CHAPTER 4

RESPONSES OF RICE TO LOW PHOSPHORUS SUPPLY IN CHANGING BETWEEN AERATED AND ANAERATED CONDITIONS

4.1 Introduction

In Chapter 3, the results have shown that growth and nutrients uptake of rice grown in the conditions of changing between aeration and waterlogging are generally better than those of rice grown in continuous waterlogging. The yield of plants in these soil-water conditions was also found significantly greater in aerobic followed by waterlogged soil than in waterlogged soil throughout. Moreover, low P application depressed plant dry weight, but increased root:shoot ratio in aerobic soil as shown previously. The adaptive significance of these responses is really unknown. I hypothesized that plants in waterlogged soil may be changed their morphological and/or physiological characteristics, and these changes may therefore, in turn, hinder nutrient uptake by rice roots. Another hypothesis is that plants after transferred from aerobic into waterlogged soil may take up more nutrients particularly P than plants kept in waterlogged soil throughout. Kirt *et al.* (1997) found that P deficiency depressed to total plant dry weight but increased root dry weight, root length as well as root surface area. In addition, Colmer (2003) reported that maximum root length of aerobic rice is longer than that of anaerobic rice but had fewer adventitious roots.

On the other hand, anaerobic rice is adversely affected by lack of O_2 supply to the roots during growing period. Growth of anaerobic rice roots therefore depends on an internal supply of O_2 which moves from the atmosphere through the shoots to the

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roots (Armstrong, 1979). The adaptation of rice to anaerobic condition is the production of numerous adventitious roots which contain aerenchyma (Drew, 1983; Justin and Armstrong, 1987; Visser *et al.,* 1996; Blom and Voesenek, 1996; Colmer *et al.,* 1998). Aerenchyma provide a low resistance internal pathway for movement of O_2 from the shoots to the roots (Armstrong, 1979). Oxygen in aerenchymatous roots may be consumed by respiration or be lost to the rhizosphere via radial diffusion from the root. Moreover, in order to reduce the radial oxygen loss, roots may induce a barrier (Colmer *et al.,* 1998). However, one possible drawback of the barrier may be inhibition of nutrient absorption by anaerobic roots (Colmer and Bloom, 1998). The adaptations of rice to either fully aerobic or anaerobic condition are reasonably well understood. However, there is limited information on morphological and physiological adaptations of rice to change between aerobic and anaerobic conditions. When nutrient uptake is limited plants are often adversely on dry weight accumulation and tillering production that will be result in low grain yield.

In fact, it is very difficult to investigate on morphological and/or physiological responses of rice roots to P application in aerobic or waterlogged soil as similar as the rainfed lowland condition by roots growing in soil because oxygen concentration and nutrient availability in soil can not be controlled. Wiengweera *et al.* (1997) reported that nutrient solution contained 0.1% of agar, "stagnant solution", can be used as simulating the slow gas movements and convection which occur in waterlogged soils. In contrast, the simulation of aerobic soil is imposed by bubbling air through nutrient solution. Moreover, utilizing nutrient solution is also favorable for transfer from aerated to stagnant condition and *vice versa.* Thus, the nutrient solution is used in this study. The study specifically examined how morphological and physiological

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responses of rice roots to low P application in changing between aerated and stagnant nutrient solution (Experiment 1).

In addition to adaptations of rice plants when grown in aerobic followed by waterlogged conditions, the effects of changing aeration and flooding of soils on P transformations, and subsequent effects on crop growth are of importance in the rainfed lowland rice. Phosphorus sorption characteristics of the soil are important properties determining P requirements for crop growth because adsorbed equilibrates with P in the soil solution and this P is, in turn, the immediate source of P for plant uptake (Fox and Searle, 1980). Phosphorus uptake by absorbing roots is often determined by the concentration of P maintained in the soil solution at the root surface. The P diffusion depends primarily on the soil-water status, and on the buffering of P in the soil solution by sorption onto the soil solid. However, depending on the mineralogy, oxidation-reduction changes in soils can significantly alter P solubility as well as the form and sorption characteristics of Fe oxides, in particular. The fact is that in aerobic soils there is little reaction between P and soil because of lacking available water in the soil bulk. Thus, Al and Fe oxides, hydrous oxides, and calcium carbonate strongly sorb P; this circumstance often occurs in uplands or lowlands during dry season when the soils are unsaturated (Ponnamperuma, 1972).

On the other hand, the net mineralization of P is reported to be far greater in flooded or submerged soils than in either dry soils or soils at field capacity (Mandal and Islam, 1979). Also, it is reported that flooding of aerobic soil causes an increase in the concentration of P in the soil solution because of the release of sorbed and co-precipitated P following the reduction of Fe^{3+} compounds. Flooding also enhances diffusion, the main mechanism of P supply to roots (Dobermann *et al.,* 2000).

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Therefore, growing in wet soil rice plant is often more favorable than in dry soil by supplied P to root surface from the soil bulk. The growth of rice in non-waterlogged and waterlogged soils is reasonably well understood; however, the practical implications of the changing of soil-water condition in the rainfed lowland system for P nutrition of rice have not been fully examined (Seng *et al.,* 1999). This study aimed to know how responses of rice growth and plant P content to low P application under two pre-transplanting soil-water conditions (Experiment 2).

4.2 Materials and Methods

4.2.1 Experiment 1: **Responses of rice to low P supply in changing aerated and stagnant conditions**

Rice plants of this experiment were grown in nutrient solutions to evaluate the effect of changes between aerobic and anaerobic conditions in the rooting medium on plant growth, root developments and plant P content. The experiment was arranged as a randomized complete block (RCB) design with factorial combinations of two concentrations of O_2 (aerated: A; stagnant: S), and two rates of P (2 and 8 ppm, designated LP and HP, respectively) with four replicates, giving a total of 48 pots for two harvests.

Phosphorus was supplied as potassium dihydrogen orthophosphate (KH_2PO_4). In addition to P, other nutrients were applied in the solution of each pot at the following rates (μM): KNO_3: 3750; NH_4NO_3: 625; NaCl: 50; SiO_2: 100; H_3BO_3: 25; Fe-EDTA: 100; $MgSO_4.7H_2O$: 400; $MnSO_4.H_2O$: 2; $ZnSO_4.7H_2O$: 2; $NiCl_2.6H_2O$: 1; $CuSO_4.5H_2O$: 0.5; $CaCl_2.2H_2O$: 1000; $Na_2MoO_4.2H_2O$: 0.5 (modified from Yoshida *et al.*, 1976). The nutrient solution was renewed weekly, and pH was adjusted to 6.5

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daily by using HCl 1N and NaOH 1N from the beginning until the end of the experiment.

The stagnant nutrient solution contained 0.1% (w/v) of agar to prevent mixing of atmospheric O_2 into the nutrient solution by convection (Wiengweera *et al.,* 1997). Oxygen concentration in the stagnant solution was 1.2-1.5%. The aerated treatment was imposed by bubbling air through the nutrient solution which had O_2 concentrations of 16.5-18.2%.

Pre-germinated seeds were sown in aerated full strength nutrient solution for 10 days, thereafter four seedlings of these plants with uniform size, healthy plants were selected to transplant to each pot, which contains 10 liters of the nutrient solution. After 12 days, the pots from each P level were split into two groups. One group continued in aerated (AA) or stagnant (SS) solution as before. The other group of aerated plants was transferred to stagnant solution (AS) and stagnant plants transferred to aerated (SA) condition.

Plants were harvested before transfer in A or S twelve days, and eight days after transfer. At each harvest, the plant samples were measured for number of tillers per plant, adventitious root number per plant, maximum root length, plant dry weight, root:shoot ratio, and root porosity. Aerenchyma appearances in adventitious roots were determined by cross sections of adventitious roots at 5 cm from the root tip under a compound microscope. The root system of each treatment was separated into thick and thin roots. Thick roots were the adventitious roots. Thin roots were smaller (less than 0.5 mm diameter) and had more lateral roots than thick roots. Roots were cut into 50 mm segments for porosity measurements. Thick and thin root porosities (% gas spaces per unit tissue volume) were measured by measuring root buoyancy

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before and after vacuum infiltration of the gas spaces in the root with water (Raskin, 1983), using the equations as modified by Thomson *et al.* (1990) as follows:

$$\% \text{ Porosity} = \frac{\text{Volume of gas in root}}{\text{Volume of root}} \times 100$$

Shoot and roots samples were separated for analysis of P concentration (molybdovanado-phosphoric acid method).

4.2.2 Experiment 2: Responses of rice to low P supply in different pre-transplanting soil-water conditions

This experiment was conducted in two different pre-transplanting soil-water regimes to evaluate plant growth and plant P content. The experiment was arranged as a randomized complete block (RCB) design with factorial combinations of two pre-transplanting soil-water regimes (W0, W+), and two rates of P (10 and 50 kg P/ha, designated LP and HP, respectively) with four replicates, giving a total of 16 pots.

Phosphorus was supplied as potassium dihydrogen orthophosphate (KH_2PO_4). In addition to P, other nutrients were applied as N (60 kg N/ha, using urea 46% N), and potassium as dipotassium sulfate (K_2SO_4). All nutrients were applied as diluted stock solutions and supplied to the soil each time by using graduated injectors. The nutrients were applied as follows: P (100%) at before transplanting two months, N (100%) at transplanting. From one week after transplanting, 0.03 g K/pot was supplied weekly to ensure that plants did not experience K deficiency at any stage.

The soil (San Sai series, Table 3.2) was mixed thoroughly before 6 kg portions were placed in a plastic lined bag into undrained PVC pots. The soil was supplied by two regimes of waters two months pre-transplanting. One regime was non-waterlogged (soil moisture content at field capacity, W0). This soil was wetted with

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freshwater to field capacity and maintained for two months pre-transplanting. At transplanting, this soil was flooded to a depth of 8-10 cm and maintained at this level until at the end of experiment by daily watering (W0+). The other regime was waterlogged (flooded throughout, W++). All pots of this water regime were flooded to a depth of 8-10 cm and maintained at this level throughout pre-transplanting for two months to at the end of experiment by daily watering.

Pre-germinated seeds were sown in a small bed, which was maintained standing water daily at depth of about 2 to 5 cm (this was begun at the same time with flooding of the soil). At two months old, four healthy seedlings were transplant into each pot of the treatments.

The plants were harvested at seventh week after transplanting. These plant samples were determined for plant height, number of tillers per plant, plant dry weight, root:shoot ratio, and plant P content. Shoot and roots samples were separated for analysis of P concentration (molybdovanado-phosphoric acid method).

Statistical analysis

For these experiments, an analysis of variance (ANOVA) for all parameters measured was carried out to determine the treatment effects using Commercial software (Statistix V.7.1, analytical Software, Inc.). When treatment effects were significant, the least significant difference (LSD) and/or standard errors (SE) were used for mean comparisons.

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4.3 Results

4.3.1 Experiment 1

The effect of P on tiller number per plant was significantly different between A and S throughout the entire experimental period (OxP significant at $P < 0.05$). Throughout 20 days, both aerated and stagnant plants gave more tillers in high P than in low P. In aerated, the tiller number increased more strongly with high P than those of plant in stagnant (Table 4.1). After transfer from S to A (SA), the plants in SA gave more tillers compared with plants kept in SS, but the tillering slowed down when plants were transferred from A to S (AS) compared with plants kept in AA.

At first 12 days, the effect of O_2 treatments (A and S) on plant dry weight was little different, while the effect of P on that was strongly different (Figure 4.1). This difference was greater in high P than in low P ($P < 0.01$). After transfer from aerated to stagnant (AS), the dry weight did not increase as fast as those of plants kept in aerated throughout (AA). Plants in AA also responded more strongly to P than those aerated then transferred to stagnant (AS). In contrast, after transfer from stagnant to aerated (SA), plants increased dry weight strongly compared with plants kept in SS. The dry weight of plants in SA did not respond to P levels.

In general, plants in low P had higher root:shoot ratio than those in high P. This difference was significantly different ($P < 0.01$). Growing in aerated, plants increased root:shoot ratio in low P, although it had no effect in high P before transition (Figure 4.2). When transferred from aerated to stagnant (AS), the root:shoot ratio did not increase much compared with plants kept in AA. With low P supply the root:shoot ratio was more depressed than in high P after transfer from A to S (AS). However, plants increased root:shoot ratio when transfer from S to A (SA) compared

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with those of plants kept in SS throughout, and that was also greater in low P than in high P ($P < 0.01$).

At first 12 days, the effect of P on plant P content in whole plant was significantly different between A and S (OxP significant at $P < 0.01$). In aerated condition, increasing P rate increased strongly plant P content while that in stagnant increased less (Table 4.2). After transfer from A to S (AS), the plant P content slowed down compared with those of plants kept in AA. However, after transfer from S to A (SA), the plant P content increased strongly compared with those of plants kept in SS throughout. In addition, the effect of P supply on plant P content was significantly different ($P < 0.01$). This difference was higher in high P than low P.

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Table 4.1 Effect of P applications on number of tillers plant^{-1} of rice grown in aerated or stagnant nutrient solution before and after transfer.

††Oxygen condition	P application		Mean	F-test	LSD $_{0.05}$
	Low P	High P			
Before transfer (12 days)					
A	8.1bA	10.1aA†	9.1A	O**	0.4
S	6.4bB	7.5aB	6.9B	P**	0.4
Mean	7.2b	8.8a		OxP*	0.6
8 days after transfer					
AS	8.3bB	10.5aB	9.4B	O**	0.5
SA	8.7bB	10.4aB	9.5B	P**	0.4
AA	9.8bA	12.8aA	11.3A	OxP*	0.7
SS	7.3bC	8.6aC	7.9C		
Mean	8.5b	10.6a			

† The lower cases and capital letters are used for comparison between rows and columns, respectively. The different letters are significantly different by LSD $_{(P<0.05)}$. †† A: aerated; S: stagnant; AA: aerated throughout; SS: stagnant throughout; AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated.

* significant at $P < 0.05$; ** significant at $P < 0.01$

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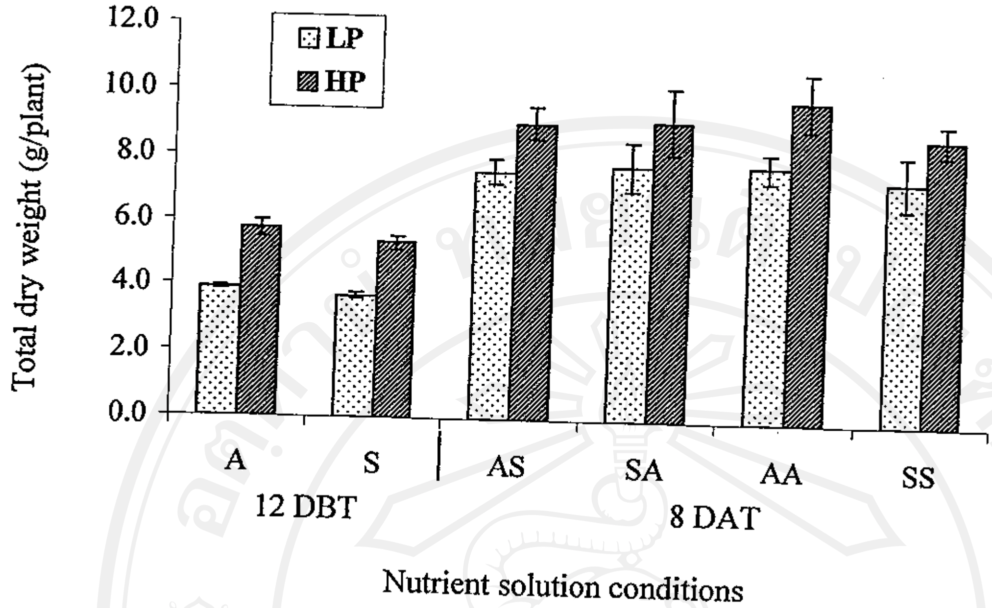

Figure 4.1 Total dry weight (g/plant) of rice grown in aerated (A) or stagnant (S) nutrient solution associated with low P (LP) or high P (HP) for 12 days then plants were transferred into another conditions for 8 days. AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated; AA: aerated throughout; SS: stagnant throughout. Each vertical bar represents mean ± standard error value of 4 replicates for comparing between O_2 applications (A or S), P levels, and the interaction between OxP. DBT = days before transfer, DAT = days after transfer

Analysis of variance

$LSD_{0.05}$	O	P	OxP
Before transfer (12 days)	0.23*	0.24**	ns
8 days after transfer	0.51*	0.36**	ns

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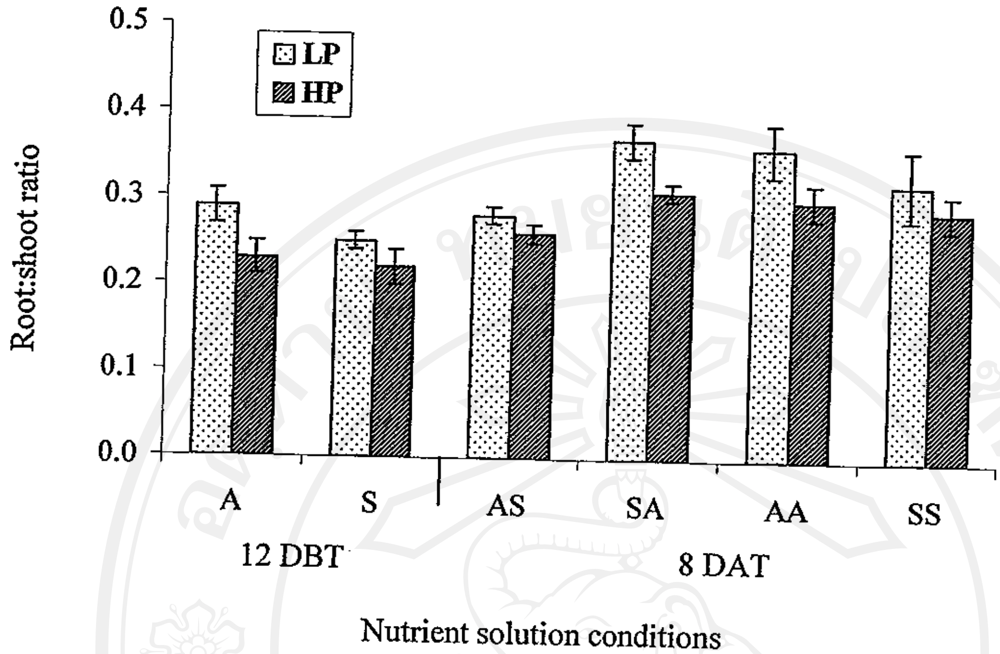

Figure 4.2 Root:shoot ratio of rice grown in aerated (A) or stagnant (S) nutrient solution associated with low P (LP) or high P (HP) for 12 days then plants were transferred into another conditions for 8 days. AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated; AA: aerated throughout; SS: stagnant throughout. Each vertical bar represents mean ± standard error value of 4 replicates for comparing between O_2 applications (A or S), P levels, and the interaction between OxP.
DBT = days before transfer, DAT = days after transfer

Analysis of variance

$LSD_{0.05}$	O	P	OxP
Before transfer (12 days)	0.01**	0.01**	0.02*
8 days after transfer	0.03**	0.02**	ns

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Table 4.2 Effect of P applications on plant P content (mg/plant) of rice grown in aerated or stagnant nutrient solution before and after transfer.

[††]Oxygen condition	P application		Mean	F-test	$LSD_{0.05}$
	Low P	High P			
Before transfer (12 days)					
A	1.18bA	2.39aA[†]	1.79A	O**	0.10
S	0.81bB	1.66aB	1.24B	P**	0.11
Mean	1.00b	2.03a		OxP**	0.15
8 days after transfer					
AS	1.33bB	2.96aC	2.15C	O**	0.17
SA	1.70bA	3.41aB	2.56B	P**	0.12
AA	1.87bA	3.76aA	2.82A	OxP**	0.23
SS	1.12bB	2.34aD	1.73D		
Mean	1.51b	3.12a			

[†] The lower cases and capital letters are used for comparison between rows and columns, respectively. The different letters are significantly different by $LSD_{(P<0.05)}$. [††] A: aerated; S: stagnant; AA: aerated throughout; SS: stagnant throughout; AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated.

** significant at $P < 0.01$

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Aerated plants gave more double maximum root length than stagnant plants throughout the entire experimental period (Table 4.3). This difference was significantly different ($P < 0.01$). Aerated plants in low P also had longer maximum root length than in high P. After transfer from A to S (AS), root elongation was slowed down in both low and high P supply compared with those of plants kept in AA. However, after transfer from S to A (SA), the roots elongated strongly compared with those of plants kept in SS. In addition, the effect of P on maximum root length was significantly different ($P < 0.01$). This difference was higher in low than high P.

At first 12 days, the effect of P on adventitious roots number was significantly different between A and S (OxP significant at $P < 0.01$). In aerated, the adventitious root number did not change with increasing P. The adventitious root number in stagnant, which increased strongly with increasing P (Table 4.4). At 8 day after transfer, the plants kept in SS still gave more adventitious roots than those of plants kept in AA ($P < 0.01$). Particularly, when transfer from A to S (AS), the adventitious root number increased strongly compared with those of plants kept in AA. However, after transfer from S to A (SA), the adventitious root number slowed down compared with those of plants kept in SS. With high P the adventitious root number was also higher than in low P ($P < 0.01$).

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Table 4.3 Effect of P applications on maximum root length (cm) of rice grown in aerated or stagnant nutrient solution before and after transfer.

[††]Oxygen condition	P application		Mean	F-test	LSD $_{0.05}$
	Low P	High P			
Before transfer (12 days)					
A	47.1aA	39.3bA[†]	43.2A	O**	1.3
S	28.9aB	26.9bB	27.9B	P**	1.3
Mean	38.0b	33.1a		OxP*	1.9
8 days after transfer					
AS	49.9aB	40.4bB	45.2B	O**	1.4
SA	40.6aC	33.9bC	37.2C	P**	0.9
AA	59.9aA	51.7bA	55.8A	OxP*	1.9
SS	33.6aD	30.5bD	32.0D		
Mean	46.0a	39.1b			

[†] The lower cases and capital letters are used for comparison between rows and columns, respectively. The different letters are significantly different by LSD $_{(P<0.05)}$ [††] A: aerated; S: stagnant; AA: aerated throughout; SS: stagnant throughout; AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated.
* significant at $P < 0.05$; ** significant at $P < 0.01$

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Table 4.4 Effect of P applications on number of adventitious root plant^{-1} of rice grown in aerated or stagnant nutrient solution before and after transfer.

††Oxygen condition	P application		Mean	F-test	LSD $_{0.05}$
	Low P	High P			
Before transfer (12 days)					
A	87.2aB	93.8aB†	90.5B	O**	6.22
S	110.7bA	136.8aA	123.7A	P**	6.23
Mean	98.9b	115.3a		OxP*	
8 days after transfer					
AS	211.4	233.2	222.3A	O**	16.7
SA	184.1	193.4	188.8B	P**	11.8
AA	190.9	200.4	195.7B	OxP^{ns}	
SS	211.3	248.6	229.9A		
Mean	199.4b	218.9a			

† The lower cases and capital letters are used for comparison between rows and columns, respectively. The different letters are significantly different by LSD $_{(P<0.05)}$ †† A: aerated; S: stagnant; AA: aerated throughout; SS: stagnant throughout; AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated.

* significant at $P < 0.05$; ** significant at $P < 0.01$; ns: not significant

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As expected, the stagnant plants had higher root porosity (% gas space) than those of aerated plants throughout 20 days of the experiment (Figure 4.3). This difference can be seen in the formation of aerenchyma (Figure 4.4). By 12 days before transfer, the effect of P on root porosity was significantly different between A and S (OxP significant at $P < 0.05$). In aerated, the root porosity did not change between low P and high P, but in stagnant the root porosity increased with high P. By 8 days after transfer, the root porosity of stagnant plants (SS) still higher than aerated plants (AA) ($P < 0.05$). After transfer from S to A (SA), the root porosity of plants was depressed compared to those of plants kept in SS. However, after transfer from A to S (AS), the root porosity increased compared with those of plants kept in AA. The effect of P on root porosity was only different in AS and SS ($P < 0.01$), but not in SA and AA. This difference was higher in high P than low P.

Root of stagnant plants had more aerenchyma than those of aerated plants (Figure 4.4). In stagnant, the aerenchyma was formed with both low P and high P, and those were more with high P than low P supply. In aerated, the aerenchyma was only formed with high P, but not with low P.

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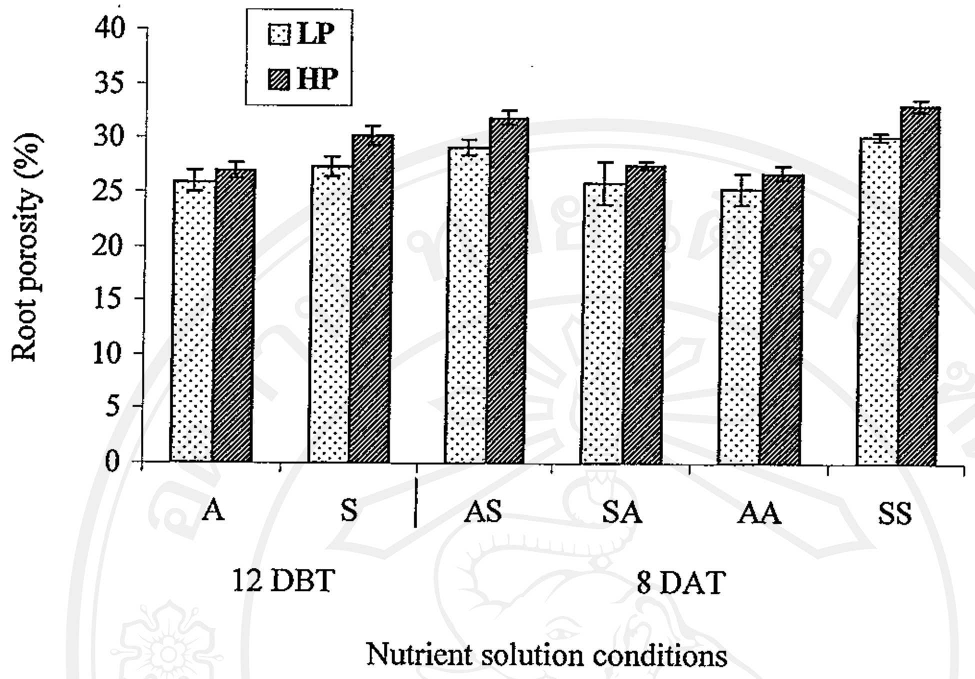

Figure 4.3 Root porosity (% gas space) of rice grown in aerated (A) or stagnant (S) nutrient solution associated with low P (LP) or high P (HP) for 12 days then plants were transferred into another conditions for 8 days. AS: aerated for 12 days followed by 8 days in stagnant; SA: stagnant for 12 days followed by 8 days in aerated; AA: aerated throughout; SS: stagnant throughout. Each vertical bar represents mean ± standard error value of 4 replicates for comparing between O_2 applications (A or S), P levels, and the interaction between OxP.
DBT = days before transfer, DAT = days after transfer

Analysis of variance

$LSD_{0.05}$	O	P	OxP
Before transfer (12 days)	0.81**	0.81**	1.14*
8 days after transfer	0.51*	0.33**	ns

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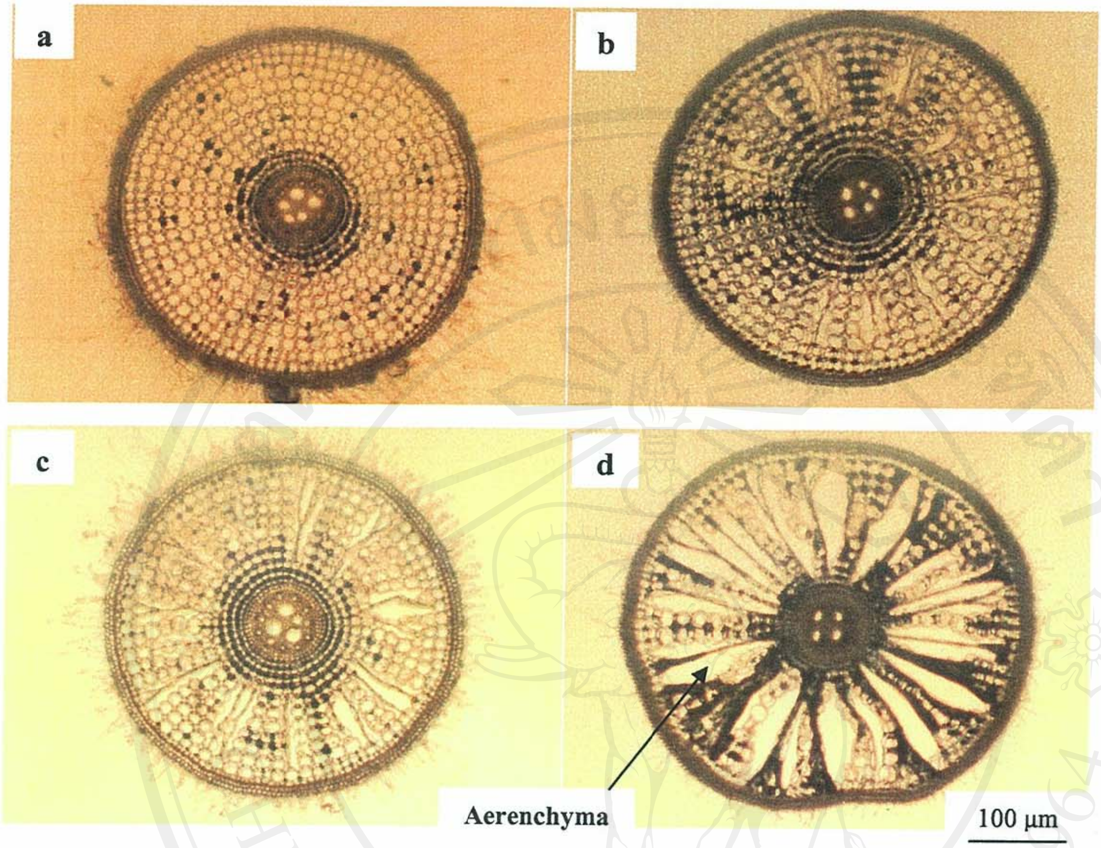

Figure 4.4 Aerenchyma appearances in adventitious roots (at 5 cm from the root tip) of rice grown in aerated or stagnant nutrient solution associated with low P or high P. (a): plant in aerated-low P; (b) plant in aerated-high P; (c) plant in stagnant-low P; and (d): plant in stagnant-high P.

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4.3.2 Experiment 2

The effect of P on tiller number per plant was higher in W0+ than in W++ throughout seven weeks of the experiment ($P < 0.01$). During first five weeks, in W0+ plants had more tiller number than those of plants in W++, and plants increased strongly tiller number with high P supply (Figure 4.5). In W++ the tiller number also increased with high P, but those did not increase as fast as tiller number of plants in W0+. At seven weeks, the plant tillering slowed down in both W0+ and W++. The effect of P on tiller number became more largely, and the difference between W0+ and W++ about tiller number was only in high P ($P < 0.01$) but not evident in low P.

The plant height in W0+ was higher than those in W++ throughout seven weeks of experimental period (Figure 4.6). The differences were greater in high P than those in low P. Plants heightened strongly during first five weeks in both W0+ and W++, and the effect of P on plant height was largely at five weeks ($P < 0.01$). High P supply, the plant height was higher than those with low P. At seven weeks, height of plants slowed down in both W0+ and W++ conditions, and those did not change between low P and high P.

The effect of P on plant dry weight was not significantly different between W0+ and W++ (Table 4.5). The effect of soil-water regime on plant dry weight was significantly different ($P < 0.01$). The plant dry weight was higher in W0+ than that in W++. In high P, the plant dry weight was also greater than that in low P ($P < 0.01$).

The root:shoot ratio did not change between W0+ and W++ (Table 4.5). The effect of P on root:shoot ratio was significantly different ($P < 0.01$). In low P plant had higher root:shoot ratio than that in high P.

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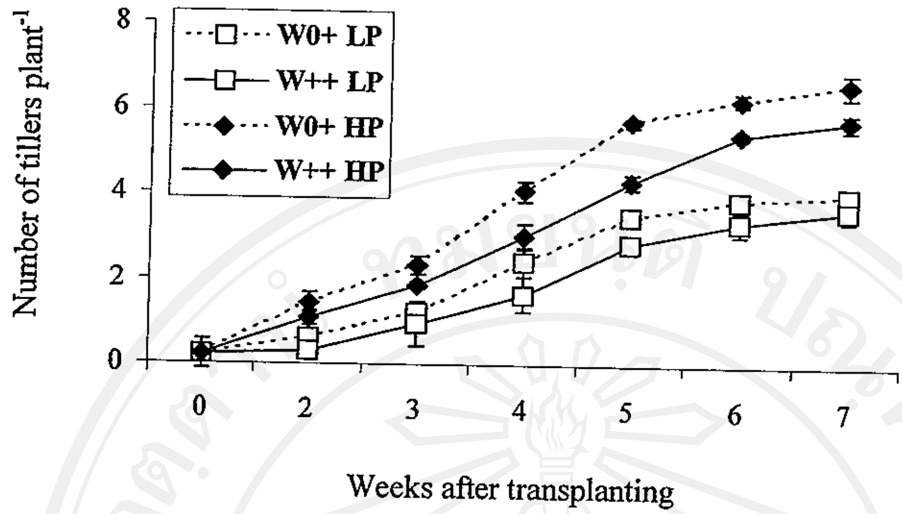

Figure 4.5 Effect of P applications (low P: LP or high P: HP) on number of tillers per plant of rice grown in two soil-water conditions (W0+: non-waterlogged soil pre-transplanting then followed by waterlogged soil at transplanting; W++: waterlogged soil throughout). Each data point is mean ± standard error value of 4 replicates for comparing between soil-water regimes (W0+ or W++), P levels and the interaction between WxP.

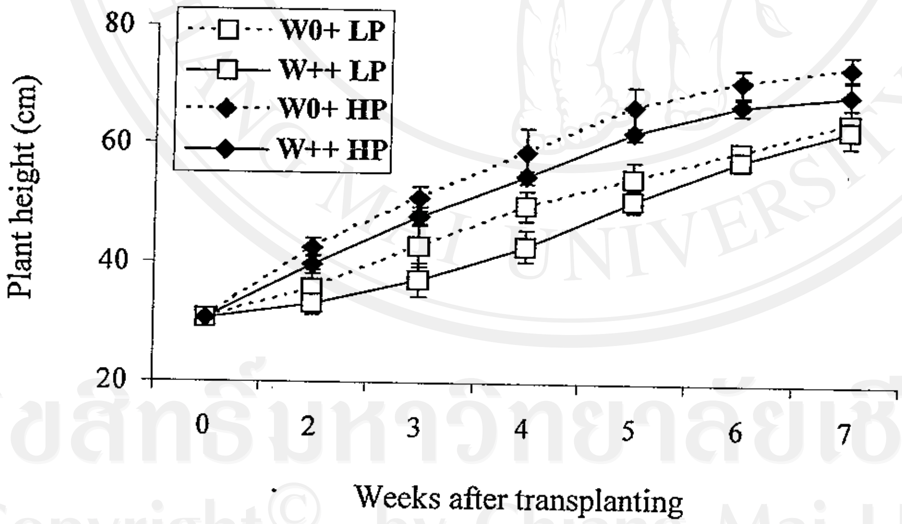

Figure 4.6 Effect of P applications (low P: LP or high P: HP) on plant height (cm) of rice grown in two soil-water conditions (W0+: non-waterlogged soil pre-transplanting then followed by waterlogged soil at transplanting; W++: waterlogged soil throughout). Each data point is mean ± standard error value of 4 replicates for comparing between soil-water regimes (W0+ or W++), P levels and the interaction between WxP.

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Table 4.5 Effect of P applications on plant dry weight (g/plant) and root:shoot ratio of rice grown in two pre-transplanting soil-water conditions.

††Soil-water condition	P application		Mean	F-test	$LSD_{0.05}$
	Low P	High P			
Total plant dry weight (g/plant)					
W0+	5.16	8.22	6.69A†	W**	0.58
W++	4.67	6.79	5.73B	P**	0.58
Mean	4.92b	7.51a		WxP^{ns}	
Root:shoot ratio					
W0+	0.59	0.49	0.54	W^{ns}	
W++	0.61	0.55	0.58	P**	0.06
Mean	0.60a	0.52b		WxP^{ns}	

† The lower cases and capital letters are used for comparison between rows and columns, respectively. The different letters are significantly different by LSD $_{(P < 0.05)}$

†† W0+: non-waterlogged soil pre-transplanting then followed by waterlogged soil at transplanting; W++: waterlogged soil throughout.

** Significant at $P < 0.01$; ns: not significant

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The effect of P on P concentration (%) in shoot of plant was not significantly different between W0+ and W++ (Table 4.6). The effect of soil-water regime on %P was significantly different ($P < 0.01$). The %P was higher in W0+ than that in W++. In high P, the %P was also greater than that in low P ($P < 0.01$).

The effect of P on P content in whole plant (mg/plant) was significantly different between W0+ and W++ (WxP significant at $P < 0.01$). In low P the P content was about the same in W0+ and W++. Increasing P increased P content in both W0+ and W++, but more strong in W0+ (Table 4.6).

Table 4.6 Effect of P applications on shoot P concentration (%) and plant P content (mg/plant) of rice grown in two pre-transplanting soil-water conditions.

[††]Soil-water condition	P application		Mean	F-test	$LSD_{0.05}$
	Low P	High P			
P concentration (%)					
W0+	0.16	0.21	0.19A[†]	W**	0.01
W++	0.14	0.19	0.17B	P**	0.01
Mean	0.15b	0.20a		WxP[ns]	
P content (mg/plant)					
W0+	0.60c	1.27a[†]	0.94A	W**	0.10
W++	0.49c	0.90b	0.70B	P**	0.10
Mean	0.55b	1.09a		WxP**	0.14

[†] The different letters are significantly different by $LSD_{(P<0.05)}$

[††] W0+: non-waterlogged soil pre-transplanting then followed by waterlogged soil at transplanting; W++: waterlogged soil throughout.

** Significant at $P < 0.01$; ns: not significant.

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4.4 Discussion

4.4.1 Growth, root development and P uptake of rice in aerated and stagnant solutions

Rice was grown in either aerated or stagnant nutrient solution (simulated waterlogging) to evaluate for growth, root development and P uptake. By comparing the growth and P uptake, the present work shows aerated plants generally grew better than stagnant plants.

The formation of aerenchyma in adventitious roots (Figure 4.4) showed that in stagnant solution (0.1% agar) the aerenchyma were stronger formed than those in aerated solution. This evidence was associated with root porosity (% gas space), which was greater in stagnant than in aerated solution throughout 20 days of experimental period. This finding is similar to the results of previous studies in rice (Colmer *et al.,* 1998), and wheat (Wiengweera *et al.,* 1997). Another study was reported that adventitious roots of wetland and dryland grass species grown in stagnant solution had more aerenchyma than those of plants grown in aerated solution (McDonald *et al.,* 2002). The present work has shown that root porosity increased after transfer from A to S (AS), but that decreased after transfer from S to A (SA) compared with plants kept in AA or SS, respectively (Figure 4.3). These findings indicate that rice differ in their constitutive porosity when grown in aerated and stagnant conditions. Drew (1983) and Visser *et al.* (1996) explained that plants adapt to waterlogged condition by formation of aerenchyma in adventitious roots. Aerenchyma development and O_2 flux to root tips increase in response to anoxic conditions (Colmer *et al.,* 1998). Oxygen may leak along the root axis, with excess leaking occurring from the older basal roots, thus limiting the amount of O_2 that can

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be delivered to the root tips. To reduce O_2 leakage from the basal regions of the root to the zhizosphere, plants induced a barrier to radial oxygen loss. These were intensive studied by McDonald *et al.* (2002); Colmer *et al.* (1998). However, one possible drawback of the barrier is, in turn, inhibition of nutrient absorption by anaerobic roots (Colmer and Bloom, 1998). Thus, the present work has shown P content in stagnant plants was lower than that in aerated plants throughout 20 days, and also AS plants was lower than in AA plants is one of possible evidences. This result was also similar to the finding in wheat when grown under stagnant and aerated solutions by Wiengweera *et al.* (2004). The physiological changes in anaerobic roots are really determined to hinder nutrient uptake by the rice roots, thus cause depress plant growth, dry weight accumulation, etc.

In addition to physiological changes, the adaptation of roots to aerated or stagnant conditions was also determined change in morphology. The data of this study have shown that plants grown in aerated condition had longer maximum root length, but less adventitious number than plants in stagnant condition (Table 4.3, 4.4). It also indicated after transfer from S to A, plants were strongly in root elongation, but slowed down the production of adventitious root numbers. In contrast, root elongation slowed down when plants were transferred from A to S, but strongly increased adventitious number. Colmer *et al.* (1998) also found that rice gave more adventitious root number when grown in stagnant compared with plants in aerated condition. Other findings in grass and tribe Triticeae were reported that aerated plants had longer maximum root length than stagnant plants (McDonald *et al.*, 2001; McDonald *et al.*, 2002). Jackson and Drew (1984) discussed that oxygen in aerenchymatous roots was consumed by respiration or was lost to the rhizosphere. Radial oxygen loss decreases

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the amount of oxygen available to the apex of roots solely dependent on O_2 from aerenchyma and therefore would decrease their maximum length in O_2-free condition. Furthermore, Bell *et al.* (2001) suggested that lowland rice usually has shallow root system while upland rice can have a deep one. They explained that rice roots under aerobic soils usually have a long maximum length to facilitate water and nutrient uptake at depth in the soil layers.

The present data on number of tiller per plant demonstrate that when grown in aerated solutions, the rice plants gave more tillers in both low P and high P compared with those of plants grown in stagnant solutions throughout 20 days of experimental period (Table 4.1). This is similar to the finding on number of tillers per plant when rice grown in aerobic or waterlogged soils in Chapter 3. However, in this work the roots of plant were not limited by nutrient supply in aerated solution while plants in stagnant solution, which were limited nutrient supply by lack of diffusion in the nutrient solution (*supported by* Wiengweera *et al.,* 1997). In previous experiment of this thesis, roots of aerobic plant were low in nutrient supply under aerobic soils while roots of waterlogged plant, which were favorable by nutrient availability in the soil solution (*discussed in* Chapter 3). Moreover, applying P increased plant dry weight, which was significantly greater in aerated than stagnant condition for 20 days. Particularly, transfer from S to A (SA) increased plant dry weight, which was 6% more than SS plant. However, transfer from A to S (AS) depressed plant dry weight by 5% less than AA plant (Figure 4.1). Previous study reported that dry weight of wheat grown in aerated greater than that of wheat grown in stagnant solution (Wiengweera *et al.,* 1997).

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In short, the responses of rice plants to aerated and stagnant, and also after transfer from aerated to stagnant conditions in present work clearly showed to be influenced by levels of P application. The effect of P deficiency was more severe on rice growth in stagnant than aerated condition.

4.4.2 Growth and P uptake of rice grown in non-waterlogged and waterlogged soils before transplanting

The result of earlier Experiment in this Chapter, which had been confirmed that the adaptation of rice roots to anaerobic condition restricts nutrient uptake by plants. In present work (Experiment 2), the result clearly showed of P uptake by rice plants at seventh week after transplanting was greater in non-waterlogging then waterlogging (W0+) than that in waterlogging throughout (W++). Applying P really increased P uptake, and the difference between W0+ plants and W++ plants about this was larger in high P than low P (Table 4.6). The difference in P uptake between W0+ plants and W++ plants of this study may cause by variations of P availability in the soil solutions, which depends on soil-water status. Bell *et al.* (2001) reported that the lack of soil fertility in rainfed lowland rice is mainly affected by a changing soil-water regime on nutrient forms and their availability in the soil. Many studies on P sorption by soils of the tropics have concerned the relative importance of Fe and Al oxide minerals (Hinga, 1973; Weaver *et al.,* 1975). In aerobic soils generally the phosphate ions (native soil-P or applied-P) in soil solution may either precipitate with the precipitating cations such as $Fe^{3+}$and Al^{3+} in acid soils, Ca^{2+} in calcareous soils, or become sorbed on clay minerals and oxy-hydroxides. However, when an aerobic soil is flooded, the concentration of P in the soil solution increase because of the release of

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sorbed and co-precipitated P following the reduction of Fe^{3+} compounds. This process increases the levels of extractable P in acidic soils, as is a major factor causing increased post-flooding P availability (Willett, 1986; Ponnamperuma, 1972; Dobermann *et al.,* 2000). Moreover, hydrolysis due to increased soil pH after flooding results in higher solubility of iron-bound phosphate ($FePO_4.2H_2O$) and aluminum-bound phosphate ($AlPO_4.2H_2O$) in acid soils (Sanyal and De Datta, 1991).

On the other hand, in continuously flooded soil, however, the concentration of Fe^{2+} in the solution stabilities, but the level of acid-soluble Fe^{2+} continues to increase (Willett, 1986). The precipitation of ferrosis hydroxides $Fe_3(OH)_8$ on prolonged flooding increases the soil capacity to adsorb P from the soil solution, which causes a decline in P concentration in the solution (Willett and Higgins, 1978). Also, Dobermann *et al.* (2000) reported that about four weeks after submergence, the initial flush of available P is followed by a decrease in availability due to the precipitation of Fe^{2+}-P compounds and the adsorption of P on clay particles and Al hydroxides, particularly the soil which containing large amount of free Fe and Al. Roots of plant in continuous waterlogging may be therefore some extent limited by supply P to the roots compared with roots of plant which after transfer from aerobic to waterlogged soil. Thus, the P uptake of rice when grown in prenon-waterlogged followed by waterlogged soil was grater than that of plant in waterlogged soil throughout is possible. Similarly, the result of this study also showed that the tiller numbers per plant and plant dry weight were higher in W0+ than in W++ condition. These could be affected by difference in P uptake when grown in W0+ and W++.

In conclusion, the growth and nutrient uptake of rice are affected by changes of root characteristics themselves to adapt to anaerobic condition. The adaptation of

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rice roots to anaeration was also observed by transfer from aerated to stagnant condition. On the other hand, phosphorus becomes more available in waterlogged soil, which after transfer from aerobic or non-waterlogged soils. Plant P uptake is higher when grown in non-waterlogged followed by waterlogged soil compared with plants grown in waterlogged soil throughout due to changes of soil chemistry, particularly P availability in soil solution. The difference in nutrient uptake by rice plants in such effects on plant growth and dry weight accumulation. Ultimately, the adaptation of plant roots themselves and changes in soil chemistry particularly soil-P under changing soil-water regime were determined to affect on plant growth, nutrient uptake, and therefore directly and/or indirectly effect on rice grain yield.

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