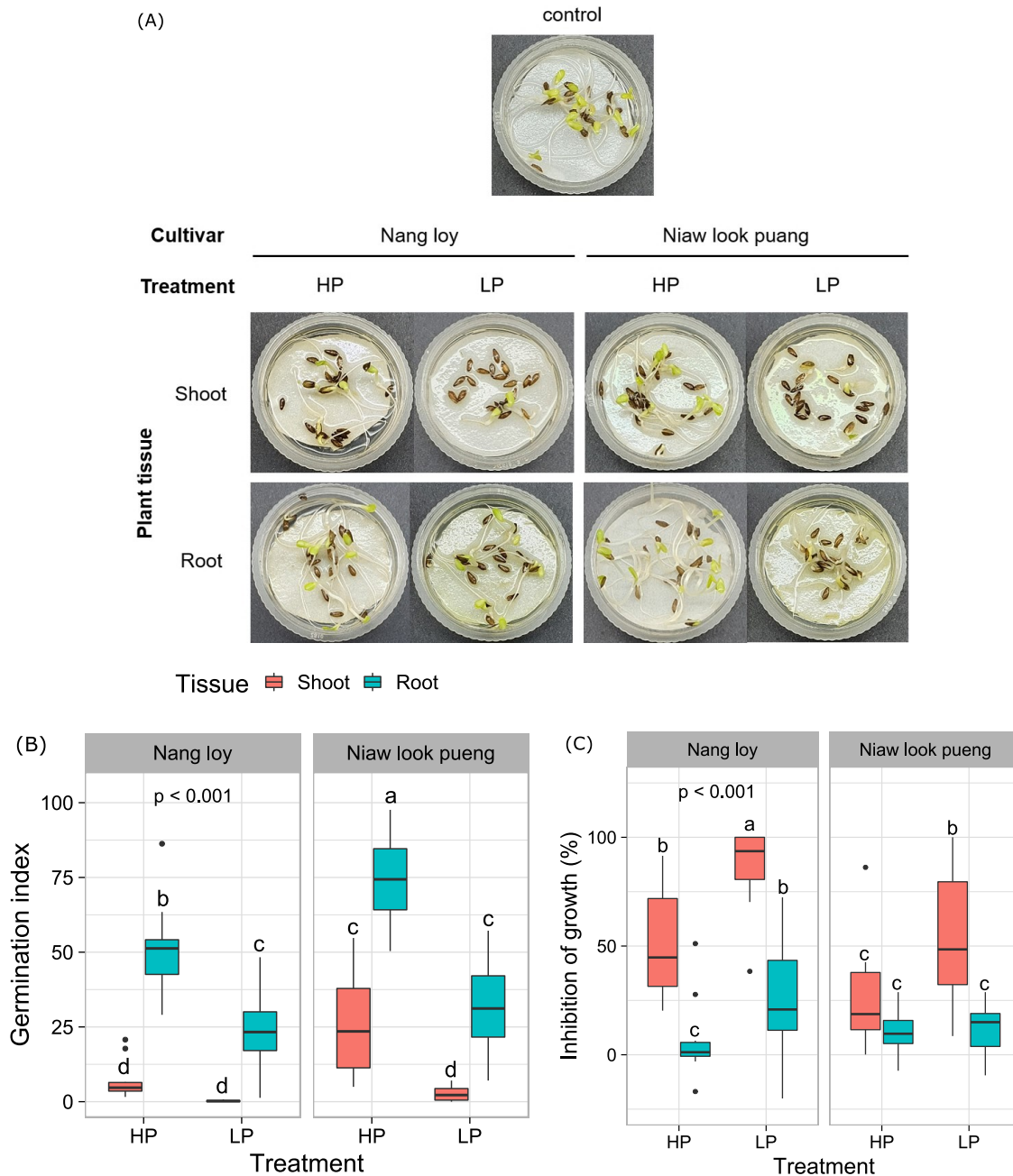


**Fig. 1** Effect of P deficiency on growth and Pi content of rice seedlings. Nang loy and Niaw look pueng *indica* rice cultivars were grown hydroponically in Yoshida solution containing normal P (HP) and low P (LP) concentrations. The boxplots show the distribution of shoot dry weight (A), root dry weight (B), and root:shoot ratio (C), shoot Pi content (D), root Pi content (E), and leaf greenness measured by chlorophyll meter at the second leaf from the top of the shoots (F) ( $n = 5$ ). Different letters indicate statistically significant differences at  $p \leq 0.05$ . N.S. indicates non-significant difference.

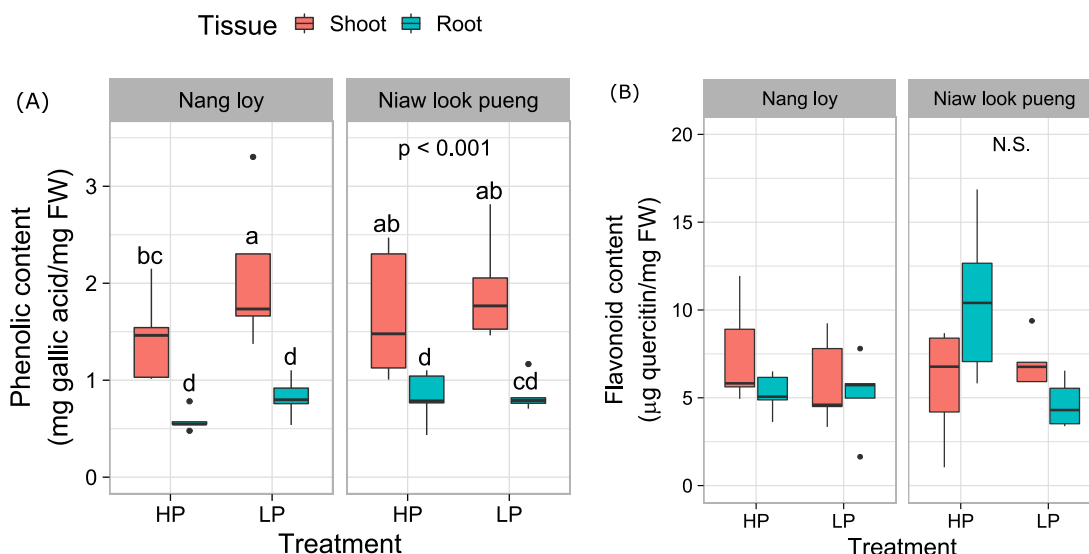
Pi contents were significantly reduced [31]. However, growth suppression due to P deficiency has been detected in rice seedlings of some rice cultivars, consistent with the higher transcription of Pi deficiency-responsive genes such as *OsIPS1*, *OsSPX1*, *OsSQD2*, *OsPAP10*, and *OsPT8* [32]. Under P deficiency, rice seedlings acquire P from the seed. At the early vegetative stage, the seed is an important P source for the growth and development of seedlings, providing P for approximately three weeks, while the seedling simultaneously takes up P via roots at the fourth day after germination [33]. Therefore, growth suppression by P deficiency in young rice seedlings is undetected. As with barley, another  $C_3$  crop, growth reduction due to P deficiency is not detected during the first two weeks of growth, whereas shoot and root Pi

contents are markedly reduced within three days of low P conditions [34]. However, we found that low P stress increased the SPAD value in the second leaf (Fig. 1F). Increased leaf greenness is a phenotypic response of rice to P deficiency [35]. Moreover, P deficiency increases the leaf greenness of other  $C_3$  grass species [36]. Thus, the reduction of Pi contents and the greener leaves in the P-deficient rice seedlings in our study indicate that the LP condition was sufficient to initiate physiological changes in the early vegetative stage.

In the present study, the allelopathy of both cultivars could be induced by P deficiency (Fig. 2), but the Nang loy cultivar showed higher allelopathic potential than the Niaw look pueng cultivar. Rice allelopathy is dependent on genetic variation [37]. Lemont



**Fig. 2** Effect of P deficiency on allelopathic activity of Nang loy and Niaw look pueng rice cultivars. Lettuce seeds were exposed to water extracts of Nang loy and Niaw look pueng seedlings grown hydroponically in Yoshida solution containing normal P (HP) and low P (LP) concentrations. Photographs of lettuce seedlings are demonstrated (A). The boxplots show the distribution of germination index (B) and inhibition of growth (C) of lettuce seedlings that received shoot (red) and root (blue) aqueous extracts of the rice cultivars. Data represent five biological replicates with two technical replicates ( $n = 10$ ). Different letters indicate statistically significant differences at  $p \leq 0.05$ .



**Fig. 3** Effects of P deficiency on total phenolic and flavonoid accumulation of Nang loy and Niaw look pueng rice cultivars. The boxplots show the distribution of total phenolic (A) and flavonoid (B) contents in shoot (red) and root (blue) of two-week old rice plants of the indica cultivars Nang loy and Niaw look pueng grown in hydroponic solution containing normal P (HP) and low P (LP) concentrations ( $n = 5$ ). Different letters indicate statistically significant differences at  $p \leq 0.05$ . N.S. indicates non-significant difference.

*japonica* rice and PI31227 *indica* rice cultivars have been used in several studies of rice allelopathy as model non-allelopathic and allelopathic rice cultivars, respectively. The allelopathic activity of PI31227 can be induced by P deficiency [38, 39]. Furthermore, co-cultivation of barnyard grass with PI31227 in the low P condition led to higher oxidative stress in the barnyard grass, indicated by lower activities of superoxide dismutase (SOD) and catalase (CAT) enzymes, but higher free radical contents and membrane lipid peroxidation [40]. It is highly likely that P deficiency brings about oxidative stress in rice seedlings, which would subsequently trigger allelopathic activity [41].

We found that the shoots of rice seedlings exhibited greater allelopathic potential than their roots (Fig. 2, which is consistent with the findings of our previous study of allelopathy among landrace rice cultivars from southern Thailand [42]. In the present study, we proved that the rice shoots accumulated greater amounts of secondary metabolites than the roots, especially phenolic compounds (Fig. 3A). Some of them might be allelopathic phenolic compounds [3, 5].

The total shoot phenolic contents were higher in plants grown in the LP condition (Fig. 3A). P is an essential element for the growth of rice [23]. Growth suppression due to P deficiency results in the production of excessive carbohydrates from photosynthesis. P deficiency might drive the allocation of excess carbon

sources toward the production of secondary metabolites, such as phenolic acids, flavonoids and terpenes, which are important allelochemicals in rice [42, 43].

The quantity of phenolic exudates, such as *trans*-ferulic acid, *p*-hydroxybenzoic acid and caffeic acid, produced by rice is correlated with allelopathic potential [44]. Some phenolic allelochemicals are highly produced in P-deficient plants in response to P deficiency [20]. In addition, P deficiency might increase the synthesis of phenolic allelochemicals through oxidative damage in plants [41]. It was reported that salicylic acid-induced stress is capable of activating the production of phenolic allelochemicals in shoots and roots of rice seedlings [45]. These and our findings suggest that the allelopathic potential of rice is induced by P deficiency and associated with the production of phenolic contents.

## CONCLUSION

This report demonstrates the effect of P deficiency on the allelopathy of *indica* rice and the different innate allelopathic activities. The growth of early-stage rice seedlings, was hardly inhibited by P deficiency, even if shoot and root internal Pi contents were markedly reduced. The reduction of shoot and root cytosolic Pi contents enhanced the allelopathic potential of rice seedlings, and shoots exerted greater allelopathic activities than roots. Shoots also accumulated more phenolic compounds in the LP condition. This correlation implies that rice seedlings might increase their

allelopathy to inhibit the growth of surrounding plants and reduce intraspecific and/or interspecific competition for P when the availability of P is limited.

**Acknowledgements:** This research was supported by the National Science, Research and Innovation Fund (NSRF) and Prince of Songkla University, Grant No. SCI6505179a (to L.K.), and by a scholarship from the Development and Promotion of Science and Technology Talents Project (DPST), Thailand (to K.N.).

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