

Common Wild Rice (*Oryza rufipogon* Griff.) and Some Tropical Rice (*Oryza sativa* L.) Varieties Response to Inorganic Phosphorus Application

Pantipa Na Chiangmai* and Phakatip Yodmingkhwan

*Faculty of Animal Sciences and Agricultural Technology,
Silpakorn University, IT Campus, Phetchaburi, Thailand.*

**Corresponding author. E-mail address: m_surin@yahoo.com*

Received July 15, 2009; Accepted May 12, 2010

Abstract

This study aimed to evaluate the effect of phosphorus on the shoot and root morphology of common wild rice (*Oryza rufipogon* Griff.) and tropical cultivated rice varieties (*O. sativa* L.) as upland rice (Sew Mae Jan) and lowland rice (KDML105, RD7 and IR68144) under 2 levels of inorganic phosphorus application (0 ppm Pi and 10 ppm Pi) 45 days after planting.

It was revealed that phosphorus availability clearly affected both rice shoot and root system excepted the primary root length. The rice varieties had different numbers of leaves/plant and senescing leaves/plant, plant height, dry shoot weight and root length. Pi-dependency value showed RD 7 and *O. rufipogon* had responded to Pi application when leaf number and dry shoot weight accumulation were assessed. Sew Mae Jan had higher dry shoot weight than other rice varieties, but it had low tillering and responded to Pi-application compared with those varieties.

Key Words: Phosphorus; Lowland rice; Upland rice; Common wild rice

Introduction

In Asia, it is generally accepted that *Oryza sativa* L. has been domesticated from the Asian wild rice species complex (*O. rufipogon* Griff.) (Morishima et al., 1963). Common wild rice is an important genetic resource for rice breeding programs for improving genetics in cultivated rice. It is also utilized to crossbreed with cultivated rice produced the fertile plant (Oka, 1988; Punyalue et al., 2006). Important characters of common wild rice can also be used in the breeding program to combat both plant

diseases, insect pests and drought tolerance (Gregorio et al., 2002; Zhou et al., 2006).

In Thailand, common wild rice, as plant genetic resource, has declined due to the reducing habitat (Chitrakorn, 1995). This situation is not favorable as desirable allells in wild rices may decrease (Sun et al., 2000) and this may affect the gene pool of wild rice which can be utilized in the breeding program. The utilization of favorable genes of the wild in breeding program is greatly restricted because of its poor agronomic characters (Zhou et al., 2006).

Although common wild rice distribution is restricted, the weedy rice (the hybrid between wild rice and crop rice) has become a problem in the rice growing area in Thailand and other regions around the world (Craigmiles, 1978; Eleftherohorinos et al., 2002; Roschevitz, 1931; Ticchiati et al., 1996). This situation is difficult to control in cultivated rice even if weed control measure is now available (Smith et al., 1977).

Weedy rice causes significant reduction of rice yield because of its high competitive ability and persistence in rice fields due to its high fecundity and seed dormancy (Federici et al., 2001). Studies on genetic diversity and origin of weedy rice have been conducted and it was concluded that some of the red rice accessions were closely related to *O. nivara* and *O. rufipogon* (Vaughan et al., 2001). Moreover, DNA analysis revealed that the invasive weeds have arisen from their wild progenitor by gene flow process. The direction of gene flow was predominately from crop to wild and crop to weedy population (Jamjod et al., 2005).

Research in the comparison between weedy rice ancestors, common wild rice and cultivated rice in responding to the nutrient deficiency is scarce. This research was conducted to assess the impact of weedy rice contribution in the rice field. Phosphorus (P) was chosen as a nutrient element to test its effect on growth of shoot and root in common wild rice and cultivated rice. This element is an essential macronutrient and has the effect on rice growth particularly at the early stages (Slaton, et al., 2002). This study aimed to identify cultivated rice varieties and common wild rice's respond to the P element supplement. The data of the selected genotypes for growth traits will be used to screen for the advantage/beneficial characters in these rice varieties for genetic improvement in the rice breeding program.

The objective of this experiment is to compare the characters of rice varieties under two Pi-application rates.

Materials and Methods

Rice varieties and seed preparation

Common wild rice (*O. rufipogon* Griff.) (anually type) was grown in culture mediums under recommended inorganic phosphorus (Pi) rate (10 ppm) (Yoshida et al., 1976) and Pi deficiency (0 ppm) compared with the cultivated rice varieties (*O. sativa* L.) such as lowland rice (Khow Dok Mali 105 or KDML105, commercial rice variety; RD7, improved rice variety and IR68144, high grain iron variety) and upland rice (Sew Mae Jan, cultivated sticky rice variety).

Both common wild rice and cultivated rice varieties were grown and seeds were harvested at Silpakorn University, IT Campus, Cha-am District, Phetchaburi Province, Thailand.

For common wild rice seeds, the seeds were incubated at 60°C in hot air oven for one week to stop seed dormancy. Seeds of these rices were soaked in tap water over night and sowed onto the designated pots.

Growing conditions

Each plastic pot (diameter of 25 cm and a depth of 22 cm) was filled with cleaned sand to 80% capacity and received a basal supply of 40 ppm N as NH_4NO_3 , 40 ppm K as K_2SO_4 , 40 ppm Ca as CaCl_2 , 40 ppm Mg as $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, and mineral elements (Yoshida et al., 1976). Two rice seedlings were planted per pot and the culture medium was given twice per day (8.00 and 16.00 A.M) (each time at 1L/pot).

Assessment

The above ground characters including the number of leaves/plant, the number of senescing leaves/plant, the number of tillers/plant and plant height were assessed at 45 days after planting (DAP). The measured plants were also uprooted

and washed in the running tap water several times to eliminate the sand particles. Root tissues were cut and separated from shoot. The root samples were photographed to determine the length of primary root (tap root). The root tissues in each plant were dried by hot air oven at 60°C until constant moisture was reached. After drying, the samples were weighed and recorded, then the fraction of shoot per root was calculated. The degree of response to P was also measured as the percentage of Pi dependency in the formula as:

$$\text{Pi dependency (\%)} = \frac{(\text{Average value at 10 ppm Pi} - \text{0 ppm Pi})}{(0 \text{ ppm Pi})} \times 100$$

Experimental design

Four cultivated varieties and common wild rice were grown under two Pi application rates (0 and 10 ppm Pi). All of the ten treatments were replicated three times. Factorial (2 x 5) in Completely Randomized Design (CRD) was employed in this experiment. Analysis of variance

procedures was conducted using SAS (SAS Inst., Cary, NC). Mean separations were performed by Fisher's protected least significant difference method at a significant level of 0.05. Duncan's multiple range test (DMRT) was employed in Pi-dependency.

Results

Pi-application had affected all eight rice characters by increasing the values of those parameters except root length.

It was found that different varieties of rice had affected the phenotypes of rice in five characters such as the number of leaves/plant, the number of senescing leaves/plant, the dry shoot weight, plant height and root length with statistical significant difference (Table 1). Different rice varieties had their own prominent characters but it was obvious that IR68144 had the average values of the characters lower than the means of varieties in both Pi application rates.

Table 1 Influence of two inorganic phosphorus application rates on eight characters in five varieties at 45 days after planting.

Pi application rates	Leaves	SL [†]	Tillers	Plant height	DSW [†]	DRW [†]	A/B [†]	RL [†]
	no./plant	no./plant	no./plant	cm	g/plant	g/plant		cm
0 ppm								
<i>Oryza rufipogon</i>	3.3	2.3	1.0	43	0.39	0.20	2.08	34.1
Sew Mae Jan	3.8	2.0	1.0	50	0.68	0.34	2.31	42.7
RD7	3.3	3.0	1.0	38	0.38	0.18	2.20	29.7
KDML105	4.5	2.2	1.0	50	0.44	0.22	2.02	33.1
IR68144	3.2	1.7	1.0	24	0.13	0.06	2.98	21.0
mean	3.6	2.2	1.0	41	0.40	0.20	2.32	32.1
10 ppm								
<i>Oryza rufipogon</i>	32.5	0.8	7.3	84	8.36	2.89	3.03	31.2
Sew Mae Jan	18.0	0.7	3.8	94	7.84	2.25	4.23	36.9
RD7	33.3	1.0	6.3	71	5.84	1.53	4.49	28.7
KDML105	24.8	1.2	4.2	89	5.28	1.56	3.99	33.4
IR68144	23.0	0.7	5.2	68	3.16	1.08	4.02	21.6
mean	26.3	0.9	5.4	81	6.10	1.86	3.95	30.4
Pool S. E.	0.69	0.08	0.22	0.82	0.19	0.10	0.20	0.76
LSD (Pi rates) (0.05)	2.898	0.348	0.915	3.439	0.780	0.437	0.819	Ns
LSD (genotypes) (0.05)	4.582	0.550	Ns [‡]	5.438	1.233	Ns	Ns	5.031
LSD (Pi rates x genotypes) (0.05)	6.480	Ns	Ns	Ns	1.744	Ns	Ns	Ns

[†] SL, Senescing leaves; DSW, Dry shoot weight; DRW, Dry root weight; A/B, Ratio of dry shoot/root weight; RL, Root length.

[‡] Ns, not significant at the 0.05 level of probability.

O. rufipogon and Sew Mae Jan had the average values of dry shoot weight/plants higher than that of the other varieties (at 4.37 and 4.26 g/plant respectively). Root length was not affected by the Pi-deficiency but it was obviously

influenced by the rice genetics. Sew Mae Jan also had highest average root length (39.8 cm) compared with these of the other varieties (Table 2).

Table 2 Influence of rice genetics on eight characters at 45 days after planting.

Rice genetics	Leaves	SL [†]	Tillers	Plant height	DSW [†]	DRW [†]	A/B [†]	RL [†]
	----- no./plant -----	-----	-----	cm	----- g/plant-----	-----	-----	cm
<i>Oryza rufipogon</i>	17.9	1.6	4.2	64	4.37	1.54	2.56	32.7
Sew Mae Jan	10.9	1.3	2.4	72	4.26	1.30	3.27	39.8
RD7	18.3	2.0	3.7	54	3.11	0.86	3.34	29.2
KDML105	14.7	1.7	2.6	70	2.86	0.89	3.01	33.3
IR68144	13.1	1.2	3.1	46	1.64	0.57	3.50	21.3
Pool S. E.	0.69	0.08	0.22	0.82	0.19	0.10	0.20	0.76
LSD (0.05)	4.582	0.550	Ns [‡]	5.438	1.233	Ns	Ns	5.031

† SL, Senescing leaves; DSW, Dry shoot weight; DRW, Dry root weight; A/B, Ratio of dry shoot/root weight; RL, Root length.

‡ Ns, not significant at the 0.05 level of probability.

In this study, there was the interaction between Pi rates and genotypes in both characters such as the number of leaves/plant and the dry shoot weight (Table 1). It was also found that the number of leaves/plant, plant height and the dry shoot weight were different among the varieties basing upon Pi-dependency value (Figure 1). The number of leaves/plant and the dry shoot weight were influenced by the interaction of Pi-application and genotypes (Table 1). *O. rufipogon* and RD7 had high Pi-dependency values when the number of leaves/plant (at 89.81 % and 89.77 % respectively) and the dry shoot weight (at 95.23 % and 93.31 % respectively) were assessed.

Plant height was not influenced by the interaction of the Pi-application rates and genotypes (Table 1). Plant height of different rice varieties, however, varied in Pi-dependency. The rice variety IR68144 had the highest Pi dependency of

64.93% (Figure 1).

In this study, it was found that Pi dependency had a negative value in the characters of the number of mature leaves/plant and root length (Figure 1). The number of tillers/plant, dry root weight per plant and ratios of dry shoot/root weight characters with statistical nonsignificant difference affected by rice varieties (Table 1) also were found nonsignificant difference between positive values on Pi dependency (Figure 1) in each character.

Using the orthogonal contrast technique to compare three groups of rice varieties (*O. rufipogon*, Sew Mae Jan and lowland rice; KDML105, RD7 and IR68144), it was found that these three groups of rice varieties were influenced by the interaction of rice genetics and the application rate of 10 ppm Pi when the number of leaves/plant and the dry shoot weight were assessed (Table 3)

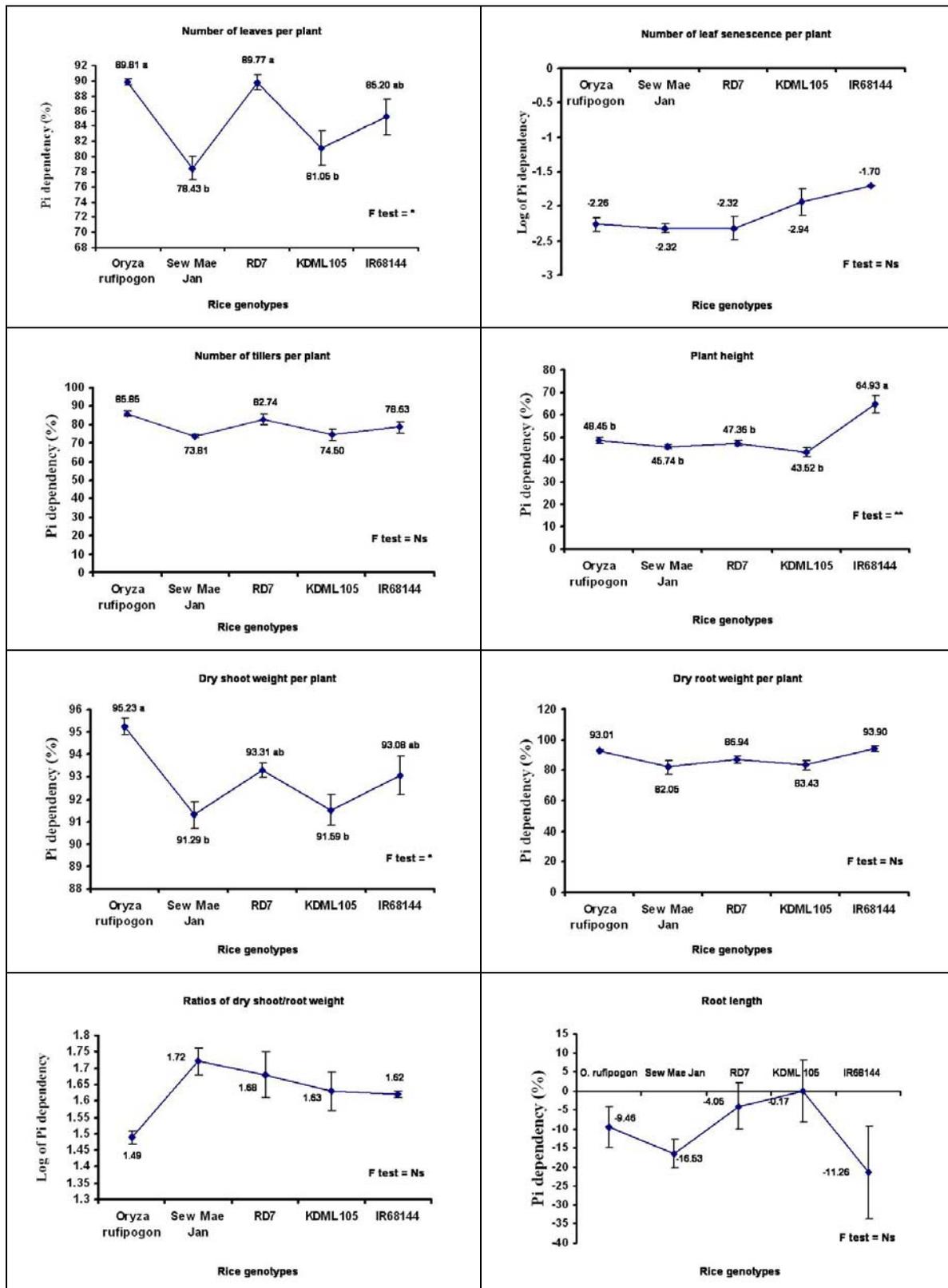


Figure 1 Pi dependency of characters in common wild rice (*O. rufipogon* Griff.), cultivated rice varieties; Sew Mae Jan, RD7, KDML105 and IR68144. Ns, not significant at the 0.05 level of probability. *, ** significant at the 0.05 and 0.01 level of probability, respectively.

Table 3 Orthogonal contrast of rice genetics in two characters was influenced by the interaction of rice genetics and inorganic phosphorus application rates at 45 days after planting.

Rice genetics	Leaves	DSW [†]	Leaves	DSW
	----- per plant -----			
	----- 0 ppm Pi -----		----- 10 ppm Pi -----	
Sew Mae Jan vs <i>O. rufipogon</i>	Ns [‡]	Ns	Ns	*
Sew Mae Jan vs KDML105, RD7, IR68144	Ns	Ns	Ns	**
Sew Mae Jan vs KDML105	Ns	Ns	**	**
Sew Mae Jan vs RD7	Ns	Ns	**	**
Sew Mae Jan vs IR68144	Ns	Ns	Ns	**
<i>O. rufipogon</i> vs KDML, RD7, IR61844	Ns	Ns	Ns	**
<i>O. rufipogon</i> vs KDML105	Ns	Ns	*	Ns
<i>O. rufipogon</i> vs RD7	Ns	Ns	*	**
<i>O. rufipogon</i> vs IR68144	Ns	Ns	*	**

† DSW, Dry shoot weight.
 ‡ Ns, not significant at the 0.05 level of probability.
 * significant at the 0.05 level of probability.
 ** significant at the 0.01 level of probability.

Interaction between Pi application rates and rice genetics did not have any influence onto the other six characteristics (Table 1). The application of the orthogonal contrast technique also revealed that Sew Mae Jan and *O. rufipogon* differed in both plant height and root length. There were also differences in both plant height and root length in the case of the comparison between Sew Mae Jan and lowland rice varieties. The

senescing leaves/plant and dry root weight were different between Sew Mae Jan and some lowland cultivated rice varieties (RD7 and IR68144). However, there were no differences in the number of tillers/plant and the ratio of the dry shoot weight and the dry root weight among these three groups of rice except *O. rufipogon* and RD7 for the number of tillers per plant (Table 4).

Table 4 Orthogonal contrast of rice genetics in six rice characters (averages across inorganic phosphorus application rates) at 45 days after planting.

Rice genetics	SL [†]	Tillers	Height	DRW [†]	A/B [†]	RL [†]
	----- per plant -----					
Sew Mae Jan vs <i>O. rufipogon</i>	Ns [‡]	Ns	**	Ns	Ns	**
Sew Mae Jan vs KDML105, RD7, IR68144	*	Ns	**	*	Ns	**
Sew Mae Jan vs KDML105	**	Ns	**	Ns	Ns	**
Sew Mae Jan vs RD7	Ns	Ns	**	**	Ns	**
Sew Mae Jan vs IR68144	Ns	Ns	**	*	Ns	**
<i>O. rufipogon</i> vs KDML, RD7, IR61844	Ns	Ns	**	Ns	Ns	Ns
<i>O. rufipogon</i> vs KDML105	Ns	Ns	**	Ns	Ns	Ns
<i>O. rufipogon</i> vs RD7	Ns	*	*	Ns	Ns	Ns
<i>O. rufipogon</i> vs IR68144	Ns	Ns	Ns	Ns	Ns	*

† SL, Senescing leaves; DRW, Dry root weight; A/B, Ratio of dry shoot/root weight; RL, Root length.
 ‡ Ns, not significant at the 0.05 level of probability.
 * significant at the 0.05 level of probability.
 ** significant at the 0.01 level of probability.

Discussion

In this experiment, almost all of the characters were affected by the level of Pi application with the exception of the value of primary root length (Table 1). This is because P is essential for cereal particularly at the early growth stages (Gutierrez-Boem and Thomas, 1998; Mengel and Kirkby, 2001; Slaton et al., 2002). These agronomic characters were also influenced by the rice genetics (Table 2).

The Pi-dependency value was applied in this study to explain the effect of either the Pi-application or the genetic of rice or the interaction of both factors on the development and growth of rice. This will help to compare the response of rice varieties to Pi-application more effectively.

The number of leaves/plant and dry shoot weight were influenced by the interaction of Pi-application and rice genetics (Table 1). Moreover, using the Pi-dependency study, the differences among rice genetics in leaf number and dry shoot weight were found (Figure 1). The difference among three rice variety groups (upland, lowland and wild rice varieties) found only at 10 ppm Pi with orthogonal contrast analysis (Table 3). Thus, the difference on these characters was influenced by the degree of each rice variety in reponding to Pi-application.

The Pi-dependency values on the number of leaves/plant and dry shoot weight was not only used to compare the degree of response to Pi-application among rice varieties, but these characters were also used to estimate the values of characters in rice genetics (because Pi-dependency values were calculated base on nonsignificant difference among varieties at 0 ppm Pi) (Table 3). *O. rufipogon* and RD7 had the highest Pi-dependency values when the number of leaves/plant and dry shoot weight were assessed (Figure 1). Thus, both varieties had high response to 10 ppm Pi-application giving rise to the high values of

number of leaves/plant and dry shoot weight than other varieties.

As a result, the obvious effects of Pi-deficiency was found on the number of leaves/plant and dry shoot weight regardless of the difference in varieties. Thus, the number of leaves/plant and dry shoot weight were good indicators for predicting the P-stress in rice plant (Dobermann and Fairhurst, 2000).

This finding emphasized the significance of Pi-application on the accumulation of rice biomass in various rice varieties. Fredeen et al. (1989) explained that P element was translocated via xylem from root to various growing young laminae and initiated leaf expansion and plant growth. Walker (1980) also reported that with the sufficient amount of P element, the photosynthetic CO₂ assimilation in the plant leaves would be enhanced. Under the P-deficient environment, ATP and RuBP synthesis would be affected and this would decrease the carboxylation process (Rao and Terry, 1989).

The number of senescing leaves/plant and plant height were clearly affected by Pi-application and genetics but not by the interaction between these factors (Table 1). As a result, the differences of the number of leaf senescence per plant and plant height could be used to observe the differences among rice varieties both in applied and non-applied Pi situation. Although the higher Pi-dependency indicated the higher response to Pi-application and the difference among rice genetics in plant height was found (Figure 1), this observation can not be used for the evaluation of these characters and made comparison among varieties.

Plant height was found to be different among the three rice groups by orthogonal contrast analysis (Figure 1 and Table 4). IR68144 is a short plant variety but it had the highest Pi-dependency on plant height (Figure 1). Thus, P element was essential and may affect plant height

in IR68144 more than the other characters. Mengel and Kirkby (2001) and Akinrinde and Gaizer (2006) also reported that plant height value correlated with the value of P-element concentration.

The number of tillers/plant, dry root weight and the ratio of dry shoot/root weight were affected by Pi-application but not affected by the genetics and the interaction between them (Table 1). Thus, these characters were similar to all varieties with nonsignificant difference in Pi-dependency among rice varieties. As a result, the mean of the ratio of dry shoot/root weight was 2.32 at non-applied Pi (0 ppm) and increased to 3.95 in applied Pi (10 ppm) (Table 1).

The number of the mature leaves/plant was negatively affected by the Pi-application as expressed in term of Pi-dependency value. The mature leaves/plant was reduced in the Pi-application setting while the number was increased in the non-Pi-application regardless of the difference in rice genetics. The expression of P-deficiency was prominent in the lower senescing leaves and the senescing process was accelerated under the P-deficiency setting (Bergmann, 1992). This phenomenon occurred because the P-element was translocated from the mature leaves to other plant parts via the phloem (Hall and Baker, 1972; Jeschke et al., 1997).

Analysis of the mean value of the primary root length showed significant difference due to the rice genetics (Table 1). The mean of root length was highest in Sew Mae Jan (39.8 cm), followed by KDML105 (33.3 cm) and *O. rufipogon* (32.7 cm), respectively (Table 2). Sew Mae Jan is an upland rice variety can also be grown in low moisture situation, thus, the high root length may be an advantage character for water supply in soil. In orthogonal contrast, the difference was observed only in plant height character between Sew Mae Jan and the other two rice groups (Table 4). However, this observation

did not apply to the dry root weight character. The dry weight of root biomass of various rice varieties was positively affected by the Pi-application as expressed in term of Pi-dependency value although the root length was reduced (Figure 1). This was because under this circumstance the rice root had more branching and the size of the root was increased with more hairy root. Similarly, roots of aerated plant in low P also had longer and slender roots than in high P (Anghinoni and Barber, 1980; Thang et al., 2006).

Root length was found to be a poor indicator to predict Pi-deficiency in rice. But root dried weight and root branching were the better indicators for evaluating the Pi-deficiency. Other root characteristic such as the number and size of hairy roots, root diameter, root surface, rooting density and root mass should also be assessed under the P-application study (Claassen and Jungk, 1984; Dobermann and Fairhurst, 2000; Itoh and Barber, 1983). Mengel and Kirkby (2001) reported that root branching initiation in monocotyledon plants occurred a few days after seed germination. Thus, root branching will be reduced during the early stage of plant growth if the plant was subject to the P-deficiency environment.

The number of rice tillers and the accumulation of root dry weight were not influenced by Pi-application as expressed in term of Pi-dependency regardless of the different in rice varieties. Rice plants responded to Pi-deficiency by having reduced tiller number although they were sufficiently applied with the other elements (Figure 1 and Table 1). It was found that the tillering growth stage was affected if P-element was insufficient in cereals. In the fruit trees, growth of new shoot and flower initiation were also impaired under P-deficiency environment (Dobermann and Fairhurst, 2000; Mengel and Kirkby, 2001).

Sew Mae Jan, an upland rice variety which had been promoted for planting, had a low tillering capacity but had quite high dry weight of shoot and root biomass. This variety had responded poorly to the Pi-application as expressed in term of the Pi-dependency value. This may be because this variety had been planted in the acidic soil with low P-element (Buresh et al., 1997; Fairhurst et al., 1999; Kirk et al., 1998). Therefore, applying more P-element to this soil, which has been planted with Sew Mae Jan, may not increase a yield as hoped for.

George et al. (2001) reported that the harvest index (HI) (grain yield/total biomass) of the traditional upland rice was low. The relationships between upland rice yield and soil fertility were also poor (Roder et al., 1995; Van et al., 2000). Therefore, increasing upland rice biomass would not only require fertilizer application but also require an improved germplasm with greater responsiveness to nutrients, partitioning of dry matter to grain and other important parameters such as tolerance to pests and abiotic stresses.

O. rufipogon was found to have greater response to Pi-application than other rice varieties as expressed in term of the P-dependency value. This may pose a risk as the F1 hybrid of the *O. rufipogon* and cultivated rice varieties may be more adaptive to the environment and more competitive in the rice field. The hybrid will be a new species of weedy rice which is difficult to eradicate. However, the positive aspect of *O. rufipogon* is that it may be used as germplasm for improving the characters of the cultivated rice varieties in responding to P-application.

Conclusion

This study emphasized the importance of Pi-application for rice production, particularly at the early growth stage in some cultivated rice

varieties and common wild rice species.

Phosphorus availability clearly affected both rice tissues aboveground (shoot) and underground (root) systems except primary root length at early growth stage.

In the Pi dependency study, it was found that RD7 and common wild rice were responsive to the Pi-application by increasing the leaf initiation and accumulating shoot biomass.

The three lowland rice genetics were all susceptible to the deficiency of Pi but KDML105 had lower accumulation of shoot biomass than the other two varieties when the P-element was applied. Sew Mae Jan also did not respond to the Pi-application in term of the accumulation of shoot biomass.

Dry weight of root biomass, root branching and size of the primary root were the characters which could be used as indicators to assess Pi-deficiency. However, the length of the primary root did not affect by Pi-deficiency.

Common wild rice species were better than the lowland varieties, when dried shoot weight, dried root weight and primary root length were assessed. However, these beneficial characteristics of the common wild rice species may have a drawback if they had cross-bred with other cultivated rice plants. This may make its hybrids more adaptable to environments and disseminate widely in the rice fields.

Acknowledgements

We gratefully thank the Faculty of Animal Sciences and Agricultural Technology, Silpakorn University, Thailand for funding this research and also thank the Plant Genetic Resource and Nutrition Laboratory, Department of Agronomy, Chiang Mai University, Thailand, for providing the materials for this research.

References

- Akinrinde, E. A. and Gaizer, T. (2006) Differences in the performance and phosphorus-use efficiency of some tropical rice (*O. sativa* L.) varieties. *Pakistan Journal of Nutrition* 5 (3): 206-211.
- Anghinoni, I. and Barber, S. A. (1980) Phosphorus influx and growth characteristic of corn roots as influenced by phosphorus supply. *Agronomy Journal* 72: 685-688.
- Buresh, R. J., Smithson, P. C., and Hellums, D. T. (1997) Building soil phosphorus capital in Africa. p. 111-149. In R. J. Buresh et al. (ed.) Replenishing soil fertility in Africa. SSSA Spec. Publ. 51. SSSA and ASA, Madison. WI.
- Bergmann, W. (1992) Nutritional disorder of plant, development visual and analytical diagnosis, Jena:Gustav Fischer.
- Chitrakorn, S. (1995) Characterization, evaluation and utilization of wild rice germplasm in Thailand. Pathum Thani Rice Research Center, Thailand Rice Research Institute, Bangkok.
- Claassen, N. and Jungk, A. (1984) Effect of K uptake rate, root growth and root hairs on potassium uptake efficiency of several plant species. *Z. Pflanzenernahr. Bodenkd.* 147: 276-289.
- Craigsmiles, J. P. (1978) Red rice, research and control. *Texas Agricultural Experimental Station Bulletin* 1270: 5-6.
- Dobermann, A. and Fairhurst, T. (2000) Rice: Nutrient disorders and nutrient management. *Potash and Phosphate Inst. (PPI), Potash and Phosphate Inst. of Canada (PPIC), and International Rice Research Institute (IRRI)*, Singapore and Los Banos.
- Eleftherohorinos, I. G., Dhima, K. V., and Vasilakoglou, I.B. (2002) Interference of red rice in rice grown in Greece. *Weed Science* 50: 167-172.
- Fairhurst, T., Lefroy, R., Mutert, E., and Batjes, N. (1999) The importance, distribution and causes of phosphorus deficiency as a constraint to crop production in the tropics. *Agroforestry Forum* 9: 2-8.
- Federici, M. T., Vaughan, D., Tomooka N., Kaga, A., Wang, X. W., Doi, K., Francis, M., Zorrilla, G., and Saldain, N. (2001) Analysis of Uruguayan weedy rice genetic diversity using AFLP molecular markers. *Electronic Journal of Biotechnology* 4(3): 130-145.
- Fredeen, A. L., Rao, I. M., and Terry, N. (1989) Influence of phosphorus nutrition on growth and carbon partitioning of *Glycine max.* *Plant Physiology* 89: 225-230.
- George, T., Magbanua, R., Roder, W., Keer, K. V., Trebuil, G., and Reoma, V. (2001) Upland rice response to phosphorus fertilization in Asia. *Agronomy Journal* 93: 1362-1370.
- Gregorio, G. B., Senadhira, D., Mendoza, R. D., Manigbas, N. L., Roxas, J. P., and Guerta, C.Q. (2002) Progress in breeding for salinity tolerance and related abiotic stresses in rice. *Field Crops Research* 76: 91-101
- Gutierrez-Boem, F. H. and Thomas, G. W. (1998) Phosphorus nutrition affects wheat response to water deficit. *Agronomy Journal* 90: 166-171.
- Hall, S. M. and Baker, D. A. (1972) The chemical composition of Ricinus phloem exudates. *Planta* 106:131-140.
- Itoh, S. and Barber, S. A. (1983) Phosphorus uptake by six plant species as related to root hairs. *Agronomy Journal* 75: 457-461.
- Jamjod, S., Maneechote, C., Nirantrayakul, S., and Rerkasem, B. (2005) The good and bad gene flow in the rice landscape. In *The International Symposium on Diversity, Management, Protection and Utilization of Local Rice Germplasm*. Chiang Mai, Thailand.

- Jeschke, W. D., Kirkby, E. A., Peuke, A. D., Pate, J. S., and Hartung, W. (1997) Effects of P deficiency on accumulation and transport of nitrate and phosphate in intact plants of castor bean (*Ricinus communis*). *Journal of Experimental Botany* 48: 75-91.
- Kirk, G. J., George, D. T., Courtois, B., and Senadhira, D. (1998) Opportunities to improve phosphorus efficiency and soil fertility in rainfed lowland and upland rice ecosystems. *Field Crops Research* 56: 73-92.
- Mengel, K. and Kirkby, E. A. (2001) Phosphorus. In *Principles of plant nutrition*. 5th Edition. Kluwer Academic Publishers. Netherlands.
- Morishima, H., Hinata, K., and Oka, H. I. (1963) Comparison of modes of evolution of cultivated forms from two wild rice species, *Oryza breviligulata* and *O. perennis*. *Evolution* 17: 170-181.
- Oka, H. I. (1988) *Origin of cultivated rice*. Japan Scientific Societies Press and Elsevier, Tokyo.
- Punyalue, A., Rerkasem, B., and Jamjod, S. (2006) Genetic diversity of common wild rice collected from various regions of Thailand. *Journal of Agriculture* 22(1): 21-25.
- Rao, I. M. and Terry, N. (1989) Phosphate status, photosynthesis and carbon partitioning in sugar beet. I. Changes in growth, gas exchange and Calvin cycle enzymes. *Plant Physiology* 90: 14-819.
- Roder, W., Phengchanh, S., and Keoboulapha, B. (1995) Relationships between soil, fallow period, weeds and rice yield in slash-and-burn systems of Laos, *Plant Soil* 176: 27-36.
- Roschevitz, R. J. (1931) A contribution to the knowledge of rice. *Appl. Bot. Genet. Plant Breeding* 27(4): 1-133.
- Slaton, N. A., Wilson, C. E., Norman, R. J., Ntamatungiro, S., and Frizzell, D. L. (2002) Rice response to phosphorus fertilizer application rate and timing on alkaline soils in Arkansas. *Agronomy Journal* 94: 1393-1399.
- Smith, R. J., Flinchum, W. T., and Seaman, D. E. (1977) Weed control in US rice production. *U S Department of Agriculture Agriculture Handbook* 497: 78.
- Sun, C. Q., Wang, X. K., Yushimura, A., and Iwata, N. (2000) Study on the genetic diversity of common wild rice (*O. rufipogon* Griff.) and cultivated rice (*O. sativa* L.) by RFLP analysis. *Acta Genetica Sinica* 27(3): 227-234.
- Thang, D. H., Jamjod, S., and Rerkasem, B. (2006). Responses of rice to low P supply in alternate aerated and stagnant solution culture. *Chiangmai Journal* : 21-35.
- Ticchiati, V., Sgattoni, S., Alois, C., and Mallengi, C. (1996) Red rice (*Oryza sativa*) control in Italian paddy rice. In *Proceedings of the Second International Weed Control Congress*. Copenhagen, Denmark.
- Van, K. K., Trebuil, G., and Goze, E. (2000) Identifying and grading limiting factors of upland rice yields in farmers's fields of northern Thailand. *Institute Rice Research Notes* 25: 32-33.
- Vaughan, L. K., Ottis, B. V., Prazak-Havey, A. M., Sneller, C., Chandler, J. M., and Park, W. D. (2001) Is all red rice found in commercial rice really *Oryza sativa*? *Weed Science* 49: 468-476.
- Walker, D. A. (1980) Regulation of starch synthesis in leaves-the role of orthophosphate. In *Physiological Aspects of Crop Productivity*. Pp. 195-207. The International Potash Institute, Bern.
- Yoshida, S., Forno, D., Cock, J., and Comez, A. K. (1976) *Laboratory Manual for Physiological Studies of Rice*. The international rice research institute. 3rd edition.
- Zhou, S. X., Tian, F., Zhu, Z. F., Fu, Y. C., Wang, X. K., and Sun, C. Q. (2006) Identification of quantitative trait loci controlling drought tolerance at seeding stage in Chinese Dongxiang common wild rice (*Oryza rufipogon* Griff.) *Acta Genetica Sinica* 33(6): 551-558.