
Root and shoot of local upland rice varieties response to various inorganic phosphorus levels

Na Chiangmai, P.^{1*}, Meetum, P.¹, Vechpong, T.² and Brooks, S.³

¹Faculty of Animal Sciences and Agricultural Technology, Silpakorn University, IT Campus, Phetchaburi, Thailand; ²Faculty of Education, Silpakorn University, Sanam Chandra Palace Campus, Nakhon Pathom, Thailand; ³School of Science, Mae Fah Luang University, Chiang Rai, Thailand.

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Abstract The influence of four inorganic phosphorus (Pi) concentrations (2.5, 5, 7.5, and 10 ppm Pi) of solid culture medium in five local upland rice (*Oryza sativa* L.) varieties: *Gi Poo*, *Pae Taw Gor Bi*, *Aung Jerng Yai*, *Row Su Ya*, and *Ni Kor* were tested. Pi deficiency caused a significant reduction in some characteristics including adventitious root number (ARN) and shoot dry weight (SDW); but only on eight weeks old seedlings. There were significant differences noted on almost all of the seedling characteristics affected by the rice varieties at seedling age of both four weeks (except SDW) and eight weeks. Trend analysis showed the response on seedling characteristics in these varieties to be varied at eight weeks old seedlings. However, only two varieties: *Aung Jerng Yai* and *Row Su Ya* responded to low Pi concentration by increased root architectures. Therefore, these two rice varieties could have the ability to adapt in low P nutrient growing condition.

Keywords: Indigenous upland rice, Phosphorus deficiency, Nutrient stress, Seedling response

Introduction

Upland rice (*Oryza sativa* L.) accounts for about 11 percent of the area under rice cultivation in Thailand (IRRI, 1998), and has been the subject of intensive study, especially in Thailand's Northern region (Pintasen *et al.*, 2007). However, hill-tribes native to many regions in Thailand also have planted upland rice primarily for household consumption. Thus, the study of upland rice has received considerable interest from researchers across Thailand includes genetic identification (Phunngam *et al.*, 2017), yield potential of each genotype (Jaruchai *et al.*, 2018) and agricultural traits related to panicle such as panicle weight and number of filled grain per panicle (Promsomboon and Promsomboon, 2016). The study of response to soil elements in upland rice genotypes, by contrast, has received relatively sparse attention. While

* **Corresponding Author:** Na Chiangmai, P.; **Email:** nachiangmai_p@silpakorn.edu

phosphorus (P) is considered an essential macro-nutrient of plant growth and development, approximately 40-50% of the arable land worldwide is lacking in this element, especially in many Asian countries (Heuer *et al.*, 2017). Niu *et al.* (2013) reported that around 5.7 billion hectares of land in the world experiences P deficiency ($<10 \mu\text{M P}$). Since less amount of P was identified in many kinds of biomass thus it raises the concern in P deficiency in the soil (Smil, 2000; Mackenzie *et al.*, 2002). Although high percent (95%), P in the Earth's crust contains mineral as calcium phosphate; but soluble P, which stimulated by weathering can be quickly immobilized into insoluble forms (Brady and Buckman, 1990). The reduction of soluble P from soil could also happen through erosion and run off to the ocean (Zin and Lim, 2015). On the other hand, the acid soil and accumulation of heavy metal often found in the arable highland area especially in tropical and subtropical regions. Moreover, with extensive use of chemicals, fertilizer, pesticide, and herbicide in agriculture practice in those area consequently the P is fixed either on surfaces of clay fractions or precipitated as inorganic salts with heavy metal such as aluminum (Al) and iron (Fe) (Tokhun and Pamonpol, 2019; Redel *et al.*, 2016; Bojórquez-Quintal *et al.*, 2017; Barra *et al.*, 2018).

Phosphorus is a critical element to support the development of rice and upland rice in most regions of the world (Slaton *et al.*, 2002; Fageria *et al.*, 2011). In some farm areas, privileged farmers are enjoying the ability to apply fertilizer to boost productivity. Nevertheless, an excessive application of inorganic fertilizer for cultivation can lead to nutrient imbalances (Heuer *et al.*, 2017), resulting in increased production costs and environmental degradation. While poor farmers choose the more suitable rice varieties that will increase the productivity, many of whom lack the resources to apply productivity factors to increase yield. Although local varieties have already existed in farmers' areas for a long time, some of them are already adaptable to the environment. However, that does not mean that planting all varieties of rice will provide high yields, or will respond well to the conditions of planting areas equally. The use of these local upland rice varieties to study its ability to grow under the limit of phosphorus content will help the farmers in the selection of rice varieties. The other benefit includes knowing the response information of each local variety that may be able to improve the breed for specific area in the future.

In this case, the upland rice varieties used in the study come from farmers' areas (minority farmers) in Pala-U village, Prachuap Khiri Khan Province in Thailand (latitude $12^\circ 30.642 \text{ N}$ and longitude $99^\circ 29.839 \text{ E}$). The mountainous terrain and the slope of areas in this village have different fertility per each area for rice cultivation. This is because the abundance of the area, especially in the highland, depends on many factors. Factors such as continuous

crop planting with, without, or less supplement for fertilizer (Mugo *et al.*, 2020) and the position and level of the slope are affecting the movement of nutrients and water (Reza *et al.*, 2011), which are causing problems in choosing the right varieties for each planting area and uneven rice productivity. For this reason, it is necessary to use local rice varieties of farmers for study. In this regard, some rice varieties that farmers still prefer to plant are also selected for testing with some varieties that are grown outside the area for comparison. Moreover, the results of the study could be applicably to the selected area as well as to adapt for testing with other local varieties in other areas.

The study on response to different concentrations of P would deliver information on the P efficiency of upland rice varieties. Therefore, the purpose of study was to determine those upland rice varieties that could best adapt to growth under conditions of P level insufficiency. This information may leverage rice farmers to increase the rice productivity.

Materials and methods

The study carried out from January to February of 2018 at Tissue Culture Laboratory in Faculty of Animal Sciences and Agricultural Technology, Silpakorn University, IT Campus, Cha-Am, Phetchaburi, Thailand.

Five upland rice varieties of indigenous upland rice varieties were collected from farmers in three provinces: Prachuap Khiri Khan (*Gi Poo* and *Pae Taw Gaw Bi* varieties), Phetchaburi (*Aung Jerng Yai* variety), and Chiang Mai (*Row Su Ya* and *Ni Kor* varieties). These varieties were grown and harvested seeds at farmer's field in Prachuap Khiri Khan Province, Thailand.

The culture media at different inorganic phosphorus (Pi) concentrations under sterile condition were used in the upland rice varieties.

Plant response to different Pi levels was tested, four Pi levels were prepared at 10 ppm, which is recommended by Yoshida *et al.* (1976) and Lu *et al.* (1999) as sufficient for plant growth and three reduced concentrations of Pi at 7.5, 5.0, and 2.5 ppm.

There were four Pi levels in Murashige and Skoog (MS) medium with modification on the amount of inorganic substances studied (Murashige and Skoog, 1962). Briefly, the modified MS medium contained different concentration of Pi including 2.5, 5.0, 7.5, and 10 ppm; then 30 g L⁻¹ sucrose and 8 g L⁻¹ agar were added. Afterwards, pH was adjusted to 5.8 with 0.1 N NaOH, medium poured into petri dishes and 8 oz culture bottle, respectively. The media were subsequently sterilized in an autoclave at 121°C for 30 minutes.

The upland rice seed of all varieties were dehusked. Seeds were then soaked in 95% ethyl alcohol and sterile distilled water for 30 seconds and 2-3

minutes in a laminar flow cabinet, respectively. The sterile dehusked seeds were soaked again in 15% and 10% mercuric chloride solution for 15 and 10 minutes, respectively. Finally, seeds were soaked in sterile distilled water for three times and cultured on MS medium (in petri dishes) until germination. Seedlings that emerged from normal MS medium were placed on modified MS medium (contained different Pi concentration) in 8 oz bottles. Seeds and seedlings were cultured in the cabinet at 25 ± 2 °C under 16-hour photoperiod. The 5x4 factorial in Completely Randomized Design (CRD) was conducted with five replications and each replication contained 10 culture bottles (8 oz) with 2 plants in each bottle.

Four weeks and eight weeks after seed cultured in modified MS medium, all seedlings were measured on five characteristics: adventitious (crown) roots numbers (ARN), adventitious root length (ARL), lateral root score (LRS), shoot dry weight (SDW), root dry weight (RDW), and ratio between shoot and root dry weight (SDW/RDW).

Analysis of variance (ANOVA) for factorial in CRD was used to analyze the results. Duncan's new multiple range test (DMRT) at 5% significant level was used for comparison of treatments. Trend analysis was employed to fit trend of graph of characteristics. Trend equation was estimated and graph created from data obtained. The data was analyzed using the R program version 3.5.2 (R Core Team, 2018).

Results

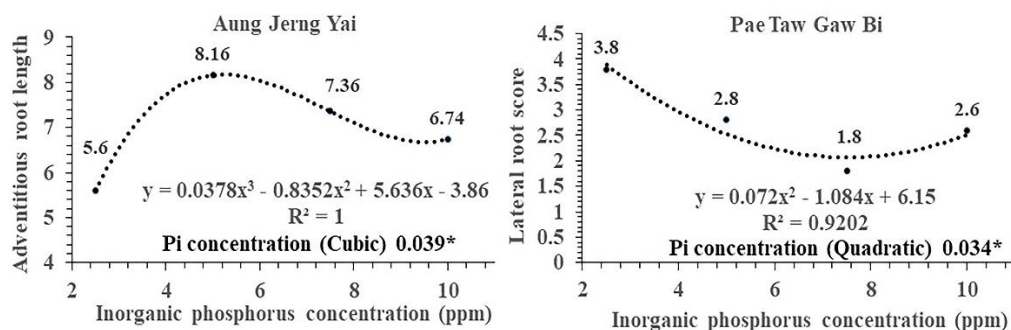
The significant differences of characteristics except SDW was affected by varieties in four weeks old seedlings. But there were no significant differences in either Pi concentration or the interaction between varieties and Pi concentration (Table 1). Root characteristics of ARN, ARL and RDW excluding LRS showed higher values on *Gi Poo*, *Paw Taw Gaw Bi* and *Ni Kor*. It was observed on different characteristics. *Aung Jern Yai* and *Row Su Ya*, that showed low values. The highest value of ratio of SDW/RDW was observed in *Aung Jerng Yai*. Trend analysis for all parameters in all varieties revealed a significant correlation only on ARL in the *Aung Jerng Yai*, and on LRS in *Pae Taw Gaw Bi* varieties (Figure 1).

A cubic relationship of values resulted from analysis on ARL in *Aung Jerng Yai*. LRS which considered both size and amount of lateral root) in *Pae Taw Gaw Bi*, it confirmed with significant consistency to the quadratic equation analyzed (Figure 1). *Pae Taw Gaw Bi* trend on LRS values declined at 2.5-7.5 ppm Pi.

Table 1. Comparison of shoot and root parameters of upland rice seed culturing on mediums supplemented with different concentrations of inorganic phosphorus (Pi) in *in vitro* condition at 4 weeks after culturing

Means of treatments in each factor	Shoot and root parameters					
	ARN ⁴	ARL ⁵ (cm)	LRS ⁶	SDW ⁷ (mg/plant)	RDW ⁸ (mg/plant)	Ratio of SDW/RDW
ppm Pi						
2.5 ppm	8.24	9.18	3.24	0.021	0.012	2.48
5.0 ppm	9.88	9.14	3.00	0.025	0.012	4.66
7.5 ppm	10.00	10.03	2.80	0.027	0.012	3.26
10 ppm	9.44	8.40	2.96	0.027	0.011	4.28
rice varieties						
<i>Gi Poo</i>	11.95 x ³	11.59 x	3.05 y	0.025	0.013 x	1.98 y
<i>Pae Taw Gaw Bi</i>	10.55 xy	9.96 x	2.75 y	0.029	0.014 x	2.64 y
<i>Aung Jerng Yai</i>	7.75 yz	6.96 y	2.75 y	0.022	0.003 y	10.81 x
<i>Row Su Ya</i>	9.20 yz	6.22 y	2.40 y	0.020	0.012 x	1.61 y
<i>Ni Kor</i>	7.50 z	11.21 x	4.05 x	0.028	0.015 x	2.14 y
F-test						
Varieties	** ¹	**	**	Ns	**	**
Pi	Ns ²	Ns	Ns	Ns	Ns	Ns
Varieties x Pi	Ns	Ns	Ns	Ns	Ns	Ns
CV ⁹ (%)	34.91	37.73	38.36	44.75	44.93	40.21

¹** Significant difference at 99% of confidence (P<0.01). ²NS, non-significant difference at 95% of confidence (P<0.05). ³x, y, z different letters in same column mean significant difference at 95% of confidence (P<0.05). ⁴ARN = adventitious root numbers/plant; ⁵ARL = adventitious root length (cm); ⁶LRS = lateral root score; ⁷SDW = shoot dry weight (mg/plant); ⁸RDW = root dry weight (mg/plant); ⁹CV = Coefficient of variation

**Figure 1.** Trend equation of changeable means of adventitious root length of seedlings in *Aung Jern Yai* (left) and lateral root score in *Pae Taw Gaw Bi* varieties (right) growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 4 weeks after culturing

The seedlings were significantly affected by different Pi concentrations on two characteristics: ARN and SDW in eight weeks (Table 2). The significant interaction effect between varieties and Pi concentration was not observed in any characteristics other than the ratio between SDW/RDW. Means of the SDW/RDW ratio in varieties are presented in line graph (Figure 2). *Row Su Ya* showed lower ratio between SDW/RDW at 2.5-5.0 ppm Pi, line graph rised at 7.5 ppm Pi and the highest value at 10 ppm Pi. By contrast, the values for *Aung Jerng Yai* and *Ni Kor* were relatively high and low, respectively. Decreased values ratio between SDW/RDW when Pi concentration increased that detected in *Gi Poo* and *Pae Taw Gaw Bi*. The higher SDW/RDW ratio is found in two varieties: *Row Su Ya* and *Aung Jerng Yai*; however, *Aung Jerng Yai* showed a relatively stable value in all concentrations of phosphorus (Figure 2).

Table 2. Comparison of shoot and root parameters of upland rice seed culturing on mediums supplemented with different concentrations of inorganic phosphorus (Pi) in *in vitro* condition at 8 weeks after culturing

Means of treatments in each factor	Shoot and root parameters					
	ARN ⁵	ARL ⁶	LRS ⁷	SDW ⁸	RDW ⁹	Ratio of SDW/RDW
ppm Pi						
2.5 ppm	13.44 n ⁴	14.61	3.16	0.07 n	0.020	4.97
5.0 ppm	18.04 m	14.57	3.60	0.09 mn	0.026	4.28
7.5 ppm	17.04 mn	14.68	3.08	0.10 mn	0.031	4.78
10 ppm	20.40 m	15.13	3.28	0.11 m	0.032	5.34
rice varieties						
<i>Gi Poo</i>	22.90 x ³	15.11 y	3.40 xy	0.10 x	0.037 x	3.76 z
<i>Pae Taw Gaw Bi</i>	20.65 x	17.00 y	3.90 x	0.11 x	0.033 x	4.27 yz
<i>Aung Jerng Yai</i>	14.75 y	10.90 z	3.00 y	0.06 y	0.013 y	6.70 x
<i>Row Su Ya</i>	12.30 y	8.66 z	3.35 xy	0.07 y	0.018 y	5.96 xy
<i>Ni Kor</i>	15.55 y	22.08 x	2.75 y	0.12 x	0.035 x	3.53 z
F-test						
Varieties	** ¹	**	**	**	**	**
Pi	**	Ns	Ns	**	Ns	Ns
Varieties x Pi	Ns ²	Ns	Ns	Ns	Ns	**
CV ¹⁰ (%)	32.66	30.33	28.68	39.04	60.95	49.32

¹** Significant difference at 99% of confidence (P<0.01). ²NS, non-significant difference at 95% of confidence (P<0.05). ³x, y, z different letters in same column mean significant difference at 95% of confidence (P<0.05). ⁴m, n different letters in same column mean significant difference at 95% of confidence (P<0.05). ⁵ARN = Adventitious root numbers/plant, ⁶ARL = Adventitious root length (cm), ⁷LRS = Lateral root score, ⁸SDW = Shoot dry weight (mg/plant), ⁹RDW = Root dry weight (mg/plant); ¹⁰CV = Coefficient of variation

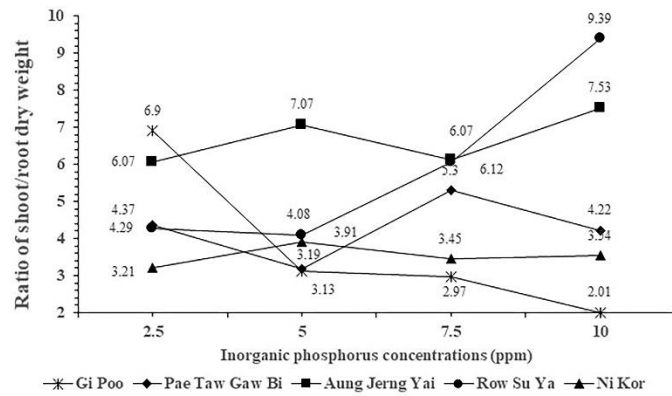


Figure 2. Response of means on ratio between shoot and root dry weight in five upland rice varieties growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 4 weeks after culturing

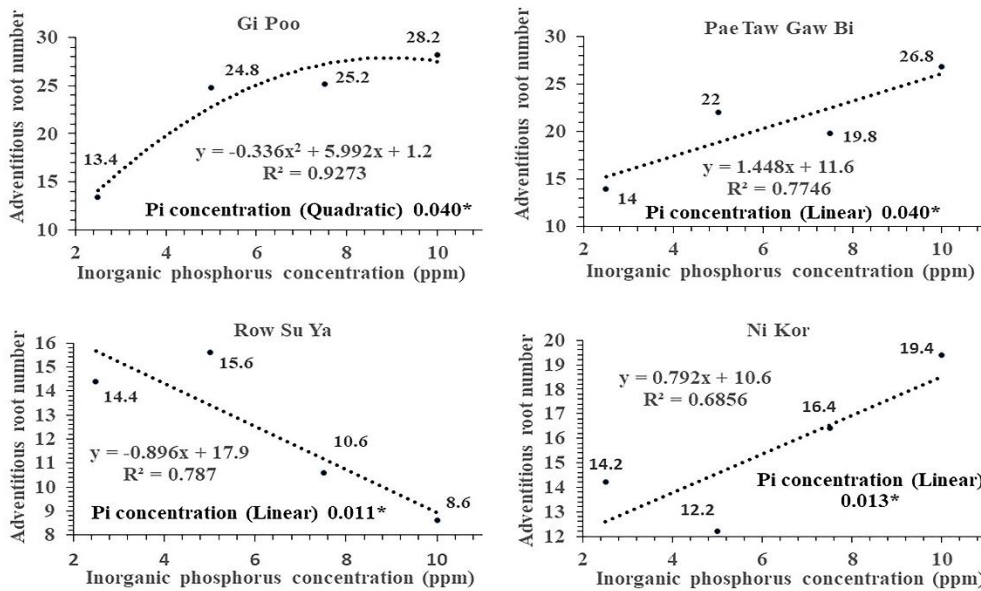


Figure 3. Trend equation of changeable means of adventitious root number of seedlings in four upland rice varieties growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 8 weeks after culturing

Trend analysis on another characteristics of seedlings at eight weeks that showed a statistically significant response to levels of Pi concentration are shown in Figures 3-7. There was significance in trend analysis on ARN in four varieties: *Gi Poo*, positive quadratic; *Pae Taw Gaw Bi*, positive linear; *Row Su*

Ya, negative linear; and *Ni Kor*, positive linear (Figure 3). For ARN in *Pae Taw Gaw Bi*, there was increased linear graph according to Pi concentrations at eight weeks old seedlings, while values were quite stable at four weeks seedlings (data not shown) (Figure 3). For *Row Su Ya*, establishment of ARN at four weeks seedlings showed the graph increased in quadratic trend but with no significant difference (data not shown). However, the ARN in *Row Su Ya* at eight weeks old seedlings showed negative linear line with significant difference (Figure 3).

Response on ARL at eight weeks old seedlings on *Gi Poo* and *Aung Jerng Yai* were significant in trend analysis, however, they trended unidirectional when graphed (positive and negative slope, respectively) (Figure 4). For *Aung Jerng Yai*, the highest ARL was observed at lowest Pi concentration at 2.5 ppm while the highest ARN was observed at eight weeks old (Figure 4). The LRS (size and density) and RDW tested by trend analysis showed statistically significance only on *Gi Poo* shown in positive linear model in both characteristics (Figure 5). SDW and the ratio between SDW/RDW tested by trend analysis yielded statistically significant results in two varieties (Figures 6 and 7). For SDW, negative linear model was most fitting on the response of increase under four Pi concentrations on *Pae Taw Gaw Bi* and *Ni Kor* (Figure 6). Finally, the ratio between SDW/RDW fitted to linear model on *Gi Poo* and *Row Su Ya* but was different in direction graphs (Figure 7).

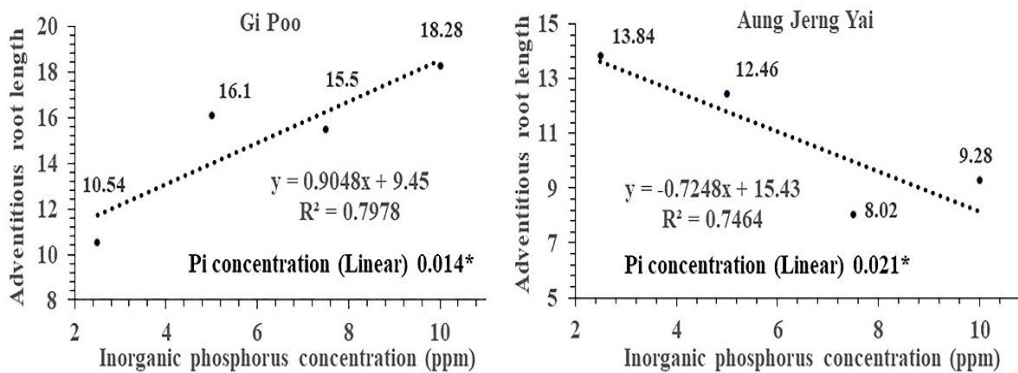


Figure 4. Trend equation of changeable means of adventitious root length of seedlings in two upland rice varieties growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 8 weeks after culturing

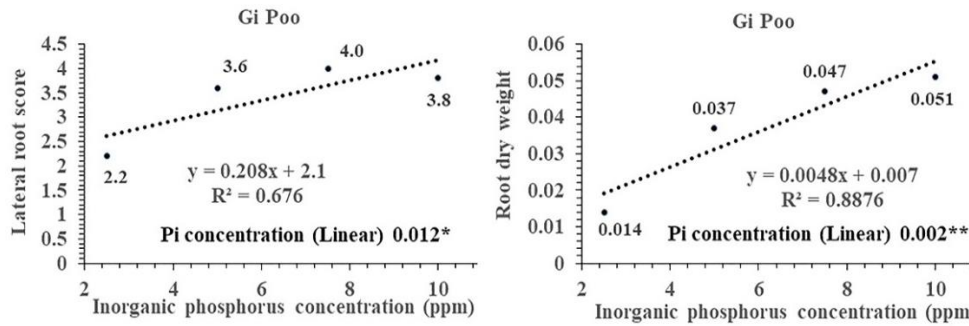


Figure 5. Change of lateral root score (Left) and root dry weight (Right) of seedlings in *Gi Poo* variety growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 8 weeks after culturing

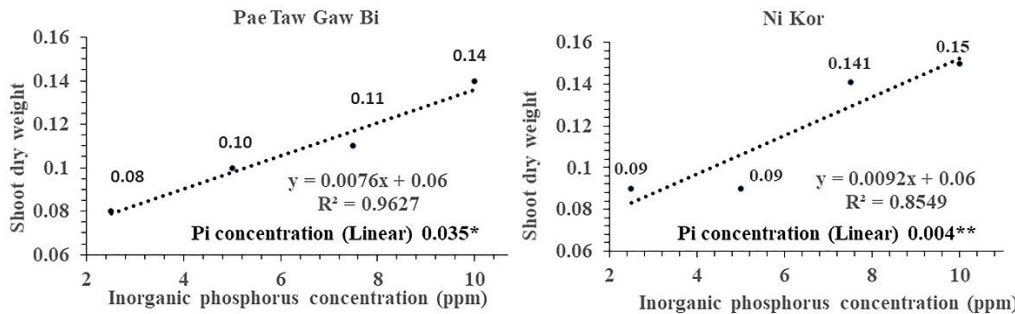


Figure 6. Trend equation of changeable means of shoot dry weight of seedlings in two upland rice varieties growing on medium contained different inorganic phosphorus (Pi) concentrations (ppm) at 8 weeks after culturing

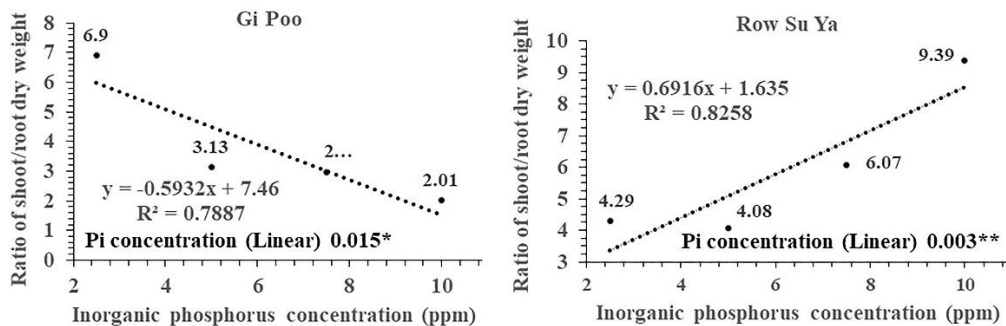


Figure 7. Trend equation of changeable means of ratio of shoot/root dry weight of seedlings in two upland rice varieties growing in mediums containing different inorganic phosphorus (Pi) concentrations (ppm) at 8 weeks after culturing

Discussion

The results did not show the influence of Pi concentration on changes in various characteristics (both root and shoot characteristics) of rice seedlings at the age of four weeks with statistical significance. Responding to the phosphorus of various characteristics by considering the trend lines of the graph in each species is necessary to proceed further. The cubic graph resulted after analysis on ARL in *Aung Jerng Yai* at four weeks after culturing showed that the rate of ARL was increasing between 2.5 to 5.0 ppm Pi and declined after that; however, it trended an increase again at 10 ppm Pi. The previous studies by Zhou *et al.* (2008) and Negi *et al.* (2016) who reported that the elongation and increasing number of the adventitious root in rice were corresponding to ability to obtain the most suitable Pi. Therefore, it may be necessary to bring the characteristics, both of the ARN and ARL for consideration. Eventhough the analysis of ARN in *Aung Jerng Yai* affected by Pi concentration was not significantly different but the ARN values changing in *Aung Jerng Yai* observed, when rice planted in different Pi concentrations tended to be similar to positive cubic graph. Thus, the determination for adaptation under insufficient Pi element should be done by observing the changing of the adventitious root by both the number and length. Which Steffens and Rasmussen (2016) confirmed that the change in root physiology is controlled by deficiency-responsive genes, thus different varieties may show different response.

For LRS characteristic plotted the graph in *Pae Taw Gaw Bi* at four weeks after culturing, this data suggested that Pi deficiency in *Pae Taw Gaw Bi* ranged at 2.5-7.5 ppm. This graph behavior showed the pattern of adaptive through rooting by increased LRS under Pi starvation in this variety. Due to the availability of phosphorus at 10-15 cm depth in soil as stated by Miller *et al.* (2003), the lateral root growth was reported to promote P solubilization, increased soil exploration, and provided an absorptive surface for nutrients (Pérez-Torres *et al.*, 2008). In addition, the response behavior of the lateral root, either elongation or enlargement in soil element deficiency, depended on plant hormones which controlled by its genetic (Vejchasarn *et al.*, 2016). By contrast, for soil with sufficiently distributed nutrients, each root type formed in different positions corresponding to the uptake of nutrients in different soil layers (Steffens and Rasmussen, 2016). Although the other rice varieties such as *Aung Jerng Yai*, *Row SuYa*, and *Ni Kor* had a similar lateral root response to each level Pi concentration as same as *Pae Taw Gaw Bi*, there was no statistical significance in those varieties mentioned.

The change of plant root architectures is varying under P insufficiency that depended on plant species and genotypes. However, these responses are

also dependent on the age of plant (Wissuwa *et al.*, 2005). In such instances, ARN and SDW at eight weeks after culturing decreased under lower Pi concentration. Relatively stable means, however, were found in both of these characteristics from 5.0 to 10 ppm Pi. Although the significant interaction at eight weeks old seedlings was found only in SDW/RDW ratio. It seems that such ratios in all rice varieties would change at all Pi concentrations. In general, the ratio between shoot per root biomass of a seedling was higher under high nutrient culturing to increase the chance for aboveground competition as stated by Maškavá and Herben (2018). However, the partitioning between shoot and root biomass is one parameter indicate the plant ability to growth under scarce resources such as lack of nutrient or water absorption (McConnaughay and Coleman, 1999). The higher and stable values of SDW/RDW in two rice varieties (*Row Su Ya* and *Aung Jerng Yai*) in all phosphorus concentrations may conclude that these rice varieties are more adaptable to Pi deficient conditions compared with the rest of rice varieties. However, the mean of both SDW and RDW in each variety at sufficient Pi concentration (10 ppm Pi) reflected the character of each variety controlled by genes.

The response to ARN on *Gi Poo* was similar between four weeks old and eight weeks old seedlings that was not significantly different affected by Pi concentration at four weeks old seedlings. Rising graph of ARN on *Gi Poo* at eight weeks old seedlings was at range of 2.5-7.5 ppm Pi, and declining occurred at 10 ppm Pi that described as sufficient concentration. At eight weeks old of seedlings (linear graph), ARN characteristic on *Pae Taw Gaw Bi* showed quite different graph trended from four weeks old seedlings (quite stable). These results can be interpreted that eight weeks old seedlings were more tolerant to Pi deficiency over than four-weeks'. This may be due to the age factor of a seedling where at eight weeks old the rice had already reached the tillering stage. For early growth stages of rice, Vinod and Heuer (2012) reported that it was very critical affected by P depletion. Upland area has usually limited P, both for low available and insoluble in soil (Shimizu *et al.*, 2008). Moreover, the behavior of farmers to sowing upland rice seeds in soil directly may cause the problem of P deficiency in the young age of seedlings more severe.

At eight weeks, *Row Su Ya* showed a negative linear line on ARN characteristic depended on increasing Pi concentration. According to the evaluated stimulation together with other characteristics, ARL and LRS were not significant difference affected by Pi concentration. Pi deficiency did not effect to ARL but it induced to increase LRS. There was a compensatory response between different roots in *Row Su Ya*, at eight weeks of seedlings grown under reduced Pi. Changing in root characteristics in root types of ARN,

ARL, and LRS was reported to cause insufficient P concentration in rice, and according to their genetic make up which also reported by Li *et al.* (2001).

On *Gi Poo* at eight weeks, similar with ARN characteristic, ARL was found to increase values according to increasing Pi concentration or non-response of these characteristics under Pi depletion. At eight weeks old seedlings, the behavior response of root characteristics was found similar among *Gi Poo*, *Pae Taw Gaw Bi*, and *Ni Kor*. The trend of graph of these characteristics (ARN and ARL) in *Aung Jern Yai* showed similarity to *Row Su Ya* seedlings in the same age. Thus, the two varieties, *Aung Jern Yai* and *Row Su Ya*, showed similar response on root characteristics which caused by varying depletion of Pi concentrations. However, *Aung Jern Yai* showed the similar responses on rooting formation between four and eight weeks old seedlings, while the compensated changing among root characteristics in seedlings at four and eight weeks observed on *Row Su Ya*. The eight weeks old seedlings showed clearly response to the different concentrations of Pi in upland rice varieties studied. Wang *et al.* (2010) and Zeng and Shannon (2000) described that rice during early seedling as well as reproductive stage showed high sensitivity to the stresses more than in other growth stages i.e. germination, tillering, and harvesting. The eight-week-old seedling was overlapped between seedling and tillage periods in upland rice. Nevertheless, this must be considered in conjunction with other characteristics, such as the dry weight of shoot and roots.

There is a similarity in the response of adventitious root characteristics (LRS and RDW) grown under varied Pi concentrations on *Gi Poo*. These data suggested that either non-responsive or no compensation under Pi deficiency element for adventitious and lateral roots may conclude on *Gi Poo*.

Due to the change, either by increased larger root system or longer seminal roots with fewer lateral roots, on rice growing in phosphate starvation was one behavior to maintain or increase uptake as reported by Sun *et al.* (2014). Thus, only two rice varieties, *Row Su Ya* and *Aung Jern Yai*, seemed to respond to Pi starvation by the increase in adventitious root architecture either in number initiation or elongation. The straight lines in regression linear on SDW on *Pae Taw Gaw Bi* and *Ni Kor* proved the important role of P for rice seedling growth as also stated by Tian *et al.* (2017). Moreover, rice grown under stress from P-deficiency for more than 16 days (or longer) found to effect in photosynthetic characteristics decreased (Xu *et al.*, 2007). Different direction of graphs on ratio of SDW/RDW between *Gi Poo* and *Row Su Ya* stimulated the establishment for these characteristics of SDW, RDW, and SDW/RDW which based on the earliest observation on root adaptation under insufficient Pi in these rice varieties.

Although the biomass of the upper part of a seedling (SDW) seemed severely affected by Pi deficiency, the root part maybe more affected by Pi starvation because it faced the nutrient stress. The lower value of SDW/RDW ratio was observed at 10 ppm Pi compared to the other Pi concentrations which means that underground root part affected by Pi depletion more than part on the above ground (shoot). Hence, non-adaptive response, especially in root system, in order to increase the tolerance ability under reduced Pi may describe the characteristic of *Gi Poo*. Oppositely, root response according to the RDW tried to keep constant values under low Pi levels on *Row Su Ya*. Thus, lower ratio SDW/RDW was observed at lower Pi concentration on *Row Su Ya* compared with higher Pi levels. Fageria *et al.* (2014) accounted that high root biomass also accumulated higher amount of nutrients to support plant growth.

For this study, many characteristics such as root architectures and shoot dry weight (SDW) varied in different rice varieties, especially for eight weeks old seedlings. Pi starvation and root architectures of ARN, ARL, and LRS responded to different Pi concentration in a variety of ways. Trend analysis showed the response of seedling characteristics in some rice varieties occurred at four weeks seedlings and almost all rice varieties at eight weeks. The increase of root characteristics at low Pi concentrations were observed only in two rice varieties which were *Aung Jerng Yai* and *Row Su Ya*; while the remaining rice varieties (*Pae Taw Gaw Bi*, *Gi Poo* and *Ni Kor*) changed to the opposite direction (decrease). Thus, *Aung Jerng Yai* and *Row Su Ya* rice varieties may have a greater adaptive response for tolerance to sustain low P nutrient via changes in root architecture at seedling stage. The concentrations showed deplete Pi crisis where changes in response in various characteristics observed range between 2.5 to 7.5 ppm Pi. Four weeks old seedlings were more susceptible to Pi deficiency based on root architectures response. However, assessment of the ability of different genetics to adapt to Pi deficiency was evident at eight weeks old seedlings.

Finally, rice varieties, such as *Aung Jerng Yai* and *Row Su Ya* showing adaptability to phosphorus deficiency are promised to be locally available in the different areas of farmers in the province of Prachuap Khiri Khan. However, it does not mean that upland rice varieties that responded well to Pi deficiency. This research finding will be able to adjust and produce high yield when grown in the farmers' fields. It is suggested to evaluate together with planting of all these rice varieties in the actual planting area of farmers to compare various characteristics including yield production.

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References

- Barra, P. J., Viscardi, S. Jorquera, M. A., Duran, P. A., Valentine, A. J. and de la Luz, M. M. (2018). Understanding the strategies to overcome phosphorus-deficiency and aluminum-toxicity by ryegrass endophytic and rhizosphere phosphobacteria. *Frontiers in Microbiology*, 9:1-12.
- Brady, N. C. and Buckman, H. O. (1990). *The nature and properties of soils*. New York, Maxwell Macmillan International Publishing, 550 pages.
- Bojórquez-Quintal, E., Escalante-Magana, C., Echevarría-Machda, I. and Martínez-Estévez, M. (2017). Aluminum, a friend or foe of higher plants in acid soils. *Frontiers Microbiology*, 8:1-12.
- Fageria, N. K., Moreira, A., Moraes, L. A. C. and Moraes, M. F. (2014). Root growth, nutrient uptake, and nutrient-use efficiency by roots of tropical legume cover crops as influenced by phosphorus fertilization. *Communications in Soil Science and Plant Analysis*, 45:555-569.
- Fageria, N. K., Santos, A. B. and Heinemann, A. B. (2011). Lowland rice genotypes evaluation for phosphorus use efficiency in tropical lowland. *Journal of Plant Nutrition*, 34:1087-1095.
- Heuer, S., Gaxiola, R., Schilling, R., Herrera-Estrella, L., López-Arredondo, D., Wissuwa, M., Delhaize, E. and Rouached, H. (2017). Improving phosphorus use efficiency: a complex trait with emerging opportunities. *The Plant Journal*, 90:868-885.
- IRRI (International Rice Research Institute) (1998). *World Rice Statistics*. Los Baños, Laguna, Philippines. Retrieved from <http://ricestat.irri.org:8080/wrsv3/entrypoin.htm>.
- Jaruchai, W., Monkham, T., Chankaew, S., Suriharn, B. and Snaitchon, J. (2018). Evaluation of stability and yield potential of upland rice genotypes in North and Northeast Thailand. *Journal of Integrative Agriculture*, 17:28-36.
- Li, H. B., Xia, M. and Wu, P. (2001). Effect of phosphorus deficiency stress on rice lateral root growth and nutrient absorption. *Acta Botanica Sinica*, 43:1154-1160.
- Lu, Y., Wassmann, R., Neue, H. U. and Huang, C. (1999). Impact of phosphorus supply on root exudation aerenchyma formation and methane emission of rice plant. *Biogeochemistry*, 47:203-218.
- Mackenzie, F. T., Ver, L. M. and Lerman, A. (2002). Century-scale nitrogen and phosphorus controls of the carbon cycle. *Chemical Geology*, 190:13-32.
- Maškavá, T. and Herben, T. (2018). Root:shoot ratio in developing seedlings: How seedlings change their allocation in response to seed mass and ambient nutrient supply. *Ecology and Evolution*, 8:7143-7150.
- McConnaughay, K. D. M. and Coleman, J. S. (1999). Biomass allocation in plants: Ontogeny or optimality? A test along three resource gradients. *Ecology*, 80:2581-2593.
- Miller, C. R., Ochoa, I., Nielsen, K. L., Beck, D. and Lynch, P. J. (2003). Genetic variation for adventitious rooting in response to low phosphorus availability: potential utility for phosphorus acquisition from stratified soils. *Functional Plant Biology*, 30:973-985.

- Mugo, J. N., Karanja, N. N., Gachene, C. K., Dittert, K., Nyawade, S. O. and Schulte-Geldermann, E. (2020). Assessment of soil fertility and potato crop nutrient status in central and eastern highlands of Kenya. *Scientific Reports*, 10:7779.
- Murashige, T and Skoog, F. (1962). A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiologia Plantarum*, 15:473-497.
- Negi, M., Sanagala, R., Rai, V. and Jain, A. (2016). Deciphering phosphate deficiency-mediated temporal effects on different root traits in rice grown in a modified hydroponic system. *Frontiers in Plant Science*. doi.org/10.3389/fpls.2016.00550.
- Niu, Y. F., Chai, R. S., Jin, G. L., Wang, H., Tang, C. X. and Zhang, Y. S. (2013). Responses of root architecture development to low phosphorus availability: a review. *Annals of Botany*, 112:391-408.
- Pérez-Torres, C. A., López-Bucio, J., Cruz-Ramírez, A., Ibarra-Laclette, E., Dharmasiri, S., Estelle, M., Herrera-Estrella, L. (2008). Phosphorus availability alters lateral root development in *Arabidopsis* by modulating auxin sensitivity via a mechanism involving the T1R1 auxin reporter. *Plant Cell*, 20:3258-3272.
- Phunngam, P., Pathumrangsang, N., Khambai, N., Tongjun, J. and Arunyawat, U. (2017). The variation of indigenous upland rice landraces in Ratchaburi, Thailand based on seed morphology and DNA sequencing. *Journal of Advanced Agricultural Technologies*, 4:48-52.
- Pintasen, S., Prom-u-thai, C., Jamjod, S. and Yimyam, N. (2007). Variation of grain iron content in a local upland germplasm from the village of Huai Tee Cha in northern Thailand. *Euphytica*, 58:27-34.
- Promsomboon, P. and Promsomboon, S. (2016). Collection and evaluation of local Thai rice varieties (*Oryza sativa* L.). *Life Science*, 10:371-374.
- R Core Team. (2018). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.
- Redel, Y., Cartes, P., Demanet, R., Velásquez, G., Poblete, G., Bol, R. and Mora, M. L. (2016). Assessment of phosphorus status influenced by Al and Fe compounds in volcanic grassland soils. *Journal of Soil Science and Plant Nutrition*, 16:490-506.
- Reza, S. K., Baruah, U., Sarkar, D. and Dutta, D. P. (2011). Influence of slope positions on soil fertility index, soil evaluation factor and microbial in acid soil of Humid Subtropical India. *Indian Journal of Soil Conservation*, 39:44-49.
- Shimizu, A., Kato, L., Komatsu, A. and Motomura, K. (2008). Genetic analysis of root elongation induced by phosphorus deficiency in rice (*Oryza sativa* L.): Fine QTL mapping and multivariate analysis of related traits. *Theoretical and Applied Genetics*, 117:987-996.
- Slaton, N. A., Wilson, C. E., Norman, R. J. and Ntamatungiro, S. (2002). Rice response to phosphorus fertilizer application rate and timing on alkaline soils in Arkansas. *Agronomy Journal*, 94:1393-1399.
- Smil, V. (2000). Phosphorus in the environment: natural flows and human interferences. *Annual Review of Energy and the Environment*, 25:53-88.
- Steffens, B. and Rasmussen, A. (2016). The physiology of adventitious roots. *Journal of Plant Physiology*, 170:603-617.
- Sun, H., Tao, J., Liu, S., Huang, S., Chen, S., Xie, X., Yoneyama, K., Zhang, Y. and Xu, G. (2014). Strigolactones are involved in phosphate- and nitrate-deficiency induced root development and auxin transport in rice. *Journal of Experimental Botany*, 65:6735-6746.

- Tian, Z., Li, J., He, X., Jia, X., Yang, F. and Wang, Z. (2017). Grain yield, dry weight and phosphorus accumulation and translocation in two rice (*Oryza sativa* L.) varieties as affected by salt-alkali and phosphorus. Sustainability. doi.org /10.3390/su9081461.
- Tokhun, N. and Pamonpol, K. (2019). Heavy metal contamination at highland agricultural soil at Dan Sai District, Loei Province, Thailand. Journal of Public Health and Development, 17:13-22.
- Vejchasarn, P., Lynch, P. L. and Brown, K. M. (2016). Genetic variability in phosphorus responses of rice root phenotypes. Rice. doi.org/10.1186/s122284-016-0102-9.
- Vinod, K. K. and Heuer, S. (2012). Approaches towards nitrogen- and phosphorus-efficient rice. AoB Plants. doi.org/10.1093/aobpla/pls028.
- Wang, Z., Wang, J., Bao, Y., Wu, Y., Su, X. and Zhang, H. (2010). Inheritance of rice seed germination ability under salt stress. Rice Science, 17:105-110.
- Wissuwa, M., Gamat, G. and Ismail, A. M. (2005). Is root growth under phosphorus deficiency affected by source or sink limitations? Journal of Experimental Botany, 56:1943-1950.
- Xu, H. X., Weng, X. and Yang, Y. (2007). Effect of phosphorus deficiency on the photosynthetic characteristics of rice plants. Russian Journal of Plant Physiology, 54:741-748.
- Yoshida, S., Forno, D. A., Cock, J. and Gomez, K. A. (1976). Laboratory manual for physiological studies of rice. The International Rice Research Institute.
- Zeng, L. and Shannon, M. C. (2000). Salinity effects on seedling growth and yield components of rice. Crop Science, 40:996-1003.
- Zhou, J., Jiao, F., Wu, Z., Li, Y., Wang, X., He, X., Zhong, W. and Wu, P. (2008). OsPHR2 is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. Journal of Plant Physiology, 146:1673-1686.
- Zin, K. and Lim, L. H. (2015). Chemical properties and phosphorus fraction in profiles of acid sulfate soils of major rice growing areas in Bruei Darussalam. Geoderma Regional, 6:22-30.

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