Songklanakarin J. Sci. Technol.
33 (6), 685-692, Nov. - Dec. 2011

SJST SONGKLANAKARIN JOURNAL OF SCIENCE AND TECHNOLOGY
http://www.sjst.psu.ac.th

Original Article

Competition of root and shoot growth between cultivated rice (*Oryza sativa* L.) and common wild rice (*Oryza rufipogon* Griff.) grown under different phosphorus levels

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Received 20 July 2011; Accepted 29 September 2011

Abstract

This study aimed to evaluate the effect of phosphorus application on shoot biomass, root biomass, and shoot/root biomass ratio of common wild rice (*Oryza rufipogon* Griff.) and two tropical cultivated rice (*O. sativa* L.) varieties, including Sew Mae Jan (an upland rice) and KDML105 (a lowland rice), under two levels of inorganic phosphorus application (0 mg P/l and 10 mg P/l) both in monoculture (specific variety growing) and mix-culture (genetic competition setting) at early stage of growth (about 45 days after planting). Results indicated that phosphorus availability at 10 mg P/l clearly affected both rice shoot and root biomass at early growth stage. Significant interaction effect was found between phosphorus levels and rice varieties both above- and underground tissues accumulating in mix-culture of rice varieties. *O. rufipogon* showed a response to phosphorus application when shoot and root dry weight accumulation was assessed. Sew Mae Jan and KDML105 did not show any significant difference on shoot biomass accumulation when grew under mix-culture condition. The relative interaction index (RII) of *O. rufipogon* showed highly competitive response for accumulating both on shoot and root biomass compared with Sew Mae Jan and KDML105.

Keywords: common wild rice, competition, lowland rice, phosphorus, upland rice

1. Introduction

Interspecific competition plays an important role in determining the species competition of plant communities. Actually, plants compete for both aerial resources (i.e. light, CO_2 etc.) and soil resources (mineral nutrients and water) (Song *et al*., 2006). Roots may be considered as soil inhabiting, heterotrophic organisms which indirectly symbioses with autotrophic above-ground parts (shoots) by exchanging carbohydrates for water and nutrients (Van Noordwijk *et al*., 1998). However, integrations between roots and shoots go far beyond such symbiotic exchanges (Van Noordwijk *et al*., 1996). Both greenhouse (Wilson, 1988) and field evidence (Cahill, 1999) demonstrated that the competition between root and shoot interacts to affect plant growth. Therefore, the relationship between root and shoot competition is not simply linear.Understanding how the competition varies in rice varieties or rice species is essential for differentiating among alternative rice genetics of plant community organization. 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 both insect pests and drought tolerance rice breeding programs for cultivated rice improvement and it could crossbreed with cultivated rice and produced the fertile plant (Punyalue *et al*., 2006; Zhou *et al*., 2006). Although common wild rice is restrict distributed,

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but weedy rice (product of natural gene flow between wild rice and crop rice was recognized as intermediate weedy form or hybrid swarm) has become a problem in the rice growing area in Thailand as well as other regions around the word (Ticchiati *et al*., 1996; Eleftherohorinos *et al*., 2002), and is difficult to control in cultivated rice (Smith *et al*., 1977). Weedy rice causes significant reduction in 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). Moreover, DNA analysis revealed that the invasive, weedy forms have arisen from their wild progenitor by gene flow process. The direction of gene flow was predominantly observed from crop to wild and crop to weedy population (Jamjod *et al*., 2005). However, the knowledge of competitive ability of *O. rufipogon* flow to weedy rice is still limited. The objective of this study was to addresses the questions essential for understanding the interaction between root and shoot competition among the two rice species *O. sativa* and *O. rufipogon* (the ancestors of weedy rice) in the normal and stressful phosphorus environments. All two target varieties of *O. sativa* and a common wild rice were grown with and without interaction with neighboring root or shoots from different genetical groups. Phosphorus (P) was chosen as an essential macronutrient because P-deficiency is an obvious problem in rice production and its effect on rice could be seen easily particularly at the early growth stage (Slaton *et al*., 2002). Apart from soluble and suspended phosphates obtaining from irrigation water, there are no natural means of increasing the quantity of this element in the soil. Since the phosphoric acid content of the soil is small, ranging from 0.02 to 0.4 per cent, and the rice crop removes a considerable quantity of this element, it might be anticipated that paddy will respond to application of phosphate fertilizers (Grist, 1986). The purpose of the investigation described in this paper was to examine these hypotheses by comparing the competitive abilities among three rice varieties, which came from two rice species, *O. sativa* and *O. rufipogon*, under two contrast environments, one highly productive and another deficient in available phosphorus. Moreover, growth performance was compared between the three varieties planted under two different conditions, mono- and mix-culture at each phosphorus availability level.

2. Materials and Methods

2.1 Study site, target varieties/species and competition treatments

Fieldwork was conducted at Silpakorn University, Phetchaburi Information Technology Campus in Cha-am district, Phetchaburi Province, Thailand. The target rice varieties were grown in September, 2007. Three target rice varieties were chosen in this study, exhibiting two different species; the common annual wild rice (*O. rufipogon* Griff.), and two cultivated rice varieties represented lowland rice (KDML105) and upland rice (Sew Mae Jan, sticky rice variety). These two cultivated rice varieties were chosen because (1) they are well-known rice varieties and grown countrywide and (2) the contrast of growth habitat, which will allow to test the factors influencing the interactions between cultivated upland rice and wild rice species. All of the target rice seeds were collected at the same site in Phechaburi Province before the study begun.

Root and shoot competition was determined by using eight treatment combinations of two rice varieties (V) x two phosphorus levels (P; 0 ppm and 10 ppm) x two cultures (C; mono- and mix-culture). There were three variety combinations; Sew Mae Jan vs *O. rufipogon*; Sew Mae Jan vs KDML105; and KDML105 vs *O. rufipogon*. Plants were grown in plastic pots with a diameter of 25 cm and a depth of 22 cm, and assumed that there were competed both intra and inter varieties in growing condition. The monoculture could provide a true control, which differs from the mix-culture only with respect to the absence of the other species; hence, a calculation of the effect of each species upon the other is possible by comparing the characters in mix-culture and monoculture.

2.2 Seed preparing and growing conditions

For common wild rice, the seeds were incubated at 60°C in hot air oven for one week to break seed dormancy. Then seeds of all rice varieties were soaked in tap water overnight and sowed onto the designated pots. Each plastic pot was filled with clean sand to 80% capacity and received a basal supply of 40 mg N/l as NH_4NO_3, 40 mg K/l as K_2SO_4, 40 mg Ca/l as $CaCl_2$, 40 mg Mg/l as $MgSO_4 \cdot 7H_2O$, as essential mineral elements (Yoshida *et al*., 1976). Two rice seedlings were planted per pot and one liter per pot of nutrient medium was given twice daily at 8:00 AM and 4:00 PM. The treatments were arranged in three replicates in a greenhouse at the conducting site in September, 2007.

2.3 Data collection and measurement of plant response to competition

During the early growth stage, each target plant was measured on growth of shoot and root, and both shoot and roots were harvested separately. After drying at 60°C for 48 hours, both parts were weighed to measure plant biomass. Plant biomass in the presence of competition in relation to with and without competition was measured as the relative interaction index (RII) of plants described by Tang *et al*. (2009) as follows:

$$RII = (B_{mix} - B_{mono}) / (B_{mix} + B_{mono})$$

where B_{mono} is biomass of the target species in monoculture and B_{mix} is biomass of the target species in mix-culture. Therefore, the combination effects of root and shoot competition may be (1) negative value (negative competitive ability), (2) positive value (positive competitive ability), or (3) zero value (no competition or no difference between mono- and mix-culture).

2.4 Experimental design and statistical analysis

Analysis of variance (ANOVA) for a factorial in CRD (2x2x2) design was used for statistical analyses of the data in each combination. Factor effects (phosphorus application rate, culture condition, and varieties) were tested against the error term, and the interaction between factors were tested against the residual error. ANOVA was performed for hypotheses testing. Duncan's new multiple range test (DMRT) at 95% confidence level was used for comparison of treatments.

3. Results

3.1 Plant growth (shoot biomass, root biomass and shoot/root biomass ratio)

The results indicated that target plant biomass was significantly affected by varieties and combinations for phosphorus applications in all measured characters. The characters that rice varieties was significant affected were root biomass in Combination 1 (Sew Mae Jan vs *O. rufipogon*), shoot biomass and shoot/root biomass ratio in Combination 2 (Sew Mae Jan vs KDML105) and both on root biomass and shoot biomass in Combination 3 (KDML105 vs *O. rufipogon*). Culture method significantly affected only on shoot/root biomass ratio in Combination 3 (KDML105 vs *O. rufipogon*) (Table 1). In the presence of phosphorus, both shoot and root increased biomass more than without phosphorus in all combinations (Table 1). The lack of phosphorus resulted in stunt of stem, produced few leaves and root branching. Phosphorus deficiency affected both on shoot and root biomass but the ratio of shoot/root increased indicated that the biomass accumulation of above-ground tissues was affected by phosphate nutrient more than underground part tissues.

3.2 Interaction between main factors

No significance in PxC interaction indicated that both mono- and mix-culture had additive effect on shoot, root biomass, and the ratio of shoot/root biomass when the phosphorus was increased. The CxV interaction had no significant effect on different characters, indicating the rice genotypes had stability on biomass accumulation performances in both mono- and mix-culture (Table 1). A significant effect of PxV interaction was found, indicating that an uniform change in the direction of varieties of plant biomass accumulation did not occur under the phosphorus application. In Combination 1, Sew Mae Jan vs *O. rufipogon*, PxV interaction had a significant effect only on root biomass (Table 1). Without application of phosphorus, two varieties showed low biomass weights and were not significantly different (0.31 and 0.35 g/plant, respectively; Figure 1A). Wild rice, *O. rufipogon*, showed greater significant response than cultivated variety with biomass of 3.19 and 1.90 g/plant for *O. rufipogon* and Sew Mae Jan respectively (Figure 1A). A better competition and higher biomass accumulation of *O. rufipogon* over neighbor varieties also appeared obviously when it was planted in the same pot with KDML105 at 10 mg P/l for both shoot (9.23 and 4.87 g/plant, Figure 1B) and root biomass (2.67 and 1.25 g/plant, Figure 1C). The ability of shoot and

Table 1. Statistical significance of different factors and factor interactions under mix culture between two varieties/species (Sew Mae Jan and *Oryza rufipogon*, Combination 1; Sew Mae Jan and KDML105; Combination 2 and KDML105 and *O. rufipogon*, Combination 3) on shoot biomass (SB; g/plant), root biomass (RB; g/plant) and ratio of shoot/root biomass (S/R) in test compartment based on CRD analysis of variance (ANOVA).

Source of variance	df	SB	RB	S/R	SB	RB	S/R	SB	RB	S/R
		Combination 1			Combination 2			Combination 3		
P levels (P) [a]	1	**	**	**	**	**	**	**	**	**
Cultures (C) [b]	1	ns	ns	ns	ns	ns	ns	ns	ns	*
Varieties (V)	1	ns	*	*	**	ns	ns	**	*	ns
PxC	1	ns	ns	ns	ns	ns	ns	ns	ns	ns
PxV	1	ns	*	ns	ns	ns	ns	**	*	ns
CxV	1	ns	ns	ns	ns	ns	ns	ns	ns	ns
PxCxV	1	ns	ns	ns	**	ns	ns	ns	ns	ns
Error	17									
Total	23									

Significance levels: ns, P>0.05; * , P<0.05; **, P<0.01. [a] P levels included 0 mg P/l and 10 mg P/l. [b] Cultures included monoculture and mix-culture.

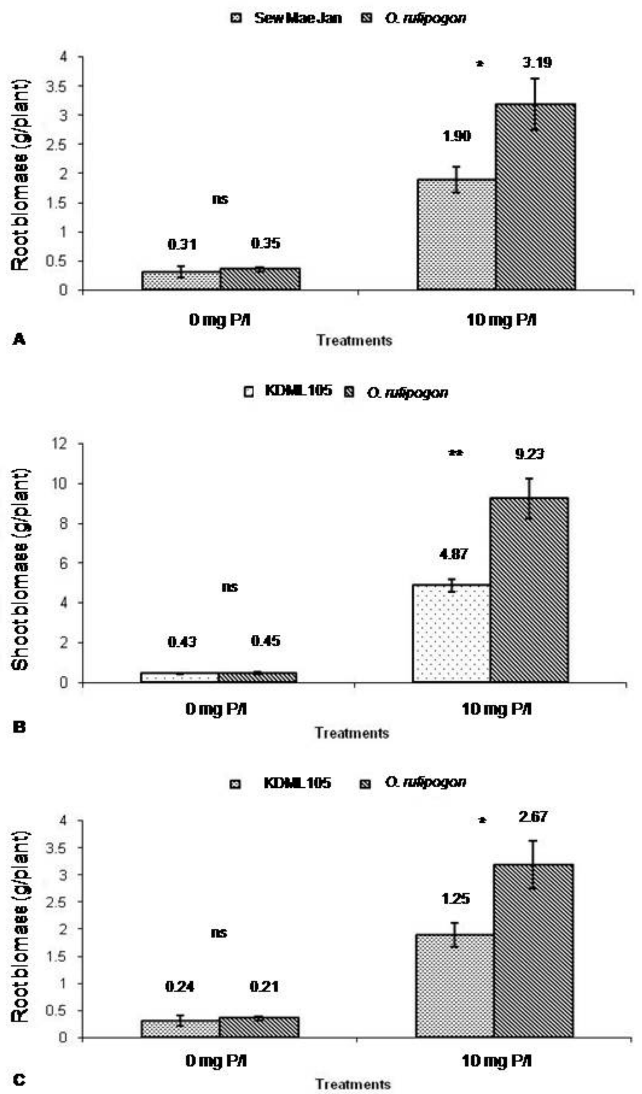

Figure 1. Root and shoot biomass as affected by the interaction between phosphorus levels and varieties in rice combinations. A, Sew Mae Jan vs *Oryza rufipogon*; B-C, KDML 105 vs *O. rufipogon*. Values are mean ± 1 SE. Significant levels are shown: ns = not significant, * = significant, ** = highly significant.

root accumulation over neighbor under 10 mg P/l was found only in *O. rufipogon*. The effect of phosphorus application and rice variety on the ability of the shoot biomass accumulation was seen in all three combinations, but the interaction occurred as a function of three factors (PxCxV) was found only in Combination 2, Sew Mae Jan vs KDML105 (Table 1; Figure 2). At 0 mg P/l, the shoot biomass of Sew Mae Jan was significantly higher than KDML105 when grew separately (0.68 and 0.44 g/plant, respectively) (Figure 2). However, this evidence was not found at 10 mg P/l (Figure 2). The positive or negative degree of changing on shoot biomass accumulation was also observed in PxCxV interaction.

3.3 Shoot biomass ratio of rice varieties

The flexible changing of shoot biomass among rice varieties in different phosphorus application levels resulted in a variation of shoot biomass ratios in all combinations (Figure 3). In Combination 1 (Sew Mae Jan/*O. rufipogon*), the shoot biomass ratio calculated from monoculture at 0 mg P/l was 1.81, indicating that growth of Sew Mae Jan was two times higher than that of *O. rufipogon*. However, the ability of shoot biomass accumulation of Sew Mae Jan was reduced when grew under mix-culture condition. Therefore, the shoot biomass ratio of Sew Mae Jan/*O. rufipogon* was less than 1.0 (0.84). However, this evidence did not occur in mono- and mix-culture at 10 mg P/l (1.04 and 1.06, respectively) (Figure 3A). In Combination 2, Sew Mae Jan developed more shoot biomass than KDML105 thus, shoot biomass ratio of KDML 105/Sew Mae Jan was less than 1 (0.65) at 0 mg P/l under monoculture. In contrast, with mix-culture condition the ratio value between these two rice varieties increased to 1.17. Despite the different ratio values in culture at 0 mg P/l, the values of shoot biomass ratio at 10 mg P/l in mono- and mix-culture were nearly the same (0.69 and 0.78, respectively) (Figure 3B). In Combination 3, the ratio of shoot biomass between KDML105/*O.rufipogon* was not different between mono- and mix-culture, both at 0 mg P/l and 10 mg P/l. However, at available phosphorus, the shoot biomass value of *O. rufipogon* tended to give higher shoot biomass and showed

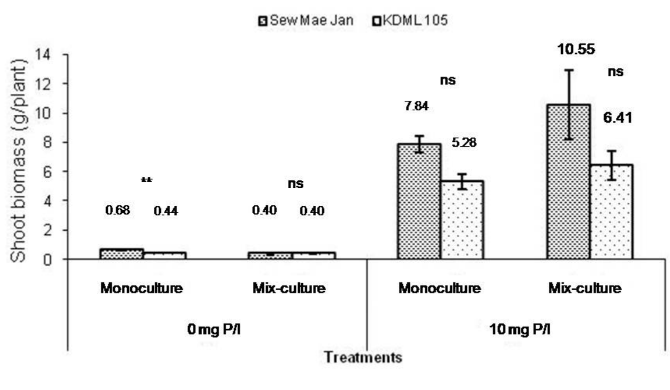

Figure 2. Shoot biomass affected by the interaction between phosphorus levels, cultures and varieties in rice combination Sew Mae Jan vs KDML105. Values are mean ± 1 SE. Significant levels are shown: ns = not significant, ** = highly significant.

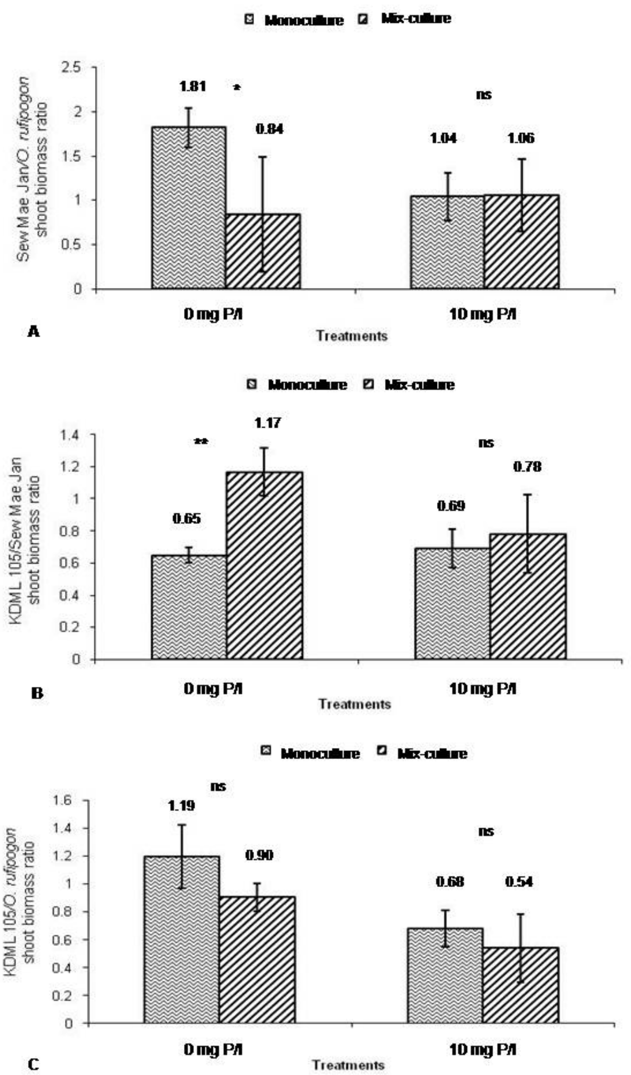

Figure 3. Shoot biomass ratio under cultures of two rice varieties. A = Sew Mae Jan/*Oryza rufipogon*, B = KDML105/Sew Mae Jan, C= KDML105/*O. rufipogon* shoot biomass. Values are mean ± 1 SE. Significant levels are shown: ns = not significant, * = significant, ** = highly significant.

ratio values less than 1 both in mono- and mix-culture (0.68 and 0.54, respectively) (Figure 3C).

3.4 The relative interaction index (RII)

The RII indicated the degree of competitive ability of individual rice genetic. Shoot and root biomass both in mono- and mix-culture were used to evaluate the ability of plant stand when grown together with neighbor rice genetics. Negative value on RII means that the biomass from monoculture was higher than that from mix-culture, or could explain that this genetic had poorer competitive ability either for overall area or fertilizer level than specific neighbor rice variety. Zero value for RII means that the biomass accumulation of target varieties from monoculture and mix-culture were not different. In addition, competitive ability might be equal in both varieties or no competitive situation occurred. Positive value on RII means that varieties had better growth under mix-culture than single stand growing with the same genotype in monoculture. In Combination 1, Sew Mae Jan showed negative RII and value was lower than 1.0 at 0 mg P/l for shoot biomass (-0.41), and gave the lowest biomass. Rice varieties had a significant effect on RII for shoot biomass but this character was not affected by phosphorus application (Table 2). The effect of rice varieties on shoot biomass could confirm that there was different competitive ability among the rice varieties. *O. rufipogon* showed stronger competition specifically at low phosphorus than Sew Mae Jan, but not at available phosphorus level.

In Combination 2 and 3, RII showed no significant effect both on shoot and root biomass from rice varieties, suggesting that these varieties grew in the same containers did not showed any competitive response to each other in mix-culture. The negative RII value appeared in Sew Mae Jan and KDML105 at 0 mg P/l on plant biomass characters. Furthermore, phosphorus deficiency greatly affected the plant biomass of all rice varieties in mix-culture. In Combination 3, KDML105 vs *O. rufipogon*, RII values of these two varieties were nearly zero both at 0 and 10 mg P/l, respectively (Table 2).

4. Discussion

This study provided evidence that response of rice growth was affected obviously by phosphorus availability under stress of mix-culture condition or enhancement the competitive condition among rice varieties. Generally, phosphorus enrichment favors plant growth for all plant varieties because phosphorus is the component of nucleic acid, phospholipids, ATP and involved in other metabolic processes, including the function in signaling and enzyme activities (Poirier and Bucher, 2002). Phosphorus is essential for cereal particularly at the early growth stages (Gutierrez-Boem and Thomas, 1998; Mengel and Kirkby, 2001; Slaton *et al.*, 2002). In our experiments, sufficient phosphorus significantly enhanced shoot and root growth in both mono- and mix-culture. The enhancement of shoot/root biomass ratio by elevating phosphorus level was found under sufficient phosphorus rather than under phosphorus deficiency for all rice varieties. These results indicated that shoot responded to phosphorus enrichment for biomass accumulating more than root system. In addition, shoot dry weight was a good indicator for predicting the P-stress in rice plant (Dobermann and Fairhurst, 2000) as the phosphorus deficiency must affect the expansion of leaf and leaf initiation (Fredeen *et al.*, 1989). This appearance was also observed in bean (*Phaseolus vulgaris*) where shoot/root ratio declined from 5 to 1.9 when grown under insufficient phosphorus (Khamis *et al.*, 1990). However, it was not documented that above-ground parts benefited more than under ground parts due to their different responses. Smith *et al.* (1990) explained root behavior that

Table 2. Relative interaction index (RII) on shoot and root biomass under P application.

Combination 1	Sew Mae Jan		*O. rufipogon*	
	0 mg P/l	10 mg P/l	0 mg P/l	10 mg P/l
Shoot biomass	-0.41 [b] ± 0.20	0.03 [a] ± 0.05	0.25 [a] ± 0.11	0.06 [a] ± 0.07
P levels = ns, Varieties = *				
Root biomass	-0.23 ± 0.21	-0.16 ± 0.24	0.46 ± 0.06	0.12 ± 0.09
P levels = ns, Varieties = *				
Combination 2	**Sew Mae Jan**		**KDML105**	
	0 mg P/l	10 mg P/l	0 mg P/l	10 mg P/l
Shoot biomass	-0.58±0.28	0.10 ± 0.16	-0.50 ± 0.09	0.09 ± 0.08
P levels = *, Varieties = ns				
Root biomass	-0.55±0.20	-0.02 ± 0.28	-0.38 ± 0.20	-0.08 ± 0.21
P levels = ns, Varieties = ns				
Combination 3	**KDML105**		***O. rufipogon***	
	0 mg P/l	10 mg P/l	0 mg P/l	10 mg P/l
Shoot biomass	0.01 ± 0.08	-0.10 ± 0.15	0.13 ± 0.16	0.09 ± 0.17
P levels = ns, Varieties = ns				
Root biomass	-0.03±0.28	-0.32 ± 0.24	0.06 ± 0.20	-0.09 ± 0.24
P levels = ns, Varieties = ns				

Values are mean ± 1 SE. Value with different lowercase letters in the same row are significantly different at P<0.05 (DMRT). Significance levels : ns, P>0.05; * , P<0.05.

tried to serve on root characteristic for uptake nutrient under deficient phosphorus condition. In addition, root morphology system was also changed under insufficient phosphorus (picture not shown). The fact that fertilization may cause shifting in the root-shoot interaction, but not in the total strength of root and shoot competition, suggests that the root-shoot interaction is itself a highly variation (Cahill, 2002). The significance of rice varieties on plant biomass accumulation in rice combination culture might affect the form of interaction between roots and shoots competition that always varied. In the phosphorus deficiency treatment, all three varieties suffered a marked reduction in growth so the biomass weights in mono- and mix-culture were not different. Some researchers explained that under low levels of resource supply, interactions between neighboring plants are rare, and competition is unimportant to plant growth (Grime, 1973; Grime and Hodgson, 1987). As resource supply increases, plant growth is greater, and there will be an increase in the total strength of competition (Huston, 1979), as well as increases in the strength of both root and shoot competition (Grime, 1973). Although the PxC interaction did not occur on plant biomass, it cannot identify the ability to compete for fertilization on rice varieties. Two ways could have happened, first, the varieties might not compete for the resource in mix-culture, and second, the competitive ability in two specific varieties was identical. All of these varieties combinations were influenced by rice genetics on differentiate characters, and PxV interaction also had a significant effect on characters studied. Sew Mae Jan vs KDML105 mix-culture showed the complicating results that there was an interaction effect between PxCxV on shoot biomass. Sew Mae Jan gave greater value than KDML105 when evaluated under monoculture condition, but this result was not found under competitive growing condition. It could be explained that Sew Mae Jan was less advantage in plant growth and biomass accumulation when growing under mix-culture condition with KDML105 at available phosphorus. On the other hand, KDML105 might have more abilities to compete over Sew Mae Jan for nutrient absorption and growth areas. Moreover, high growth rice variety might have more abilities to shift on plant morphologies and thus alter the competitive ability between above- and below-ground parts in response to the environment changes (Song *et al*., 2006). In Sew Mae Jan vs *O. rufipogon*, the RII value of *O. rufipogon* was significantly higher than that of Sew Mae Jan, both on shoot and root biomass (Table 2). This evidence suggests that *O. rufipogon* has a more advantageous performance than Sew Mae Jan under competitive setting. In this study, it is assumed that shoot competition is less than root competition because the container had restricted area and fertilizer was applied, but the space above ground area and light were not limited. Thus, the decrease in shoot biomass was mainly due to the consequence of root competition under plant standing with the neighbors.

However, the evidence of container effect was not quite clear under field condition. The response of plant to one form of competition may alter their abilities to compete in another form of competition, thus the combination effects will not be simple sum of the parts (Cahill, 2002). Moreover, the ability to make morphological shifts in response to change in the environment is quite species-specific. It is also likely that interactions between roots and shoots competition vary greatly among species. The intensity of competition experienced by individual plants is not characteristic for the community (competitive intensity), instead, an interaction between the neighborhood surrounding, an individual plant, and that plant's ability to respond are physiologically complex (Cahill, 2002). The RII values in combination were close to zero in characters implying that the competitive response seemed to occur in phosphorus deficiency condition and showed strong effect to reduce plant biomass at mix-culture. Zero on RII value suggested that rice varieties had poor or no competitive response, or the competitive ability among plant varieties in mix-culture were quite similar.

5. Conclusion

The experiment clearly showed that phosphorus application was necessary for growth of both above- and underground tissue parts at the early growth stage in all rice varieties and common wild rice species. The biomass characters were influenced by rice genetics. Further, the relationship between phosphorus level and rice genetic was found significant in mix-culture between *O. rufipogon* vs Sew Mae Jan and *O. rufipogon* vs KDML105. *O. rufipogon* responded to phosphorus application on shoot biomass more than Sew Mae Jan, and KDML105 both on shoot and root biomass. Shoot biomass of Sew Mae Jan did not differ from KDML 105 under mix-culture although it had higher shoot biomass accumulation under monoculture. The common wild rice species had beneficial characteristics over both lowland and upland rice varieties under the competitive culture. This evidence may have a drawback effect if common wild rice crossbreeds with other cultivated plant, making their offspring more adaptable to various environments and disseminating widely in the rice fields as noxious weeds.

Acknowledgements

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

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