Chapter 2

Responses of upland and wetland rice cultivars to flooded and well-drained soil water conditions

2.1 Introduction

Rice cultivated areas are classified by source of water supply as rainfed or irrigated. The rainfed rice ecosystem lacks irrigation and usually experiences discontinuous waterlogging of soil during crop growth. The amount and timing of water supply in rainfed rice ecosystems is variable and considered to be the most severe constraint to productivity. Thus, the rice yield in the rainfed wetlands is generally less than 50 % of the irrigated rice except in the more favourable sub-ecosystem, where rainfall distribution is effective in maintaining soils in flooded conditions (Wade *et al.*, 1999). When soil becomes waterlogged, oxygen in soil is rapidly depleted. Thongbai *et al*. (2001) studied the dynamics of oxygen concentration at 15 cm depth from the soil surface in an irrigated clay soil. They found that 48 hrs after irrigation, oxygen in the soil declined to close to zero. In general for waterlogged soil, redox potential declines and soil pH increases to about 6-7, and availability of phosphorus, iron, and manganese was increased (Ponnamperuma, 1972). In contrast, availability of nitrogen as nitrate form and the mineralization of organic matter were decreased. Therefore, rice plants in the rainfed ecosystem have to adapt to fluctuation of water regimes and nutrient availability. The adaption of rice plants varies among cultivars.

Rice cultivars are classified by rice ecosystem into upland, lowland, deepwater and floating rice types. Based on improvement, they can also be classified as traditional or local rice and improved rice. Moreover, rice types are either may be non-photoperiod sensitive or photoperiod sensitive rice. According to the differences in rice group, many studies determined the response of rice cultivars from different types especially based on rice ecosystem. Colmer *et al.* (1998) studied the response of three rice types; upland, lowland, and deepwater rice to aerobic and anaerobic conditions. Colmer (2003a) confirmed the responses in the same three rice groups with 12 cultivars. Rice plants in two studies were grown in aerated and stagnant nutrient solution and the responses of root constitutive porosity (%) and radial oxygen loss (ROL) from root in anaerobic condition were different in rice cultivar types (Colmer *et al.*, 1998). They concluded that upland cultivars showed less adaption to stagnant solution and deduced that these cultivars were less well adapted to flooded soil. Hence the differential adaptation of upland and lowland rice cultivars in Thailand to change in water regime may provide insights for nutrient management technologies or rice breeding strategies that will increase productivity and response of rice to well-drained and waterlogged conditions. However, at present very few Thai cultivars have been examined and the previous work was only conducted in solution culture where for example rhizosphere effects on nutrient availability are not expressed. Therefore, the study in this chapter was an opportunity to test the findings of Colmer *et al*. (1998) in flooded soil and to extend the number of cultivars studied in waterlogged and well-drained conditions. The aim of the experiments was to examine responses of root and shoot growth and nutrient accumulation of Thai rice cultivars (upland and lowland rice), to waterlogged and well-drained soil conditions.

2.2 Materials and Methods

2.2.1 Experiment 1: Responses of rice in waterlogged and well drained soils

Two soil water conditions were imposed on four rice cultivars. Soil conditions were waterlogging (W+, the soil surface was submerged under 10 cm water) and well drained (W0, daily watering of the plant but no water standing in the pot). Four Thai rice cultivars were Sew Mae Jan (SMJ); Kae Noi (KN: traditional upland rice cultivars); Chainat1 (CNT1: improved non-photoperiod sensitive cultivar for irrigated areas), and; Khao Dawk Mali 105 (KDML105: aromatic photoperiod sensitive rainfed wetland rice cultivar). Sew Mae Jan was previously grown in aerated and stagnant nutrient solution by Colmer *et al.* (1998) but referred to by a slightly different name of Sei Maj Un. Three 7 day-old rice plants were transplanted in each pot one week before the treatments started. Each earthenware pot was lined with a plastic bag and contained 5 kg of soil (San Sai series; Table 2.2.1.1). Basal fertilizer was applied at the rate of 0.37 g N/pot as urea, 0.26 g P/pot and 0.26 g K/pot two weeks after transplanting and repeated four weeks later. There were separated pots for each harvest at 2, 4, 8 and 10 weeks after the treatments started. There were three replicates for each treatment and harvest.

At each harvest, maximum root length, maximum shoot length, root and shoot dry weight, total root volume, aerenchyma appearance and nutrient contents were assessed. Maximum root length was measured as the longest undamaged adventitious root. Maximum shoot length was measured from the base of stem to the tip of the terminal, fully expanded leaf blade. The total root volume was measured by displacement of water in a cylinder of water. Root and shoot dry weights were measured after oven drying at $70^{o}C$ for 48 hrs. Aerenchyma development (% of root cross sectional area) was measured on samples of adventitious roots. A sample of 3 root tips (5 cm in length) was collected from each pot (1 root tip/plant) for examination of aerenchyma development by cross sectioning and scanning under a compound microscope. The aerenchyma formation was determined as a percentage of aerenchyma appearance in root cortex. Shoot and root samples were digested in sulfuric acid then analysed by the Kjeldahl method for N. The tissue samples were ashed at $535^{o}C$ for 8 hrs and dissolved in 0.1 N HCl and then P was determined by using a colorimetric assay (molybdovanado-phosphoric acid method) and a spectrophotometer (Murphy and Riley, 1962). K concentration in plant sample was determined by using an atomic absorption spectrophotometer.

2.2.2 Experiment 2: Responses of rice in fluctuation of soil water regimes

Three selected rice cultivars from the previous experiment were grown in two water conditions. Kae Noi (KN), Chainat1 (CNT1), and KDML105 were grown in waterlogged (W+, the soil surface was submerged under 10 cm of water) and well drained soils (W0, the plant was watered everyday but did not have water standing in the pot) at different times from 2-9 weeks after sowing. The treatments comprised waterlogging continuously for 2-9 weeks (W++++) or waterlogged with periods of drainage at 2-3 (W0+++), 4-5 (W+0++), 6-7 (W++0+), and 4-9 weeks (W+000).

Four days after germination, the seedlings were transplanted into the plastic pots, which were lined with a plastic bag, and containing 10 kg of mixed 5 kg of soil and 5 kg of coarse sand. Five rice plants of each cultivar were transplanted per pot, and allowed to establish for one week before starting of waterlogging treatment. Plant pots were separated for each harvest at 3, 5, 7, and 9 weeks. Pots were arranged in a randomised completed block design with three replicates. At each harvest, maximum root length, maximum shoot length, root and shoot dry weight, total root volume, aerenchyma appearance and nutrient contents were assessed as described above for experiment 1. However, in this experiment, aerenchyma appearance (Percentage of root cross sectional area) was measured on samples of adventitious roots at 2, 3 and 5 cm from the root tip.

2.2.3 Statistic analysis

Analysis of variance was conducted based on a factorial model with treatment arranged in a Randomized Complete Block Design (RCBD). Data were analyzed using two-way analysis on variance (ANOVA) to determine the main effects and interactions among cultivar, and water treatment. Means were compared using Least Significant Difference (LSD) at $P<0.05$.

Table 2.2.1.1 General characteristics of San Sai soil series used for all experiments.

San Sai soil characteristics	
Texture	Sand
pH (KCl)	4.5-5.5
CEC	Low
Slope	0 – 3%
Other characteristics	Low humus, low available phosphorus
	Low organic matter, poor irrigation, poor fertility
	Land use for rice cultivation and some soybeans,
	peanut, corn, garlic, tomato etc.

Source: Land Development Department, Bangkok, Thailand (2002)

2.3 Results

2.3.1 Experiment 1: Responses of rice in waterlogged and well drained soils

After the first two weeks maximum root length of wetland rice cultivars was enhanced by W+. By contrast, the longest root length of the upland rice KN was increased in W0 soil; SMJ had similar length of the longest root in both W+ and W0 soils (Table 2.3.1.1). At 4-10 weeks the longest root length of KN was similar in both W+ and W0 soils. Whereas, SMJ and wetland cultivars the root elongation was increased by W+ (Table 2.3.1.1). At 10 weeks, the rice cultivars were approaching or had reached in the panicle initiation stage. There was no increase in root length, especially in W+ soil. At this stage, the longest root length showed a clear difference in responses to soil water condition between the upland and wetland rice cultivars. Water regime did not affect to the root length of upland rice, while in wetland rice had longer roots in W+ soil than in aerated soil (Table 2.3.1.1).

Waterlogging significantly increased the total root volume of all rice cultivars (Table 2.3.1.2). Total root volumes of four rice cultivars were equal (data not shown). While at 10 weeks CNT1 showed the highest increase on total root volume in W+ soil but the other wetland rice, KDML105 was the poorest in both W+ and W0 soils. In W0 soil, KN was the highest on total root volume while SMJ had the same response on total root volume as CNT1 (Table 2.3.1.2). The other characteristics of root growth measured in this study were root dry weight. At first two weeks in treatments, root dry weight was separated by rice cultivar groups. At two weeks, wetland rice; CNT1 and KDML105 had 62-65 % higher root dry weight than upland rice; KN and SMJ (Table 2.3.1.3). Then, root dry weight of rice when grown in treatments for 10 weeks showed the influence of water and cultivar interaction effects. At 10 weeks, root dry weight in W0 soil for three cultivars (CNT1, KDML105 and SMJ) was about half that in W+ soil. In contrast KN had the same root dry weight in both soil water conditions. CNT1 in W+ had higher root dry weight than other cultivars. In W0 soil, CNT1 had the same value of root dry weight as KN and higher than KDML105 and SMJ by about 50% (Table 2.3.1.3).

Table 2.3.1.1 The longest root length (cm) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 2, 8 and 10 weeks.

Cultivars	The longest root length (cm)					
	2 weeks		8 weeks		10 weeks	
	W+	W0	W+	W0	W+	W0
SMJ	13.4 Aa	12.4 Aa	43.4 Aa	37.6 Bb	36.0 Ca	37.4 Ba
KN	8.2 Bb	12.5 Aa	45.5 Aa	44.2 Aa	41.8 Ba	44.0 Aa
CNT1	13.0 Aa	6.8 Bb	45.2 Aa	38.0 Bb	40.3 Ba	31.8 Cb
KDML105	12.1 Aa	7.8 Bb	45.1 Aa	26.7 Cb	46.1 Aa	33.8 Cb
F-test	C x W*		C x W*		C x W*	
$LSD_{(P<0.05)}$	2.2		3.3		3.2	

* Significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effect. The difference between water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.1.2 Total root volume (ml) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 10 weeks.

Cultivars	Water soil conditions	
	W+	W0
SMJ	36.3 Ca	24.0 Bb
KN	45.5 Ba	31.7 Ab
CNT1	62.3 Aa	20.7 Bb
KDML105	33.0 Ca	12.3 Cb
F-test	C x W*	
$LSD_{(P<0.05)}$	7.44.	

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effect. The difference between water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.1.3 Root dry weight (mg/plant) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 2 and 10 weeks. Values at 2 weeks are means of three replicates ± standard errors.

Cultivars	Root dry weight (mg plant^{-1})				
	2 weeks			10 weeks	
	W+	W0	Mean	W+	W0
SMJ	7 ± 2	11 ± 1	9 B	3.857 Ba	2.069 Bb
KN	9 ± 3	9 ± 1	9 B	3.464 Ba	3.557 Aa
CNT1	32 ± 1	19 ± 1	26 A	5.534 Aa	3.255 Ab
KDML105	28 ± 8	19 ± 2	24 A	4.154 Ba	2.161 Bb
F-test		C*		C x W*	
$LSD_{(P<0.05)}$		7.0		0.725	

* significant at P< 0.05. C, and C x W indicate F-test for cultivar, and cultivar and soil water condition interaction effects. The difference between water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

After two weeks shoot length of KDML105 was higher than CNT1, SMJ and KN respectively. At 4-10 weeks, shoot length was affected by cultivar and water interaction effects, most cultivars increased shoot length when grown in W+ soils, except KN at 4 and10 weeks. In W+ at 10 weeks, KDML105 had the longest shoots followed by SMJ and KN, which are also traditional varieties, with the semi-dwarf CNT1 the shortest, only two-thirds of KDML105 (Table 2.3.1.4). Shoot length was shortened in W0 soil most strongly in KDML105, followed by SMJ, while CNT1 and KN had about the same height in W+ and W0 soil (Table 2.3.1.4). Likewise, shoot dry weight at two weeks responded on rice cultivars as shoot length being highest in KDML105. Shoot dry weight of rice plants at two weeks was highest in W0 soil (data not shown), whereas at four weeks, tillering stage, shoot dry weight of all cultivars were increased by W+ soil conditions (Table 2.3.1.5). Responses of the rice cultivars to water condition were not distinguishable during early growth. The differences became evident by 8-10 weeks. As shown for week 10 (Table 2.3.1.6), in W+ soil CNT1, KDML105 and SMJ had about the same dry weight, whereas KN was lower. Responses to W0 soil were in accordance with the upland or wetland status of the cultivars. Dry weight of the upland cultivars KN and SMJ was about the same in W+ as in W0 soil, while that of the wetland cultivars KDML105 and CNT1 in W+ was double of that in W0 soil.

The efficiency of root for shoot production was measured as root/shoot ratio. At two weeks, all rice cultivars were higher in root/shoot ratio when grown in W+ soil and CNT1 was the highest. At four weeks, root/shoot ratio of all cultivars was increased and higher than other harvest time. At this stage, upland rice cultivars had no different on root/shoot ratio when grown in both W+ and W0 soil conditions, whereas root/shoot ratio of wetland rice cultivars increased in W+. At 10 weeks, KN had higher root/shoot ratio than other cultivars and root/shoot ratio was increased when grown in W+ soil (Table 2.3.1.7).

This study found that all rice cultivars formed aerenchyma when grown in both W+ and W0 soils. Aerenchyma formation in SMJ was the same as KDML105 regardless of soil water conditions. Similarly in CNT1 at eight weeks was no different on aerenchyma in both water soil conditions. Whereas, at 5 cm from the root tip, KN in W0 soil formed more aerenchyma than others and more increased when grown in W+ soil (Figure 2.3.1.1). Generally, rice plants in W+ soil had higher N, P and K content than rice in W0 soil (Table 2.3.1.8). Moreover, in different water conditions, nutrient uptake efficiency by each cultivar was different. In W+ soil, SMJ had the same N content as KDML105 and higher P and K contents than the other cultivars. Nutrient contents were higher in W+ soil, but with different W0/W+ ratios in the different cultivars and different nutrients. Nutrient uptake in KDML105 was depressed the most in W0 condition compared with W+. Although its N, P, K contents were among the highest in W+, they were among the lowest in W0 soil. While, KN was the highest in N, P and K accumulation in plant when grown in W0 soil, but KDML105 was the lowest.

Table 2.3.1.4 The maximum shoot length (cm) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 10 weeks.

Cultivars	Water soil conditions	
	W+	W0
SMJ	80.6 Ba	69.6 Ab
KN	73.2 Ca	70.4 Aa
CNT1	60.3 Da	55.0 Cb
KDML105	92.2 Aa	63.3 Bb
F-test	C x W*	
$LSD_{(P<0.05)}$	4.5.	

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effect. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.1.5 Shoot dry weight (g plant^{-1}) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for four weeks.

Cultivars	Water soil conditions		Mean
	W+	W0	
SMJ	0.81	0.49	0.65 B
KN	0.52	0.51	0.51 B
CNT1	0.98	0.74	0.86 A
KDML105	1.03	0.75	0.89 A
Mean	0.83 a	0.62 b	
F-test	C *	W*	C x W ^{ns}
$LSD_{(P<0.05)}$	0.14	0.10	-

ns, * are nonsignificant and significant at P< 0.05, respectively. C, W and C x W indicate F-test for cultivar, soil water condition and cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.1.6 Shoot dry weight (g $plant^{-1}$) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 10 weeks.

Cultivars	Water soil conditions	
	W+	W0
SMJ	13.01 ABa	11.71 Aa
KN	8.92 Ba	11.20 Aa
CNT1	15.61 Aa	8.92 Ab
KDML105	17.49 Aa	11.08 Ab
F-test	C x W*	
$LSD_{(P<0.05)}$	4.54.	

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.1.7 Root/shoot ratio of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for 10 weeks. Values are means of three replicates ± standard errors.

Cultivars	Water soil conditions		Mean
	W+	W0	
SMJ	0.30 ± 0.01	0.18 ± 0.01	0.24 B
KN	0.39 ± 0.04	0.32 ± 0.02	0.35 A
CNT1	0.36 ± 0.04	0.37 ± 0.04	0.36 A
KDML105	0.25 ± 0.04	0.21 ± 0.06	0.23 B
Mean	0.32 a	0.21 b	
F-test	C*	W*	
$LSD_{(P<0.05)}$	0.08	0.05	

* significant at P< 0.05. C and W indicate F-test for cultivar and soil water condition effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

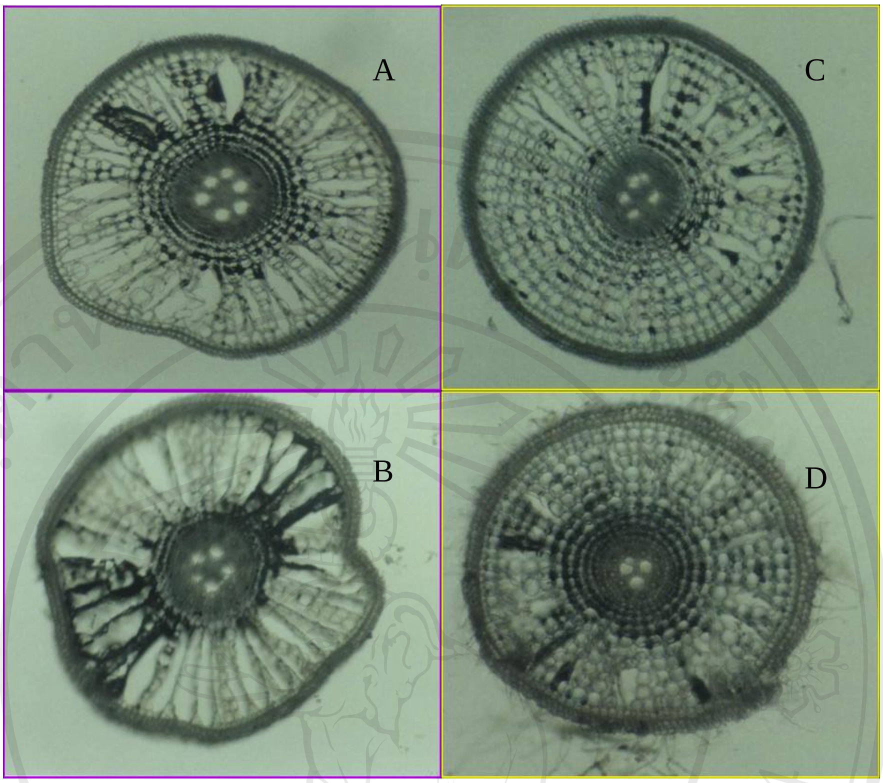

Figure 2.3.1.1 Aerenchyma appearance in adventitious roots at 5 cm from the root tip of KN when grown in well drained (A) and waterlogged (B) soil conditions compared with KDML105 when grown in well-drained (C) and waterlogged (D) soil conditions.

Table 2.3.1.8 Nitrogen (N), phosphorus (P) and potassium (K) contents (mg plant^{-1}) of four rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions for eight weeks.

Cultivars	N contents (mg)		P contents (mg)		K contents (mg)	
	W+	W0	W+	W0	W+	W0
SMJ	48.5 Aa	20.7 BCb	4.6 Aa	1.7 Bb	61.3 Aa	27.8 Ab
KN	37.4 Ca	30.3 Ab	4.4 Aa	2.3 Ab	45.9 Ba	28.3 ABb
CNT1	39.5 BCa	22.5 Bb	4.0 Ba	2.5 Ab	36.9 Ca	32.6 Aa
KDML105	44.8 ABa	14.5 Cb	4.0 Ba	1.2 Cb	40.2 BCa	21.8 Bb
Mean	42.6	22.0	4.3	1.80	46.1	27.6
	F-test	$LSD_{(P<0.05)}$	F-test	$LSD_{(P<0.05)}$	F-test	$LSD_{(P<0.05)}$
	C ^{ns}	-	C *	0.16	C *	5.05
	W*	3.49	W*	0.11	W*	3.57
	C x W*	6.99	C x W*	0.22	C x W*	7.14

ns = non significant $_{(P<0.05)}$, * significant at P< 0.05. C, W and C x W indicate F-test for cultivar, soil water condition and cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

2.3.2 Experiment 2: Responses of rice in fluctuation of soil water regimes

At three weeks, root length of CNT1 in waterlogged soil was longer than in well-drained soil but in KN root length displayed the was the opposite longest in well-drained soil condition (data not shown). By contrast, root length of KDML105 was the same in waterlogged and well-drained soil. At seven weeks, the cultivars did not show any difference in root length response to water condition. Root length of all cultivars was longer in continuously waterlogged soil and the root length of KN was longer than other cultivars (Table 2.3.2.1). Total root volume increased with waterlogging at five weeks in all cultivars but at seven weeks root volumes of the cultivars were not different, excepted KDML105 in W+00 was lower than other conditions (Table 2.3.2.2). Likewise, total root volume of KN in continuously waterlogged soil was more than in treatments continuous without standing water. At five weeks, lack of waterlogging at the early stage dramatically decreased root dry weight over though they were rewatered (W0+). Lack of waterlogging 2-3 weeks after transplanting, reduced root dry weight more than the lack of waterlogging in period of 4-5 weeks. Similarly, shoot dry weights at three and five weeks, were higher in the continuously waterlogged soil condition that in those with a period of no standing water (Table 2.3.2.3). At seven and nine weeks, shoot dry weight of CNT1 was higher than other cultivars, except KDML105 in nine weeks was equal.

Aerenchyma formation at 2 cm from the tip was found in all cultivars and they were clearly different at 5 cm with more aerenchyma appearance with the length of root. At three weeks, aerenchyma appearance at 5 cm in roots of CNT1 was higher in lack of waterlogging than in waterlogged soil condition, KN formed higher aerenchyma when grown in waterlogged soil whereas, aerenchyma formation in

KDML105 was not different regardless of water regimes. After nine weeks, aerenchyma formation in KN and CNT1 was higher than KDML105 but none of the treatment effects were significant.

In all cultivars, N content at three weeks in waterlogged soil condition were more than in well-drained soil condition. Nitrogen concentrations declined with time in shoots, and in general differences among treatments diminished. Nitrogen concentration at five weeks of all cultivars in W0+ condition were more than other water soil conditions. At seven weeks, N concentration of CNT1 in all water soil conditions were not different and the same as other cultivars in the each of water soil condition, except in W+0+ which higher than KN and in W+00 which lower than KN (Table 2.3.2.4). At nine weeks, the N concentration in W+000 conditions of all cultivars was higher than other water soil conditions. Phosphorus contents of all cultivars in the thorough waterlogged soil at all harvests were higher than other conditions, except CNT1 at three weeks was equal (Table 2.3.2.5). In W+++ condition at nine weeks, the P content was the same as other conditions, except in W+000 conditions. Phosphorus contents and concentrations of CNT1 were lower than other cultivars in most of conditions and harvests, whereas KN was higher. Potassium contents were the same as P contents but at nine weeks KN was lower than other cultivars. Potassium concentrations at seven weeks, KN in all conditions were not different and lower than other cultivars, while in continuous waterlogged condition was the same (Table 2.3.2.6). Whereas, K concentration in KDML105 in W+00 condition was the highest and the same as nine weeks.

Table 2.3.2.1 Maximum root length (cm) of three rice cultivars when grown in treatments including waterlogging 2-9 weeks (W++++) and drainage at 2-3 (W0+++), 4-5 (W+0++), 6-7 (W++0+), and 4-9 weeks (W+000), values for harvests at seven and nine weeks.

Cultivars	Water soil conditions					Mean
7 weeks	W++0	W+0+	W+00	W0++	W+++	
KN	41.4	42.0	41.1	40.0	44.2	41.7
CNT1	42.6	40.9	40.6	40.1	42.7	41.4
KDML105	37.1	37.2	38.4	42.9	47.6	40.6
Mean	40.4 b	40.0 b	40.0 b	41.0 b	44.8 a	
F-test	W*		$LSD_{(P<0.05)}$		3.0	
9 weeks	W++0+	W+0++	W+000	W0+++	W++++	
KN	38.1	46.9	43.5	44.7	47.5	44.1 A
CNT1	42.1	40.4	37.8	40.9	37.5	39.7 B
KDML105	41.0	39.8	35.6	38.5	39.9	39.0 B
Mean	40.4	42.4	39.0	41.4	41.6	
F-test	C*		$LSD_{(P<0.05)}$		3.6	

* significant at P< 0.05. C and W indicate F-test for cultivar and soil water condition effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.2.2 Total root volume (ml) of three rice cultivars when grown in when grown in treatments including waterlogging 2-7 weeks (W+++) and drainage at 2-3 (W0++), 4-5 (W+0+), 6-7 (W++0), and 4-7 weeks (W+00) soil conditions at seven weeks.

Cultivars	Water soil conditions				
	W++0	W+0+	W+00	W0++	W+++
KN	9.20 Aa	8.47 Aa	9.13 Aa	7.64 Aa	15.20 Ab
CNT1	10.67 Aa	11.73 Aa	10.05 Aa	10.40 Aa	10.23 Ba
KDML105	9.80 Aab	10.45 Aa	6.80 Ab	9.33 Aab	9.93 Bab
F-test			C x W*		
$LSD_{(P<0.05)}$			3.27		

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.2.3 Root dry weight and shoot dry weight (g $plant^{-1}$) of three rice cultivars when grown in treatments including waterlogging 2-5 weeks (W++) and drainage at 2-3 (W0+), 4-5 (W+0) in soil at five weeks.

Cultivars	Water soil conditions			Mean
Root Dry Weight	W+0	W0+	W++	
KN	0.573	0.478	0.853	0.635
CNT1	0.677	0.542	0.675	0.631
KDML105	0.680	0.429	0.569	0.559
Mean	0.643 a	0.483 b	0.699 a	
F-test		W*		
$LSD_{(P<0.05)}$		0.146		
Shoot Dry Weight	W+0	W0+	W++	Mean
KN	0.726	0.723	1.272	0.907
CNT1	1.170	0.849	1.058	1.026
KDML105	0.979	0.662	1.025	0.889
Mean	0.958 ab	0.745 b	1.118 a	
F-test		W*		
$LSD_{(P<0.05)}$		0.232		

* significant at P< 0.05. W indicates F-test for soil water condition effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.2.4 Nitrogen concentration (%) of three rice cultivars when grown in when grown in treatments including waterlogging 2-7 weeks (W+++) and drainage at 2-3 (W0++), 4-5 (W+0+), 6-7 (W++0), and 4-9 weeks (W+00) soil conditions at seven weeks.

Cultivars	Water soil conditions				
	W++0	W+0+	W+00	W0++	W+++
KN	0.831Ab	0.730Bb	1.183Aa	0.788Ab	0.799Ab
CNT1	0.829Aa	0.850ABa	0.842Ba	0.817Aa	0.738Aa
KDML105	0.880Aab	0.926Aa	0.970Ba	0.847Aab	0.767Ab
F-test	C x W*				
$LSD_{(P<0.05)}$	0.154				

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.2.5 Phosphorus content (mg plant^{-1}) of three rice cultivars when grown in waterlogged (W+) and well drained (W0) soil conditions at three weeks.

Cultivars	Water soil conditions	
	W0	W+
KN	0.064 Aa	0.074 Ba
CNT1	0.050 Bb	0.075 Ba
KDML105	0.051 ABb	0.095 Aa
F-test	C x W*	
$LSD_{(P<0.05)}$	0.014	

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

Table 2.3.2.6 Potassium concentration (%) of three rice cultivars when grown in when grown in treatments including waterlogging 2-7 weeks (W+++) and drainage at 2-3 (W0++), 4-5 (W+0+), 6-7 (W++0), and 4-9 weeks (W+00) soil conditions at seven weeks.

Cultivars	Water soil conditions				
	W++0	W+0+	W+00	W0++	W+++
KN	3.13 Ba	3.21 Ba	3.25 Ba	3.34 Ba	3.26 Aa
CNT1	3.52 Aa	3.52 Aa	3.27 Bb	3.40 Bab	3.30 Aab
KDML105	3.36 ABc	3.60 Ab	4.00 Aa	3.65 Ab	3.33 Ac
F-test	C x W*				
$LSD_{(P<0.05)}$	0.23				

* significant at P< 0.05. C x W indicates F-test for cultivar and soil water condition interaction effects. The difference between soil water treatments in the same row is indicated by lower case letters. The difference between cultivars in the same column is indicated by upper case letters.

2.4 Discussion

Thai rice cultivars responded differently to waterlogged and well-drained soil conditions after 8-10 weeks of experiment 2.2.1 and after 5-7 weeks of experiment 2.2.2, which correspond with tillering and panicle initiation stages. This period is the most important for rice productivity because the number of tillers and root development during this stage determine the success of reproductive stage and yield (De Datta, 1981). In this study, all rice cultivars were more productive growing in waterlogged soil except KN grew better than in well drained soils. Likewise, Ponnamperuma (1975) reported that rice yields less on well drained soils than on the same soil when waterlogged. Poorer growth of rice was attributed by Ponnamperuma (1975) to unfavourable chemical properties for rice in well drained soil such as iron deficiency and low availability of nitrogen, phosphorus and silica. Moreover, waterlogged soil contained continuous standing water, which eliminates water stress, neutralizes toxic Al levels, controls weeds, regulates the microclimate, and provides a favourable pH and microbiological environment for the rice roots. On the other hand, Fe toxicity may arise in flooded soils, but not in well-drained soils. Nutrient uptake, especially phosphorus content, was generally higher in waterlogged soils. This may reflect the fact that in waterlogged soil, soil reduction increases the availability of phosphate. Nitrogen availability in waterlogged soils, ammonia is the major form of nitrogen available for rice. Rice tolerates and uses ammonia efficiently at relatively high concentration (Yoshida, 1981). Ammonia supported growth of lowland rice when grown in submerged soils. In dry soils, fertilizer response is poor because of low moisture supply from rain and poor water holding capacity of soil. For phosphorus deficiency is more commonly a limiting factor for rice in well drained soils (Ponnamperuma, 1975). Rhizosphere modification by rice under well-drained conditions and under flooded conditions can be significant for improved P uptake but the mechanisms of rhizosphere modification involve organic acid excretion or ROL, respectively (Kirk and Du, 1997; Huguenin-Elie *et al.*, 2003).

However, the cultivar differences in growth under waterlogged and well-drained conditions suggest that root/shoot ratio might be a more significant trait than rhizosphere modification. KDML105 which is a lowland rice cultivar had a similar shoot production and P uptake in well drained soil to the upland rice cultivars These showed that KDML105 had the overlap on characteristics of upland rice cultivars. It may in part account for the popularity of KDML105 in rainfed lowland ecosystems of Thailand.

KN, which grew better in well drained soils than other cultivars and grew better under these soil water conditions than in waterlogged soil was different in its adaption to most previous cultivars. A notable trait of KN was that it constructed more roots in well drained soils, about the same as in waterlogged soils. The higher root growth seems to account for improved N and P uptake by KN in well-drained soil. This suggests that KN in well drained soil had no advantage on specific root uptake efficiency.

In waterlogged soil, rice plants develop aerenchyma to facilitate internal transport of oxygen from the shoot atmosphere to root tips (Justin and Armstrong, 1987; Drew *et al.*, 1994; Drew, 1997; Aschi-Smiti *et al.*, 2003; Colmer, 2003a). Fan *et al*. (2003) also suggested that aerenchyma might be an advantageous trait by decreasing the respiratory energy costs of maintaining a root system. However, aerenchyma formation might decrease symplastic nutrient transport across the roots to the main transport vessels in the stele (Drew and Saker, 1986; Kronzucker *et al.*, 1998). The strong aerenchyma development of KN under waterlogged soils may reflect an adaption of this cultivar to maximize root surface area and length for nutrient uptake, without undue respiratory costs for maintenance growth of the roots. In the present study with rice in soils, aerenchyma development of SMJ was not different in two water condition. Whereas, Colmer *et al.* (1998) studied the same cultivar, in nutrient solution culture and found that root porosity of SMJ was lowest in the aerated solution, but the stagnant solution treatment increased the porosity of this cultivar by 2.3 fold. These indicated that rice plants in stagnant solution culture were more limited by oxygen deficiency. Stagnant solution simulated the waterlogged condition by mixed 0.1 % agar in solution culture to prevent the oxygen diffusion and convection (Wiengweera *et al.*, 1997). Whereas, in waterlogged soil in this study; soil surface was submerged under 10 cm, oxygen may diffuse and solve in water resulted in root of SMJ in waterlogged soil formed aerenchyma equal in well drained soil.

Contrary to the suggestion of Colmer *et al*. (1998), the responses of rice cultivars to soil water conditions were not determined by whether they were upland or lowland cultivars. Some responses of the upland cultivar, SMJ in waterlogged soils were similar to those of lowland rice cultivars. Similarly some responses of KDML105 in well-drained soil resembled those of the upland cultivars. In contrast, in KN, root and shoot growths were not different in both waterlogged and dry condition and compared to the other three cultivars had the longest of root length. Traditional upland cultivars are generally intermediate or tall-statured, low tillering and root deeper than lowland rice (Chang and Vergara, 1975 cited by De Datta, 1981). By contrast, CNT1, which has been bred for irrigated lowland ecosystems, had higher root dry weight in waterlogged soil than in other cultivars.

In conclusion, waterlogging generally promoted root dry weight and root length in all cultivars except in KN. Increases in root volumes of all cultivars were evident at 2-4 weeks after waterlogging commenced and continued throughout. Aerenchyma appeared in both waterlogged and well-drained soil conditions of all cultivars. By contrast, root lengths of KN in well-drained soil were greater than other cultivars. Waterlogging generally stimulated nutrient uptake but upland cultivars responded more slowly, especially KN. Shoot growth responses generally corresponded to those of root growth. The upland rice, KN expressed greatest root growth in well drained soil whereas CNT1 a cultivar for irrigated lowland environments had the lowest. SMJ and KDML105 were intermediate in responses to waterlogging. However, the lack of water in any growth stage, especially on seedling dramatically reduced growth of rice. Overall, the adaptive response of roots and shoots to waterlogging overlapped between upland and lowland cultivars. The root/shoot ratio best explained the adaptation of rice cultivars to well drained soil conditions.