Chapter 5

Genotypic variation in responses to phosphorus stress under aerobic and anaerobic conditions

5.1 Introduction

Rice has many genotypes which vary with cultivation system, origin, history of crop improvement and varietal selection. Generally, rice production systems are classified based on source of water supply into rainfed and irrigated; based on land into upland and lowland, and based on genetic improvement into traditional and improved rice cultivars. However, among groupings of rice there is overlapping variation and differences in growth and adaption to varied soil conditions (Colmer, 2003a). Water and nutrient stress are major problems in the rainfed rice ecosystem. Several previous works on genotypic variation of rice responses to fluctuating soil water regimes were reported (Kamoshita *et al.*, 2000; Banoc *et al.*, 2000a; Banoc *et al.*, 2000b). In these studies, difference in the seminal root system development among rice genotypes was examined under soil water fluctuations. Results confirmed genotypic variation in responses of rice root morphology as a key trait for the adaptation of rice plants to the fluctuation of soil water regimes.

Nutrient stress such as phosphorus deficiency was also examined in rice. George *et al.* (2001) worked on upland rice response to phosphorus fertilization and they found that improved upland rice varieties produced higher yield grain than traditional upland varieties, due to a larger proportion of biomass partitioned to grain. Moreover, differences among rice genotypes in their soil phosphorus uptake, growth and yield when grown in a P deficient soil in Thailand were studied by Koyama *et al.* (1973). However, these previous works did not explore the adaption of rice genotypes to exposure to both oxygen and nutrient deficiency. Therefore, the present work studied the variation of rice genotypes in their adaptation to alternate aerobic and anaerobic conditions at low P supply.

5.2 Materials and Methods

5.2.1 Experiment 1: Responses of Thai rice cultivars to P stress in solution culture

This experiment examined the P stress tolerance of 10 Thai rice cultivars in stagnant and aerated nutrient solution. Rice cultivars were: three selected from previous experiments (KDML105, CNT1 and KN), two upland cultivars (R258 and SMJ), three rainfed cultivars (RD6, NSG19 and RD7) and two deepwater cultivars (LMN111 and PCB1). Phosphorus levels were low P (1.6 μM) and adequate P (200 μM). The composition of nutrient solution was the same as the previous experiment (Chapter 3 experiment 3.2.4). There were four replicates. Twenty seedlings with 2 cm root length (three days after germination) were transplanted in each pot. Each plastic pot contained 40 litres of nutrient solution which was renewed every week and adjusted to pH 6.5 every day. The rice plants were harvested at six weeks after transplanting. Maximum root length, maximum shoot length, numbers of leaves, roots and tillers, root number per tiller, root and shoot dry weights, root/shoot ratio and N, P, K content in shoots were assessed.

5.2.2 Experiment 2: Short term responses of RD7 to P stress in solution culture

In the experiment 5.2.1 RD7 out-performed other cultivars at low P in term of shoot growth and dry weight and root dry weight. This suggest its that RD7 has P efficiency traits. In the present experiment RD7 was compared with another lowland cultivar, Chainat 1 (CNT1) to examine the short term responses of the two cultivars to aerated and stagnant solution at low P. There were three replicates per treatment. Five 14 day-old seedlings were transplanted to each pot of full strength nutrient solution for 14 days before transition. Each plastic pot contained 10 L of nutrient solution, renewed every week and adjusted to pH 6.5. The rice plants were harvested after 14 days in aerated high P supply nutrient solution (before transition to treatments), and again 2, 4 and 8 days after transition to stagnant and aerated at 1.6 (low P) and 200 μM (high P). Porosity of adventitious root (percentage of gas space per volume), aerenchyma formation in root cross sections, root and shoot dry weights, root/shoot ratio, and P content in plants were measured.

5.2.3 Experiment 3: Phosphorus stress tolerance of Three Australian rice cultivars

This experiment examined the P stress tolerance of three Australian rice cultivars in stagnant and aerated nutrient solution. Australian rice cultivars were Langi, Amaroo and Kyeema. Phosphorus levels were 50, 100, 200 and 400 μM for first two weeks (harvest 1) and changed to 1.6, 8, 40 and 200 μM, respectively after two weeks (harvest 2). There were four replicates. Six (two plants of each cultivar) 14 day-old seedlings were transplanted in each pot. Each plastic pot contained 12 L of nutrient solution which was renewed every day and adjusted to pH 6.5 every day. The rice plants were harvested at two and four weeks after transplanting. Maximum root length, maximum shoot length, number of leaves, roots and tillers, porosity of adventitious root (percentage of gas space per volume), root and shoot dry weights, root/shoot ratio and aerenchyma formation were assessed. For porosity measurement, adventitious roots from each plant were cut into 50 mm segments and measured by using the method described by Raskin (1983), and the equations as modified by Thomson *et al*. (1990). Aerenchyma formation was assessed in root cross section as describe in the chapter 2 experiment 2.2.1.

5.2.4 Statistical analyses

Data on root and shoot growth, root porosity, and tissue P were analyzed using linear models as general analyses of variance (ANOVA) to determine the main effects and interactions among treatments for a three way factorial combination. Effects of treatments at each harvest time were analyzed as separate data sets in experiment 5.2.2. Means were compared using Least Significant Differences (L.S.D) at P = 0.05.

5.3 Results

5.3.1 Experiment 1: Responses of Thai rice cultivars to P stress in solution culture

Ten rice cultivars in aerated solution culture had greater maximum root length than grown in stagnant solution culture regardless of P levels, (Table 5.3.1.1). The greatest decrease in root length in stagnant solution which found in four cultivars, NSG19, SMJ, R258 and LMN111. In six cultivars, KDML105, KN, R258, SMJ, RD7 and PCB1 maximum root length increased by low P whereas in other cultivars were no effect of P supply on the maximum root length.

Oxygen supply strongly affected root numbers increasing it in CNT1, NSG19, RD7, decreasing it in KN and R258 and having no effect on root numbers of other cultivars. In all cultivars low P strongly decreased root numbers with the largest decreases in CNT1, RD6, NSG19, RD7 and PCB1. Phosphorus and oxygen affected on root numbers appeared to be correlated (R^2= 0.7) (Figure 5.3.1.1). That is in cultivar where low P strongly decreased root numbers stagnant solution also had largest effect on decreasing root numbers. NSG19 and CNT1 were two cultivars where low P and stagnant had the largest effect on root numbers whereas KN and R258 had relatively small effects on root numbers due to low P and were the only cultivars where stagnant solution increased root numbers (Table 5.3.1.2).

In all cultivars, low P depressed root dry weight regardless of oxygen supply except for R258 and RD7 which maintained root dry weight under low P in aerated solution. In RD7, R258 and KDML105, root dry weight was strongly depressed by low P in stagnant solution compared to aerated solution. Whereas, NSG19, LMN11 and PCB1 root dry weight was depressed by stagnant solution with both high and low P (Table 5.3.1.3).

Overall cultivars shoot dry weight in stagnant solution decreased significantly by 46-59 %. Similarly, low P strongly decreased shoot dry weight in both aerated and stagnant solutions (Table 5.3.1.4). RD7 appeared to produce greater shoot dry weight under low P than other cultivars, matching its superior root dry weight in low P aerated solution. Tiller and leaf numbers in RD7 under low P also tended to be greater than in other cultivars in both aerated and stagnant solutions (Table 5.3.1.5 and 5.3.1.6). RD7 is distinctive in having shorter shoot and relatively short root length compared to other cultivars (Table 5.3.1.7).

Table 5.3.1.1 Maximum root lengths (cm) of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	77.1	56.8	50.9	31.5
Kae Noi	69.9	63.8	48.5	39.1
Chainat 1	72.7	72.1	43.3	39.8
R258	86.9	76.8	45.1	40.1
Sew Mae Jan	79.0	76.7	38.2	31.4
RD6	58.5	65.2	36.2	32.7
Nam Sa Gui1 9	72.2	72.1	37.1	32.0
RD7	62.3	51.8	33.0	31.4
Leb Mue Nang 111	80.1	78.0	39.4	35.5
Prachinburi 1	72.8	67.6	37.5	33.2
F- test	O x C*		P x C*	
LSD $_{(P<0.05)}$	7.1		7.1	

* significant at P< 0.05. O x C and P x C indicate F-test for oxygen condition and cultivar interaction, and P level and cultivar interaction effects, respectively.

Table 5.3.1.2 Root numbers of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars /	Aerated		Stagnant	
Conditions	Low P	High P	Low P	High P
KDML105	42.8	122.5	31.0	130.5
Kae Noi	24.3	73.8	38.3	98.3
Chainat 1	41.3	146.0	31.0	139.0
R258	37.3	81.5	31.3	110.5
Sew Mae Jan	27.5	101.5	26.5	115.3
RD6	32.0	126.8	30.0	132.0
Nam Sa Gui1 9	40.3	155.8	36.0	131.5
RD7	62.5	141.8	43.3	145.3
Leb Mue Nang 111	26.5	102.8	26.8	108.5
Prachinburi 1	34.3	129.0	26.3	142.8
F- test	O x C*		P x C*	
LSD $_{(P<0.05)}$	13.9		13.9	

* significant at P< 0.05. O x C and P x C indicate F-test for oxygen condition and cultivar interaction, and P level and cultivar interaction effects, respectively.

Table 5.3.1.3 Root dry weight (g plant^{-1}) of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	0.48	1.00	0.19	0.84
Kae Noi	0.56	1.02	0.42	1.25
Chainat 1	0.46	1.13	0.23	1.27
R258	1.11	1.04	0.36	1.31
Sew Mae Jan	0.50	1.29	0.24	1.10
RD6	0.30	0.80	0.15	0.96
Nam Sa Gui1 9	0.47	1.36	0.20	0.83
RD7	0.82	1.01	0.34	1.08
Leb Mue Nang 111	0.65	1.73	0.21	1.34
Prachinburi 1	0.63	1.72	0.28	1.25
F- test	O x C*	P x C*	O x P x C*	
LSD $_{(P<0.05)}$	0.19	0.19	0.27	

* significant at P< 0.05. O x C, P x C and O x P x C indicate F-test for oxygen condition and cultivar interaction, P level and cultivar interaction, and oxygen condition, P level and cultivar interaction effects, respectively.

Table 5.3.1.4 Shoot dry weight (g plant^{-1}) of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	1.30	6.38	0.40	2.99
Kae Noi	0.99	6.07	0.59	3.33
Chainat 1	1.01	5.80	0.41	3.28
R258	1.02	4.75	0.47	3.21
Sew Mae Jan	1.05	5.97	0.42	3.39
RD6	0.90	4.93	0.27	3.04
Nam Sa Gui1 9	1.30	7.90	0.47	3.35
RD7	1.93	6.76	0.65	3.31
Leb Mue Nang 111	1.24	6.70	0.38	3.38
Prachinburi 1	1.42	7.11	0.33	3.36
F- test	O x P*	O x C*	P x C*	
LSD $_{(P<0.05)}$	0.81	0.61	0.61	

* significant at P< 0.05. O x C, P x C and O x P indicate F-test for oxygen condition and cultivar interaction, P level and cultivar interaction, and oxygen condition and P level interaction effects, respectively.

Table 5.3.1.5 Tiller numbers of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	2.0	9.3	0.0	3.5
Kae Noi	1.0	4.3	0.0	3.0
Chainat 1	2.7	11.8	0.0	6.3
R258	1.3	5.0	0.3	3.0
Sew Mae Jan	1.3	4.8	0.0	3.3
RD6	2.0	6.0	0.0	3.3
Nam Sa Gui1 9	2.0	9.0	0.0	2.8
RD7	3.0	13.3	1.5	7.3
Leb Mue Nang 111	1.8	6.3	0.0	2.7
Prachinburi 1	2.0	10.5	0.0	4.8
F- test	O x P*	O x C*	P x C*	O x P x C*
LSD $_{(P<0.05)}$	0.6	1.1	1.1	1.6

* significant at P< 0.05. O x C, P x C, O x P and O x P x C indicate F-test for oxygen condition and cultivar interaction, P level and cultivar interaction, oxygen condition and P level interaction, and oxygen condition, P level and cultivar interaction effects, respectively.

Table 5.3.1.6 Leaf numbers of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	8.3	40.3	3.5	17.5
Kae Noi	5.3	22.0	2.8	15.3
Chainat 1	11.0	56.5	3.3	29.0
R258	7.0	25.3	3.5	16.0
Sew Mae Jan	6.8	26.0	3.0	15.8
RD6	7.5	30.3	2.3	16.0
Nam Sa Gui1 9	9.3	40.8	3.0	16.3
RD7	15.5	59.8	5.5	44.0
Leb Mue Nang 111	7.0	33.5	3.3	15.0
Prachinburi 1	9.0	51.8	8.0	24.5
F- test	O x P*	O x C*	P x C*	
LSD $_{(P<0.05)}$	3.1	5.7	5.7	

* significant at P< 0.05. O x C, P x C and O x P indicate F-test for oxygen condition and cultivar interaction, P level and cultivar interaction, and oxygen condition and P level interaction effects, respectively.

Table 5.3.1.7 Maximum shoot lengths (cm) of 10 rice cultivars when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) for six weeks.

Cultivars / Conditions	Aerated		Stagnant	
	Low P	High P	Low P	High P
KDML105	64.3	99.3	46.2	87.5
Kae Noi	65.1	102.1	64.0	88.8
Chainat 1	48.6	81.0	48.4	70.6
R258	54.0	94.9	41.4	79.7
Sew Mae Jan	69.6	112.3	54.9	99.0
RD6	58.9	105.0	43.5	89.5
Nam Sa Gui1 9	60.9	99.3	50.7	90.8
RD7	43.8	72.0	35.9	57.1
Leb Mue Nang 111	71.8	117.6	56.3	105.6
Prachinburi 1	63.8	100.1	50.7	84.9
F- test	O*	P	C*	P x C*
LSD $_{(P<0.05)}$	3.1	1.7	3.8	5.3

* significant at P< 0.05. O, P, C and P x C indicate F-test for oxygen condition, P level, cultivar, and P level and cultivar interaction effects, respectively.

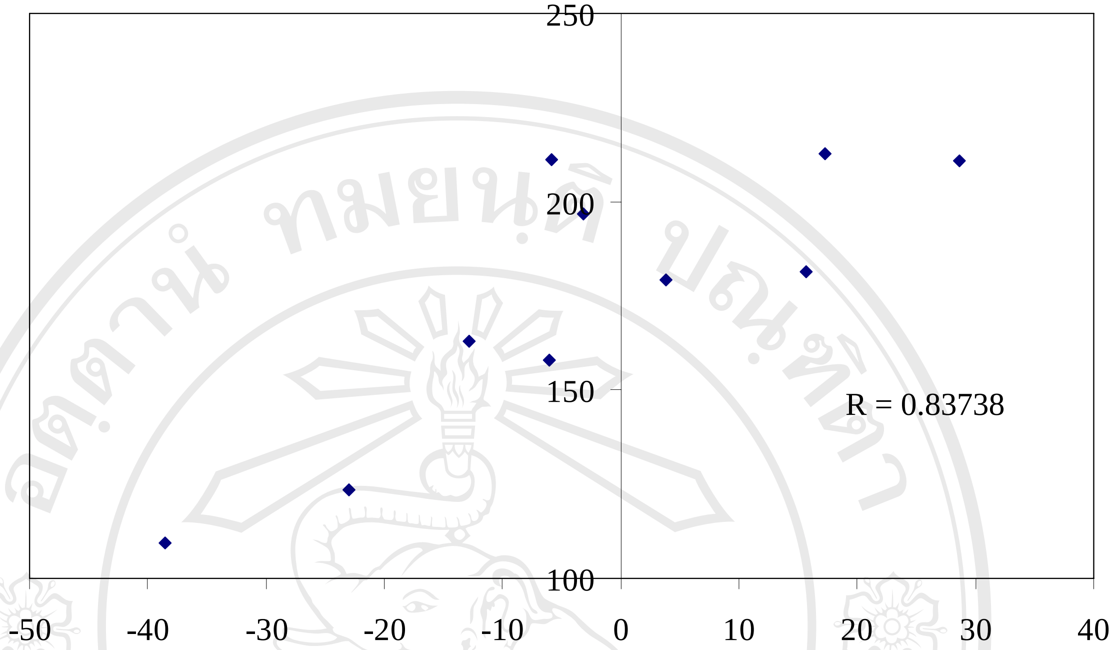

Figure 5.3.1.1 Relationship between P level and oxygen effects on root numbers of rice when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 µM (high P) for six weeks.

5.3.2 Experiment 2: Short term responses of RD7 to P stress in solution culture

From the start, and throughout the experiment RD7 had shorter maximum root length than CNT1. Nevertheless, stagnant solution decreased root length significantly from two days after transfer, and the differences in maximum root length between aerated and stagnant solution increased with time. By contrast, P had smaller effects on root length even at day 8 when low P increased root length in aerated solution by 2 cm and decreased its by 2 cm in stagnant solution (Figure 5.3.2.1). Root numbers responses at two and four days where inconsistent. At eight days, root numbers increased in stagnant solution and decreased in low P and generally high in CNT1 than RD7 unlike the responses in experiment 1. However, it is worth noting that four week-old seedlings grown with adequate P and aeration were used in the present experiment whereas three day-old seedlings were used in experiment 5.2.1 and exposed to treatments for six weeks. The only consistent root dry weight response was the increase in the stagnant solution which was evident from two days after treatments began. Shoot dry weight did respond to treatments in the eight day period apart from a week P effect (data not shown). However, tiller numbers were depressed by low P at eight days. RD7 had higher P content in whole plant than CNT1 and stagnant solution decreased P content. Phosphorus uptake per unit root weight was also consistently higher in RD7 than in CNT1 including both stagnant and aerated solutions and low and high P supply.

At eight days, root porosity of CNT1 was higher than RD7, and it was 8-15 % increased in stagnant culture. While, root porosity of RD7 in all treatments was the same, excepted it was 9-17 % lower in aerated at high P supply.

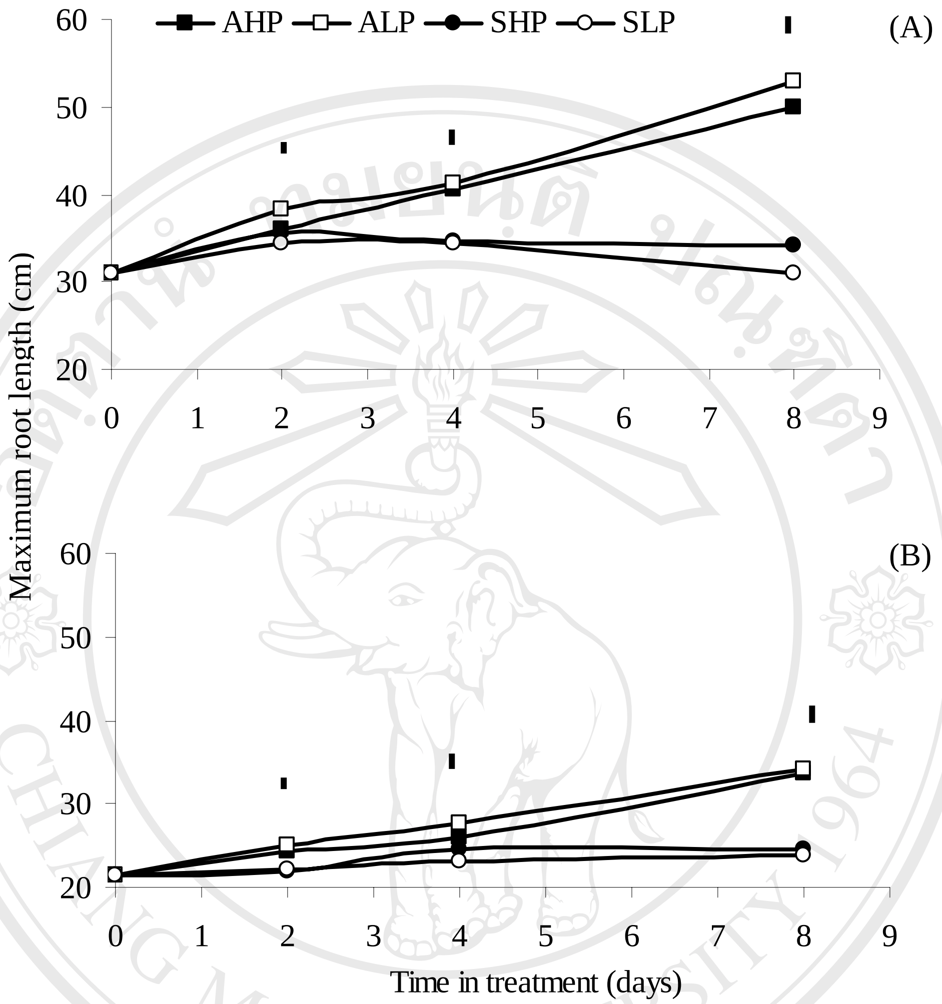

Figure 5.3.2.1 Maximum root length (cm) of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for oxygen level, P level and cultivar interaction effects at two days in treatments are 1.4; for oxygen level and cultivar interaction effects at four days in treatments are 1.8; for oxygen level and cultivar interaction , and oxygen level and P level interaction effects at eight days in treatment are 1.9.

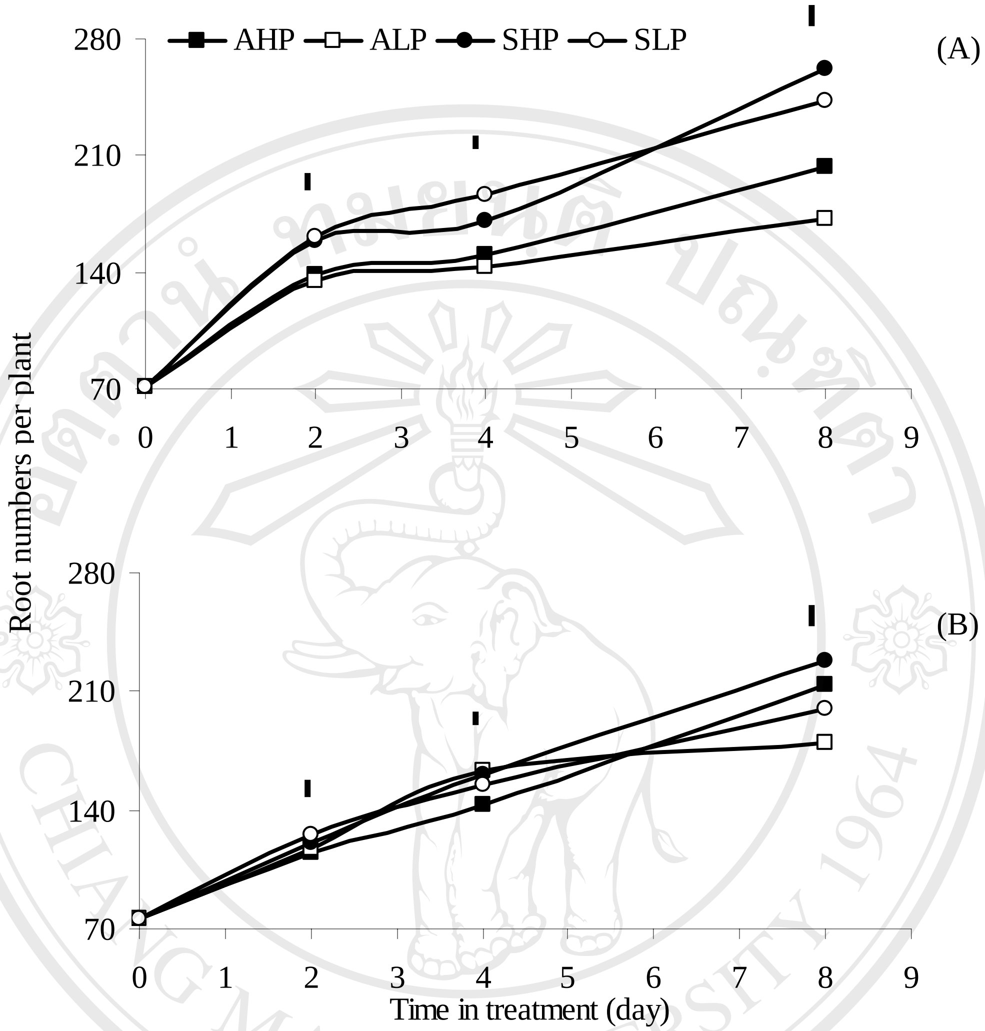

Figure 5.3.2.2 Root numbers per plant of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for oxygen level and cultivar interaction effects at two days in treatments are 6.7; for oxygen level, P level and cultivar interaction effects at four days in treatments are 8.8; for oxygen level and cultivar interaction effects at eight days in treatment are 12.9.

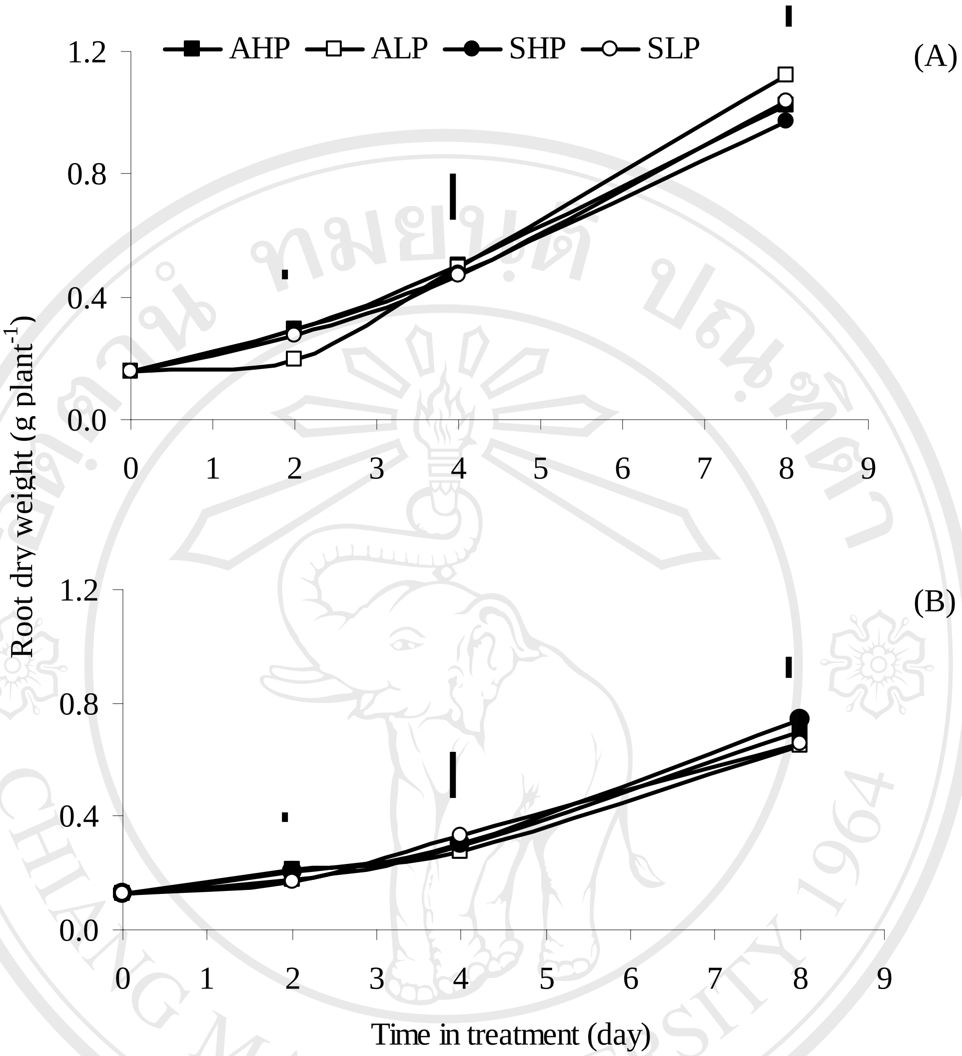

Figure 5.3.2.3 Root dry weight (g plant^{-1}) of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for oxygen level and P level interaction effects at two days in treatments are 0.035; for oxygen level effect at four days in treatments are 0.155; for oxygen level effect at eight days in treatment are 0.070.

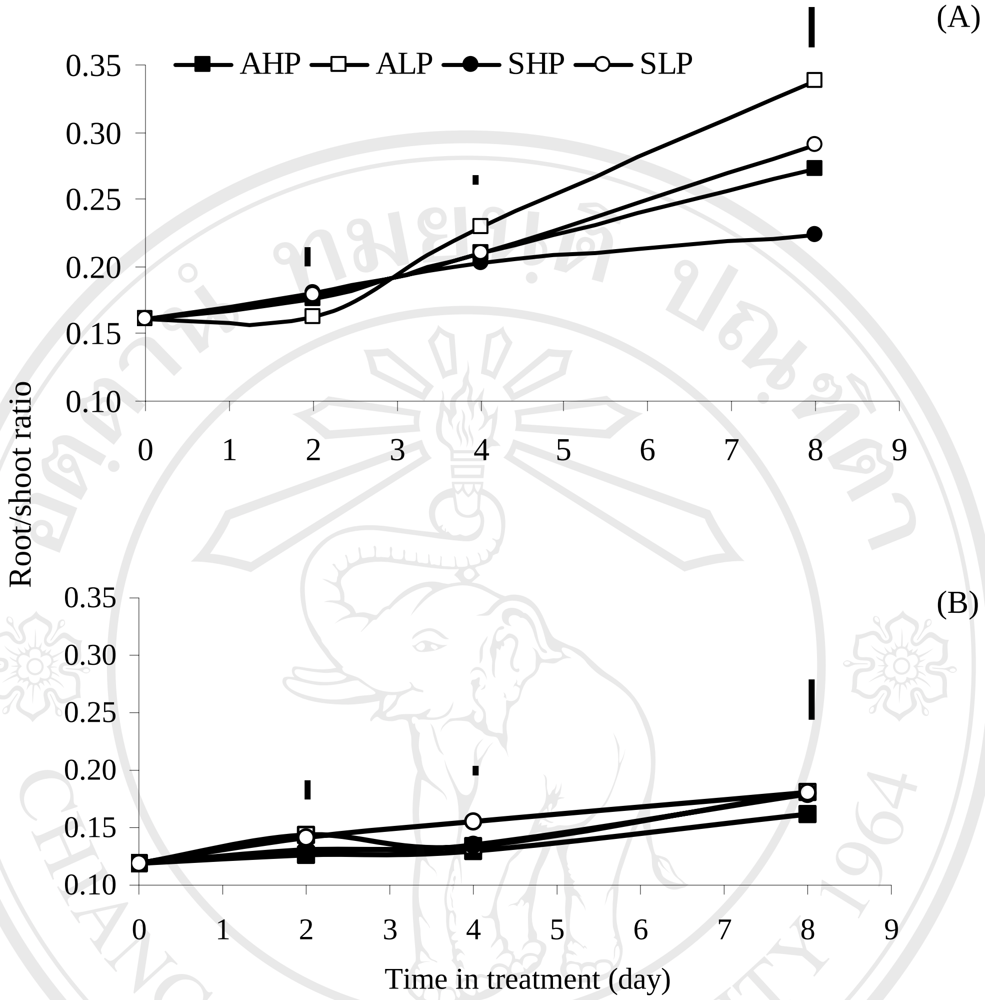

Figure 5.3.2.4 Root/shoo ratio of CNT1 (A) and RD7 (B) when grown in aerated at low or high P and stagnant at low or high P solution cultures at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for cultivar effect at two days in treatments are 0.02; for cultivar effect at four days in treatments are 0.01; for cultivar effect at eight days in treatment are 0.04.

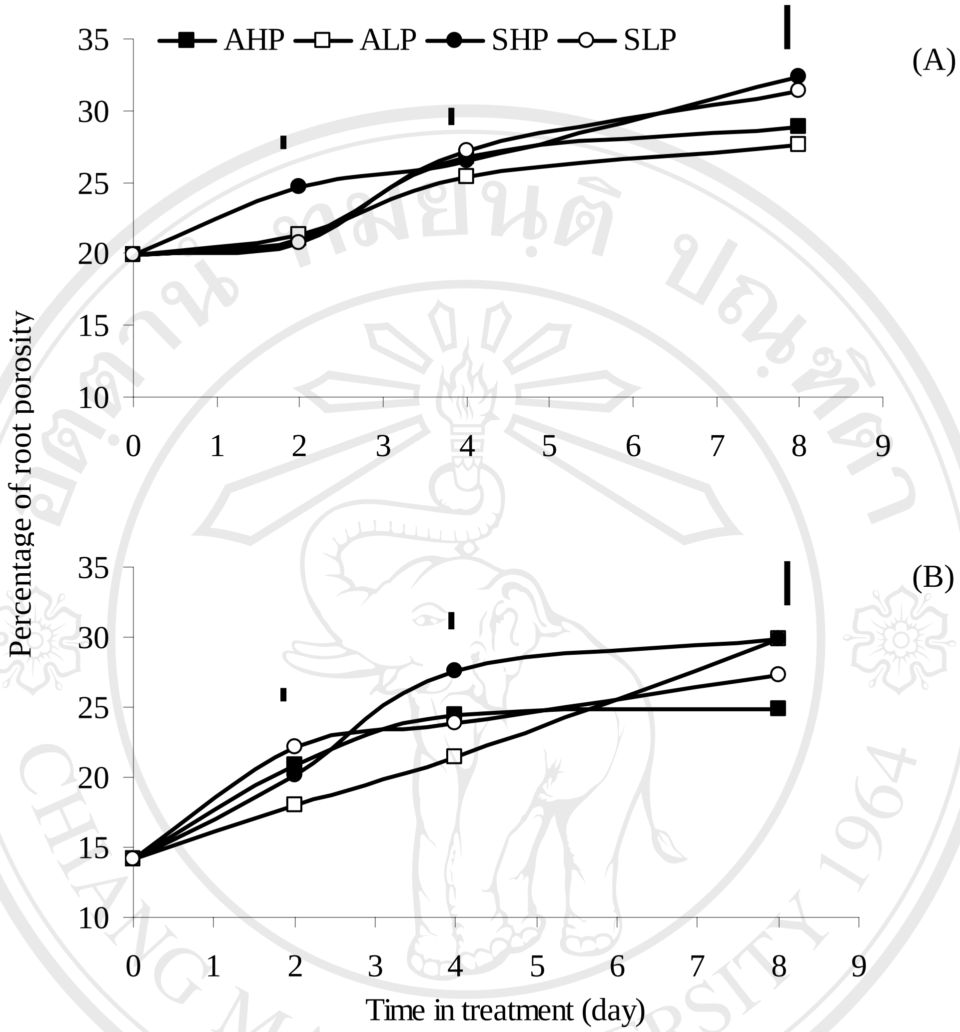

Figure 5.3.2.5 Root porosity (%) of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences (P<0.05) for oxygen level, P level and cultivar interaction effects at two days in treatments are 1.1; for oxygen level, P level and cultivar interaction effects at four days in treatments are 1.3; for oxygen level, P level and cultivar interaction effects at eight days in treatment are 3.2.

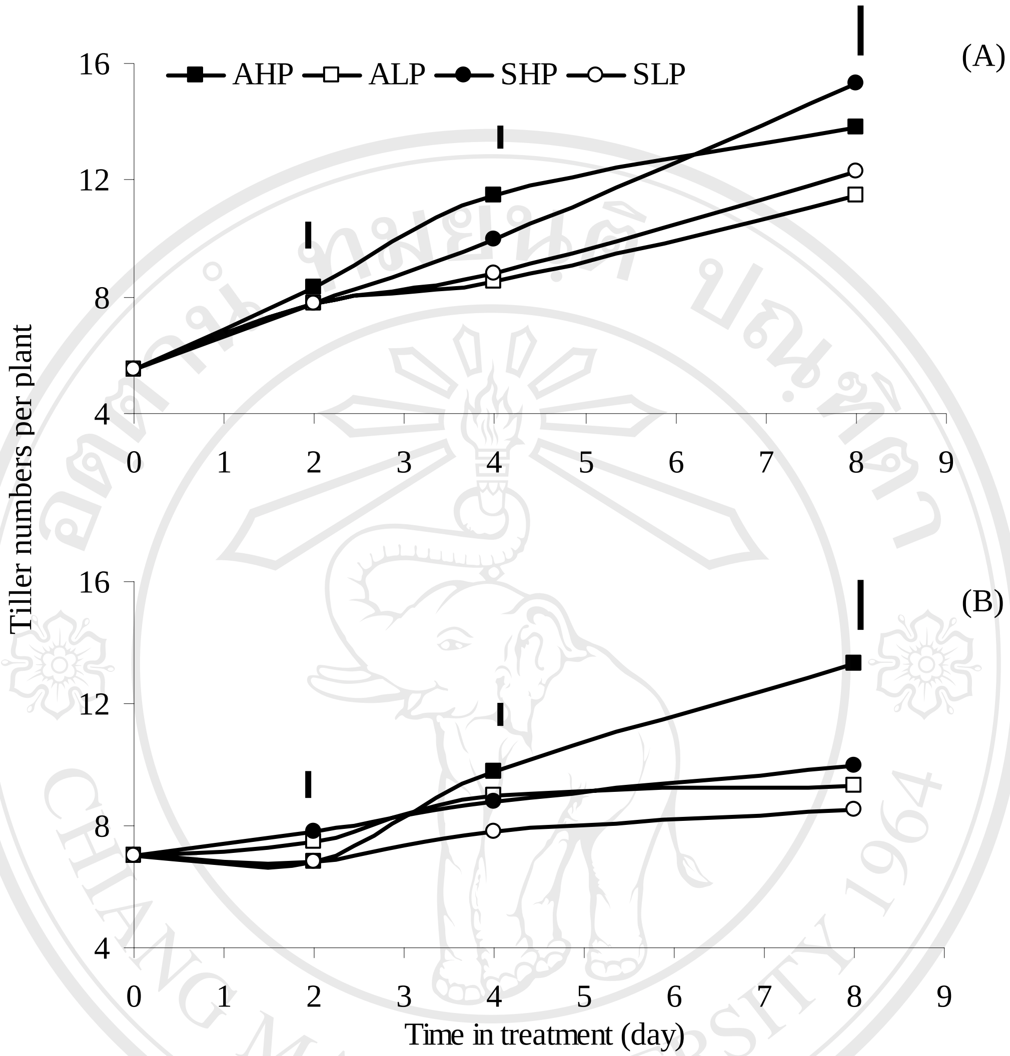

Figure 5.3.2.6 Tiller numbers per plant of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for oxygen level, P level and cultivar interaction effects at two days in treatments are 0.9; for cultivar effect at four days in treatments are 0.8; for oxygen level, P level and cultivar interaction effects at eight days in treatment are 1.7.

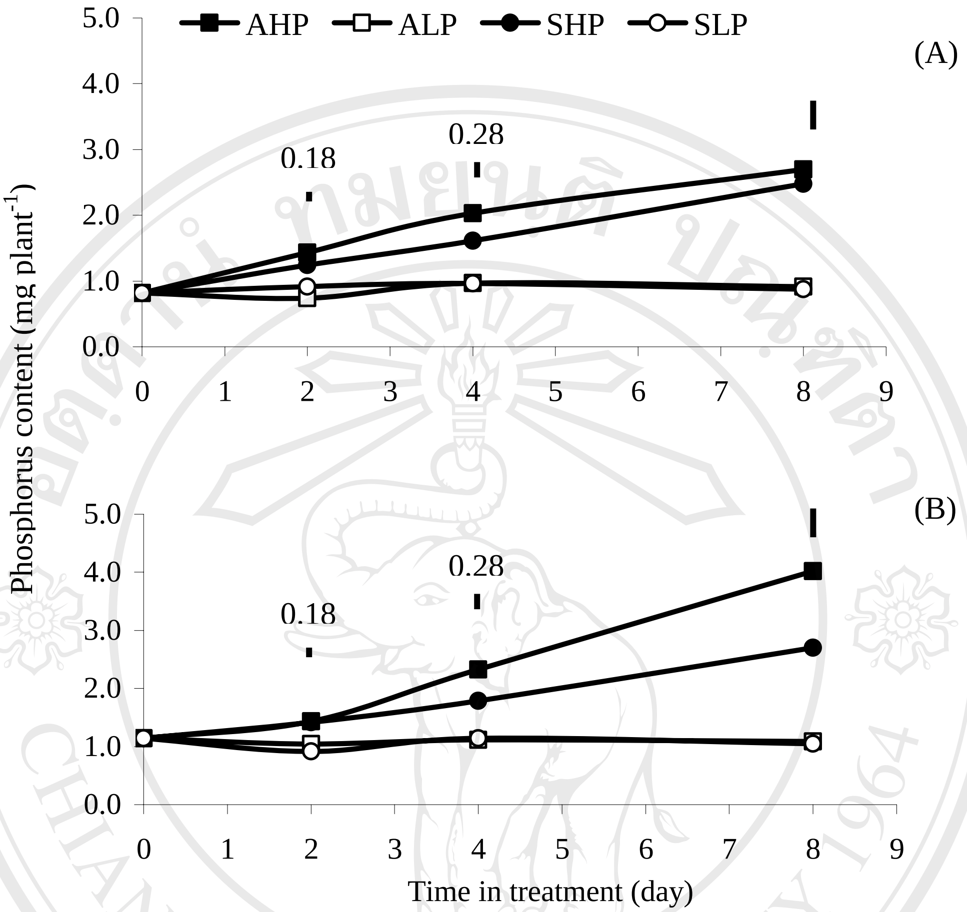

Figure 5.3.2.7 Phosphorus content (mg plant^{-1}) of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences (P<0.05) for oxygen level and cultivar effects at two days in treatments are 0.13 and 0.18; for oxygen level and cultivar effects at four days in treatments are 0.20 and 0.28; for oxygen level effect at eight days in treatment are 0.52.

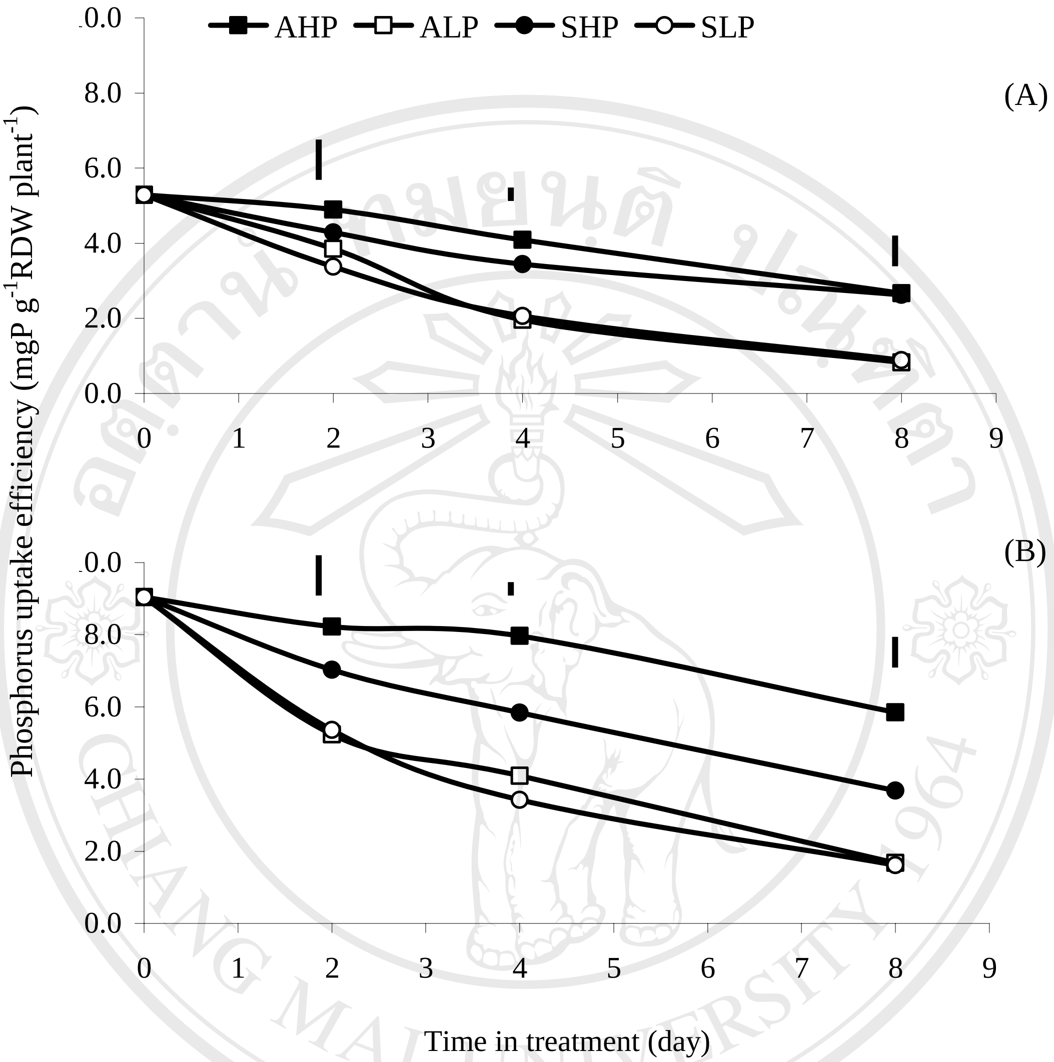

Figure 5.3.2.8 Phosphorus uptake efficiency (mgP g^{-1} root dry weight) of CNT1 (A) and RD7 (B) when grown in aerated and stagnant nutrient solution at 1.6 (low P) and 200 μM (high P) at initial, 2, 4 and 8 days. Least significant differences ($P<0.05$) for oxygen level, P level and cultivar interaction effects at two days in treatments are 1.12; for oxygen level, P level and cultivar interaction effects at four days in treatments are 0.40; for oxygen level, P level and cultivar interaction effects at eight days in treatment are 0.85.

5.3.3 Experiment 3: Phosphorus stress tolerance of Three Australian rice cultivars

At first two weeks in aerated and stagnant solution cultures at different levels of P supply, all Australian rice cultivars generally increased root elongation when plants grown in aerated culture (Table 5.3.3.1). Moreover, root elongation of all cultivars in aerated culture was varied in different levels of P supply by rice plants had the longest root length when obtained 100 μM P, and they were the shortest at 50 μM P, while P level at 200 and 400 μM resulted in roots were intermediate length. Whereas, the shorter root in stagnant culture was more reduced root length when plant gained higher P supply, which the highest of root length was at 50 μM P and the lowest was at 400 μM P. Root numbers were only affected by cultivars effect, which Amaroo produced the highest of root numbers, Kyeema was intermediate root numbers between Amaroo and Langi (Table 5.3.3.2). The root dry weight was supported by root numbers, which resulted in Amaroo and Kyeema had 13 % higher root dry weight than Langi (Table 5.3.3.3). In addition, root dry weight was varied by P supply, which at 100 and 400 μM P promoted root dry weight. In contrast, P supply at 200 μM P 27 % reduced root dry weight when compared with root dry weight at 100 μM P. For shoot growth, only shoot length was affected by cultivars effect, which Kyeema was the highest in the maximum shoot length, while Amaroo and Langi were the same length (Table 5.3.3.4).

Table 5.3.3.1 Maximum root length (cm) of three rice cultivars when grown in aerated or stagnant at 50, 100, 200 and 400 µM P of nutrient solution cultures for two weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		50	100	200	400	
Langi	Aerated	16.2	19.7	16.5	17.6	15.4
	Stagnant	14.2	12.8	13.6	12.5	
Amaroo	Aerated	16.5	16.3	14.8	16.1	14.5
	Stagnant	14.1	13.9	12.2	12.0	
Kyeema	Aerated	13.3	16.2	15.3	16.9	14.0
	Stagnant	12.8	13.3	11.7	12.2	
Aerated		15.3 Ac	17.4 Aa	15.5 Abc	16.9 Aab	
Stagnant		13.7 Ba	13.3 Ba	12.5 Ba	12.2 Bb	
Means of conditions		Aerated	16.3	Stagnant	12.9	
F- test		Con*	Cul*	Con x P*		
LSD $_{(P<0.05)}$		-	-	1.5		

*Significant at P< 0.05, Con, P, Cul and Con x P indicate F test for conditions of solution culture, phosphorus levels, cultivars and conditions of solution culture and phosphorus levels interaction effects, respectively. ns indicates no significant difference. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.2 Root numbers per plant of three rice cultivars when grown in aerated or stagnant at 50, 100, 200 and 400 µM P of nutrient solution cultures for two weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		50	100	200	400	
Langi	Aerated	18.0	17.0	18.0	18.0	18.5 B
	Stagnant	17.0	20.0	20.0	20.0	
Amaroo	Aerated	20.0	20.0	21.0	18.0	20.5 A
	Stagnant	23.0	20.0	20.0	22.0	
Kyeema	Aerated	19.0	18.0	18.0	17.0	19.4 AB
	Stagnant	21.0	21.0	20.0	21.0	
Means of P levels		19.7	19.3	19.5	19.3	
Means of conditions		Aerated	18.5	Stagnant	20.4	
F- test		Con ^{ns}	P ^{ns}	Cul*		
LSD $_{(P<0.05)}$		-	-	1.4		

*Significant at P< 0.05, Con, P and Cul indicate F test for conditions of solution culture, phosphorus levels and cultivars effects, respectively. ns indicates no significant difference. The upper case is used for comparison between cultivars.

Table 5.3.3.3 Root dry weight (g plant^{-1}) of three rice cultivars when grown in aerated or stagnant at 50, 100, 200 and 400 µM P of nutrient solution cultures for two weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		50	100	200	400	
Langi	Aerated	0.016	0.025	0.022	0.026	0.020 B
	Stagnant	0.016	0.020	0.017	0.020	
Amaroo	Aerated	0.025	0.026	0.020	0.023	0.023 A
	Stagnant	0.023	0.025	0.018	0.021	
Kyeema	Aerated	0.023	0.028	0.021	0.024	0.023 A
	Stagnant	0.023	0.026	0.015	0.024	
Means of P levels		0.021 bc	0.025 a	0.019 c	0.023 ab	
Means of conditions		Aerated	0.023	Stagnant	0.021	
F- test		Con ^{ns}	P*	Cul*		
LSD $_{(P<0.05)}$		-	0.004	0.002		

*Significant at P< 0.05, Con, P and Cul indicate F test for conditions of solution culture, phosphorus levels and cultivars effects, respectively. ns indicates no significant difference. The upper and lower cases are used for comparison between cultivars and phosphorus levels, respectively.

Table 5.3.3.4 Maximum shoot length (cm) of three rice cultivars when grown in aerated or stagnant at 50, 100, 200 and 400 µM P of nutrient solution cultures for two weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		50	100	200	400	
Langi	Aerated	46.7	46.9	47.2	49.3	47.1 B
	Stagnant	45.5	47.4	44.0	50.0	
Amaroo	Aerated	49.7	46.9	47.1	44.3	47.7 B
	Stagnant	50.6	49.5	44.2	49.0	
Kyeema	Aerated	49.5	52.8	48.7	51.4	50.5 A
	Stagnant	51.2	52.4	47.8	50.5	
Means of P levels		48.9	49.3	46.5	49.1	
Means of conditions		Aerated	48.4	Stagnant	48.5	
F- test		Con ^{ns}	P ^{ns}	Cul*		
LSD $_{(P<0.05)}$		-	-	1.7		

*Significant at P< 0.05, Con, P and Cul indicate F test for conditions of solution culture, phosphorus levels and cultivars effects, respectively. ns indicates no significant difference. The upper case is used for comparison between cultivars.

In first two weeks in adequate P supply, rice growth shown no clear responses to P and all plants were healthy in appearance even at 50 μM P (see Appendix G). Therefore, the levels of P supply were reduced from 50, 100, 200 and 400 μM P to 1.6, 8, 40 and 200 μM P, respectively. New imposed P treatments use the same plants in aerated and stagnant as the previous two weeks treatment. After two weeks plant in stagnant solution had reduced maximum root length, increased root numbers, slightly lower in root dry weight but similar shoot dry weight to plant in aerated solution. The following presentation focused on growth responses between two and four weeks with the lower P levels.

The maximum root length of all rice cultivars was decreased by 45 % when grown in stagnant solution, which it was without P level effect (Table 5.3.3.5). Root numbers were depressed by 1.6 μM P compared to higher P levels and also increased by stagnant solution (Table 5.3.3.6). Root dry weight of all cultivars in aerated culture at 8 and 200 μM P supply was lower than in stagnant culture, while root dry weight of plant in aerated at 1.6 and 40 μM P supply was the same weight as in stagnant culture at the same P levels (Table 5.3.3.7). In aerated culture, plants at 40 μM P supply produced 17 – 20 % higher root dry weight than other P levels, while all plants in stagnant culture in all P supply were the same in root dry weight. The ability of rice roots in root porous construction was affected by culture conditions, P levels and cultivars interaction effects. Root porosity (%) of all cultivars was generally increased when grown in stagnant culture, otherwise there was no clear effect of P on root porosity level part from and increased at low P in Kyeema in aerated solution (Table 5.3.3.8). Overall shoot dry weight was slightly decreased by stagnant solution and decreased by 25 % at low P (Table 5.3.3.9). Overall Amaroo produced more biomass and leaf numbers including apparently at 1.6 μM P (Table 5.3.3.10). Amaroo also produced more tiller than other cultivars in those aerated and stagnant solution and was the only cultivar which tillers in aerated solution at 1.6 μM P (Table 5.3.3.11). The maximum shoot length of all cultivars was generally the same in all conditions, excepted the maximum shoot length of plants in stagnant culture at 1.6 μM P supply was lower than others (Table 5.3.3.12).

Table 5.3.3.5 Maximum root length (cm) of three rice cultivars when grown in aerated or stagnant at 1.6, 8, 40 and 200 µM P of nutrient solution cultures for four weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	35.1	32.3	42.9	28.0	26.2
	Stagnant	16.0	18.2	19.5	17.5	
Amaroo	Aerated	31.6	31.5	47.5	25.2	26.7
	Stagnant	20.8	19.2	20.5	17.5	
Kyeema	Aerated	23.9	25.2	32.9	42.6	23.9
	Stagnant	16.2	16.8	17.9	16.0	
Means of P levels		23.9	23.9	30.2	24.5	
Means of conditions		Aerated	33.2 a	Stagnant	18.0 b	
F- test		Con*	P [ns]	Cul [ns]		
LSD $_{(P<0.05)}$		11.4	-	-		

*Significant at P< 0.05, Con, P and Cul indicate F test for conditions of solution culture, phosphorus levels and cultivars effects, respectively. ns indicates no significant difference. The lower case is used for comparison between conditions.

Table 5.3.3.6 Root numbers per plant of three rice cultivars when grown in aerated or stagnant at 1.6, 8, 40 and 200 μM P of nutrient solution cultures for four weeks.

Cultivars	Conditions	Phosphorus levels (μM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	27.8	29.0	29.8	31.3	29.9 B
	Stagnant	24.5	32.3	30.3	34.0	
Amaroo	Aerated	32.5	28.3	37.0	38.5	36.0 A
	Stagnant	29.8	42.0	41.3	38.5	
Kyeema	Aerated	27.5	28.8	32.0	32.3	32.1 B
	Stagnant	26	34.0	37.0	38.3	
Means of P levels		28.1 b	32.4 a	34.6 a	35.5 a	
Means of conditions		Aerated	31.2	Stagnant	34.0	
F- test		Con ^{ns}	P*	Cul*		
LSD $_{(P<0.05)}$		-	3.8	2.5		

*Significant at P< 0.05, Con, P and Cul indicate F test for conditions of solution culture, phosphorus levels and cultivars effects, respectively. The upper and lower cases are used for comparison between cultivars and phosphorus levels, respectively.

Table 5.3.3.7 Root dry weight (g $plant^{-1}$) of three rice cultivars when grown in aerated or stagnant at 1.6, 8, 40 and 200 µM P of nutrient solution cultures for four weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	0.078	0.073	0.096	0.082	0.084
	Stagnant	0.091	0.088	0.077	0.083	
Amaroo	Aerated	0.099	0.094	0.121	0.100	0.110
	Stagnant	0.086	0.118	0.120	0.139	
Kyeema	Aerated	0.077	0.078	0.088	0.070	0.087
	Stagnant	0.098	0.104	0.090	0.092	
Aerated		0.085 Ab	0.082 Bb	0.102 Aa	0.084 Bb	
Stagnant		0.092 Aa	0.103 Aa	0.096 Aa	0.105 Aa	
Means of conditions		Aerated	0.088	Stagnant	0.099	
F- test		Con*	Cul*	ConxP*		
LSD $_{(P<0.05)}$		-	-	0.015		

*Significant at P< 0.05, Con, Cul and ConxP indicate F test for conditions of solution culture, cultivars, and conditions of solution culture and phosphorus levels interaction effects, respectively. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.8 Root porosity (%) of whole root system of three rice cultivars when grown in aerated or stagnant at 1.6, 8, 40 and 200 μM P of nutrient solution cultures for four weeks.

Cultivars	Conditions	Phosphorus levels (μM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	21.9 Bb	28.5 ABa	27.0 Aa	22.4 Bb	27.0
	Stagnant	27.6 ABa	30.5 Aa	28.3 Aa	29.7 Aa	
Amaroo	Aerated	24.4 Ba	24.6 Ba	19.2 Bb	24.9 Ba	25.9
	Stagnant	28.0 ABa	27.2 ABa	27.7 Aa	31.3 Aa	
Kyeema	Aerated	28.8 Aa	24.6 Aab	20.4 Bb	21.5 Bb	26.2
	Stagnant	27.4 ABa	27.2 ABa	28.6 Aa	31.0 Aa	
Means of P levels		26.4	27.1	25.2	26.8	
Means of conditions		Aerated	24.0	Stagnant	28.7	
F- test		ConxP*	PxCul*		ConxPxCul*	
LSD $_{(P<0.05)}$		2.4	3.0		4.3	

*Significant at P< 0.05, ConxCul, PxCul and ConxPxCul indicate F test for conditions of solution culture and cultivars interaction, phosphorus levels and cultivars interaction, and conditions of solution culture, phosphorus levels and cultivars interaction effects, respectively. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.9 Shoot dry weight (g plant^{-1}) of three rice cultivars when grown in aerated or stagnant nutrient solution at 1.6, 8, 40 and 200 µM P for four weeks.

Cultivars	Conditions	Phosphorus levels (µM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	0.260	0.328	0.333	0.362	0.315 B
	Stagnant	0.249	0.294	0.327	0.365	
Amaroo	Aerated	0.355	0.453	0.484	0.497	0.422 A
	Stagnant	0.372	0.450	0.442	0.326	
Kyeema	Aerated	0.250	0.312	0.387	0.371	0.330 B
	Stagnant	0.280	0.324	0.367	0.350	
Means of P levels		0.294 b	0.360 a	0.390 a	0.379 a	
Means of conditions		Aerated	0.366 a	Stagnant	0.346 b	
F- test		Con*	P*	Cul*		
$LSD_{(P<0.05)}$		0.018	0.040	0.032		

* significant at P< 0.05. Con, P and Cul indicate F test for conditions of solution culture, cultivars, and cultivars effects, respectively. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.10 Leaf numbers per plant of three rice cultivars when grown in aerated or stagnant nutrient solution at 1.6, 8, 40 and 200 μM P for four weeks.

Cultivars	Conditions	Phosphorus levels (μM)				Aerated	Stagnant
		1.6	8	40	200		
Langi	Aerated	5.8	6.0	6.5	6.3	6.2 Ba	5.4 Bb
	Stagnant	3.8	5.5	6.3	6.0		
Amaroo	Aerated	6.3	8.0	8.5	9.0	8.0 Aa	6.2 Ab
	Stagnant	4.5	6.8	7.0	6.3		
Kyeema	Aerated	5.5	5.8	5.5	6.0	5.7 Ba	6.2 Aa
	Stagnant	3.5	5.8	5.8	6.0		
Means of P levels		4.9	6.3	6.6	6.6		
Means of conditions		Aerated	6.6	Stagnant	5.6		
F- test		Con*	P*	Cul*	ConxCul*		
LSD $_{(P<0.05)}$		-	-	-	0.6		

*Significant at P< 0.05, Con, P, Cul and ConxCul indicate F test for conditions of solution culture, phosphorus levels, cultivars, and conditions of solution culture and cultivars interaction effects, respectively. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.11 Tiller numbers per plant of three rice cultivars when grown in aerated or stagnant nutrient solution at 1.6, 8, 40 and 200 μM P for four weeks.

Cultivars	Conditions	Phosphorus levels (μM)				Aerated	Stagnant
		1.6	8	40	200		
Langi	Aerated	0.0	0.0	0.3	0.3	0.2 Ba	0.0 Ba
	Stagnant	0.0	0.0	0.0	0.0		
Amaroo	Aerated	0.5	1.8	1.8	1.8	1.5 Aa	0.5 Ab
	Stagnant	0.0	0.5	1.0	0.5		
Kyeema	Aerated	0.0	0.0	0.0	0.0	0.0 Ba	0.0 Ba
	Stagnant	0.0	0.0	0.0	0.0		
Langi		0.0 Ba	0.0 Ba	0.2 Ba	0.2 Ba		
Amaroo		0.3 Ab	1.2 Aa	1.4 Aa	1.2 Aa		
Kyeema		0.0 Ba	0.0 Ba	0.0 Ba	0.0 Ba		
F- test		Con x Cul*		P x Cul*			
LSD $_{(P<0.05)}$		0.3		0.4			

*Significant at P< 0.05, ConxCul and PxCul indicate F test for conditions of solution culture and cultivars interaction, and phosphorus levels and cultivars interaction effects, respectively. The upper and lower cases are used for comparison between columns and rows, respectively.

Table 5.3.3.12 Maximum shoot length (cm) of three rice cultivars when grown in aerated or stagnant at 1.6, 8, 40 and 200 μM P of nutrient solution cultures for four weeks.

Cultivars	Conditions	Phosphorus levels (μM)				Means of cultivars
		1.6	8	40	200	
Langi	Aerated	61.7	64.5	61.3	64.9	62.4
	Stagnant	50.6	61.4	66.0	68.9	
Amaroo	Aerated	64.5	66.2	65.6	69.6	64.6
	Stagnant	54.8	64.8	66.8	64.5	
Kyeema	Aerated	63.3	66.2	68.6	68.6	64.7
	Stagnant	53.3	64.7	66.7	66.4	
Aerated		63.2 Aa	65.6 Aa	65.2 Aa	67.7 Aa	
Stagnant		52.9 Bb	63.6 Aa	66.5 Aa	66.6 Aa	
Means of P levels		58.0	64.6	65.8	67.2	
Means of conditions		Aerated	65.4	Stagnant	62.4	
F- test		P*	Cul*	ConxP*		
LSD $_{(P<0.05)}$		-	-	4.8		

*Significant at P< 0.05, P, Cul and ConxP indicate F test for phosphorus levels, cultivars and conditions of solution culture and phosphorus level effects, respectively. The upper and lower cases are used for comparison between columns and row, respectively.

5.4 Discussion

The cultivar which out-performed all others in term of shoot dry weight and root dry weight especially in aerated solution was RD7. RD7 is lowland cultivar, characterized by short stem, many leaves and relatively shallow root. It is also reported to be acid tolerant (DOA, 2003). Compared to CNT1, RD7 had higher P uptake efficiency. RD7 may therefore be a P efficient rice genotype. It superior performance at low P was more obvious in aerated solution than in stagnant solution. R258 also produced high root dry weight at low P in aerated solution. However, unlike RD7, its maximum root length was above average for the cultivars tested and its root numbers and shoot dry weight did not respond under low P. In stagnant solution there was no clear evidence of P efficient cultivars. None of the cultivars produced more than 10 % of the maximum shoot biomass possible in high P aerated solution. This suggested that with low P at 1.6 μM, P deficiency was too severe especially under oxygen limited condition for the expression of differences in P efficiency.

Generally, adequacy of aeration and nutrient supplies culture promoted growth of plant, this work also consistently responded. Shoot growth of all ten Thai rice cultivars were promoted when grown in aerated at high phosphorus supply and they had the same responses to different nutrient solution conditions. Shoot dry weight of plants only in aerated culture differed among several rice cultivars. Deepwater (LMN111 and PCB1) and rainfed rice groups (NSG19, RD7 and KDML105) are quite higher in shoot dry weight than upland rice group, whereas stagnant culture regardless of phosphorus stress depressed them to the same weight. The variation in responses to aerated and stagnant culture presented low degree of anaerobic tolerance in all cultivars, including rainfed type and even in the deepwater cultivars which are normally grown in high water regime. However, it should be noted that the deepwater rice cultivars used in this study are of the 'floating rice' type, which escapes anaerobiosis by rapid stem elongation to keep upper leaves and growing point above the flood water. The shoot dry weight of deepwater and rainfed types was depressed by stagnant solution as upland types. This may be because from they were in prolonged anaerobic stress since three days after germination to 45 days. The young seedling had no time to acclimate to the anaerobic condition, and so suffered more from the long period of stress. The genotypic variation of rice in responses to waterlogging was also found by Colmer (2003a) among upland rice, paddy and deepwater types cultivars, but there was no typical response specific to each group. It was suggested on these responses of upland rice that waterlogging can be common in many upland soils used to cultivate rice (IRRI, 1975; Moormann and van Breemen, 1978; Grist, 1986). In this study tiller numbers were also promoted by aeration at high P, there was an exception among the upland types. KN was the one upland cultivar that showed no tillering response to aeration in high P supply. These confirmed the report of Colmer (2003a) on the genotypic variation that three of seven upland rice cultivars produced the same number of tillers when grown in drained soil as in waterlogged soils, while three cultivars had more tillers in well drained soil and one cultivar tillered more in waterlogged soil.

Low P supply generally decreased root growth especially in root numbers and root dry matter due to P is essential for plant growth (Marschner, 1995). Root is a sink of nutrients and energy and for oxygen supply. When P stress was synchronized with oxygen deficiency all cultivars were unable to acclimate in term of root numbers or root dry mass but only in root elongation. The ability in root elongation supported the increase root surface area for nutrient acquisition as the report of Bates and Lynch (1996) who work on increased in root hair elongation of Arabidopsis plant under limited P condition. This work presented the difference among rice cultivars on root elongation by upland types and one rainfed cultivars (KDML105) were longer in maximum root length when grown in all conditions except in stagnant at high P supply. Noticeably, all rice cultivars in this work when grown in stagnant at high P supply were the same in the maximum root length and they were shorter than other conditions. In stagnant culture was mixed with 0.1 % agar to protect the convection of oxygen (Wiengweera *et al.*, 1997) resulted in root had no oxygen supply, possibly not enough energy for elongation. Moreover, there would have been adequate P supply around root, and no need to acquire nutrient in deeper solution. However, root in stagnant at high P supply adapted to increase oxygen transportation by increased the aerenchymatous adventitious root number. Similarly, all 12 rice cultivars reduced in root elongation when grown in stagnant culture but adventitious roots per plant were increased, which they contained the higher porosity in roots (Colmer, 2003a).

The short term responses of Thai rice to aerated and stagnant cultures in limited P condition were measured within eight days after they had been grown in full strength aerated solution for 28 days following germination. CNT1 and RD7 were improved cultivars for irrigated cultivation as short length of shoot and more tiller production. Noticeably, at the initial of root growth of CNT1 was generally higher than in RD7, whereas shoot growth of RD7 was higher than in CNT1. Within eight days treatments, both of CNT1 and RD7 were generally responded to solution culture conditions the same as prolonged treatments period. However, there were some major differences between these two cultivars in their response to aeration and stagnant condition. CNT1 showed more significant difference between aerated and stagnant in morphological responses of root elongation, root numbers, root dry weight, while RD7 obviously presented in physiological responses as root porosity and P uptake efficiency.

Three Australian rice cultivars were also responded to aerated and stagnant culture the same as Thai rice cultivars by depressed growth when grown in stagnant. Root elongation was also reduced with higher P concentration in solution culture. The P supply for the Australian rice experiment is higher than previous experiments for 30 times higher in low P supply and 2 times higher in high P supply, while causing no difference in root number production. The one of different response to P supply was root dry weight, three cultivars was reduced in P levels at 50 and 200 but increased in 100 and 400 μM. These were still in doubt and can not be explained due to most root dry weight increased when increased P supply. The results seem suggested that at 100 μM was adequate P supply for rice growth but this is not consistent with the higher P levels at 200 μM. Therefore, the differences of these responses should be clarified in future. The P supply in the two weeks prolonged treatments was reduced in each P levels, which the lowest and highest P concentrations were 1.6 and 200 μM the same as previous experiments, respectively. However, three rice cultivars were still not different in root elongation by P effect, they were only increased in aerated culture. These may have resulted from the previous P accumulation in rice plants, therefore they were not suffering from low P supply two weeks later. However, root numbers were increased when grown in high

P supply since 8 μM, these indicated that at 1.6 μM was low enough P supply for presented P deficient symptom in nutrient solution culture which this level was 10 times lower than phosphorus concentration in Kirk and Du (1997). This work used too low P levels to more clarify responses to P deficiency, although they obtained adequate P supply. The genotypic variation of Australian cultivars in aerated and stagnant culture at low or high P levels was found in root porosity (%), leaf and tiller number characteristics. These responses can be concluded that the overlapped responses found in within and among rice types and there were differences in characteristically responses of rice to aeration and nutrient stress.

Phosphorus acquisition and uptake of plant in aerated soil with low P supply was enhanced by increasing mechanism on production and secretion of phosphatases, exudation of organic acids (Vance *et al.*, 2003). Moreover, Bolan (1991) and Smith and Read (1997) reported that more than 90 % of land plants had the symbiotic associations with mycorrhizal fungi. The fungi hyphae were an important role in the acquisition of P for the plant (Bolan, 1991; Smith and Read, 1997).

In waterlogged soil, plants had the different mechanism for P uptake by rhizosphere acidification from ROL and H^+ secretion (Kirk and Du, 1997). Jones (1973) reported that some grasses in waterlogged soil reduced P uptake resulting from inhibition of iron plaque on roots. Zhang *et al*. (1999b) found that iron plaque had a great capacity to adsorb phosphorus from the solution and the release of root exudates as phytosiderophores increased iron availability and also increased phosphorus uptake.

The different in mechanism for adaption to waterlogged condition in stress was also reported in *Carex* species, flooding tolerant of *C. remota* when grown in periodically flooded habitats presented a similar root anatomy to *C extensa* under aerobic conditions, whereas a cortex with fine intercellular spaces throughout most of the root under anaerobic conditions. While, flooding tolerant *C. pseudocyperus* when grown in permanently flood developed an intact cortex over most of root length under both growth in conditions (Moog, 1998a). Moreover, the different plant characteristics may differ in stress tolerant evaluation. The study of Jan and Pettersson (1993) on the effects of low Al levels on growth and nutrient relatives in three rice cultivars with different tolerances to Al, also suggested that the cultivars could not be so clearly separated into different Al-tolerant class when compared data on total dry matter but different on fresh weight. It was confirmed on the can not be separated the Al-tolerant classes in other rice cultivars by Coronel (1980), Sarkunan and Biddappa (1982), and Fageria *et al*. (1988).

In the present work I have confirmed that rice in the same types may differ in the mechanisms for adaption to oxygen and nutrient stress. Moreover only eight days in stress period dramatically affected rice growth, especially on root. Growing rice in nutrient solution culture has been shown to be promising to simulate soil P supply, and thus for screening for P efficiency rice for aerated and waterlogged soils.