Chapter 4

Morphological and physiological responses of upland rice in tolerance to Al toxicity in nutrient solution

4.1 Introduction

In the previous study, the popular varieties in Tee Cha village showed differentiation in plant growth, nutrient uptakes and grain yield on acid soil in the field (Chapter 2). Genotypic variation for Al tolerance was identified in the short term screening in nutrient solution (Chapter 3). On the basis of their RRL (root length in 30 mg Al L^{-1} Al relative to nil Al), some upland rice varieties were found to be more tolerant to Al than improved rice varieties. After rapid screening, therefore, better understanding of Al tolerance mechanisms in these upland rice varieties should be useful in the selection for key Al tolerance traits for rice breeding program and rice varieties for acid soil regions.

Up to date, Al tolerance mechanisms in rice are still being debated. Organic acid secretion from roots has been suggested as the primary mechanism of Al tolerance in several crops i.e. wheat and maize (Delhaize *et al.*, 1993; Pellet *et al.*, 1995), but not in rice (Ishikawa *et al.*, 2000; Ma *et al.*, 2002). Another mechanism for Al tolerance suggested is Al accumulation in different plant parts. Differential Al accumulation in the rice roots has been reported in different studies (Jan and Pettersson, 1993; Watanabe and Okada, 2005; Xu *et al.*, 2004). Some evidence suggested that efficient retention of Al in root may be one key characteristic of Al tolerance (Marschner, 1995; Sierra *et al.*, 2006).

Aluminum tolerant mechanism in plants may also be associated with more efficient uptake and utilization of nutrients. In fact, Al inhibits root growth, thereby causing the uptake of water and nutrient elements to be reduced. Aluminum may be competitive for common binding sites at or near the root surface and therefore the uptakes of K, Ca and Mg to be reduced (Fageria and Carvalho, 1982). Moreover, Al toxicity and P deficiency often appear together. Under low pH and high Al concentration, P is fixed as Al-phosphate, which is highly insoluble and unavailable to plants (Rao *et al.*, 1993). Some Al tolerant varieties tended to increase the pH of the rhizosphere more than that in Al sensitive varieties. The increasing in pH not only decrease the solubility and toxicity of Al by precipitation, but the binding sites of Ca and Mg in the root apoplasm can be increased (Foy, 1984; Marschner, 1995).

Therefore, this study aimed to determine the response in growth, efficient for taken up nutrient and Al accumulation of upland rice varieties in tolerant to Al toxicity by nutrient solution method. This may confirm the efficiency of RRL parameter that used to classify genotypic variation for tolerance to Al in short term screening and may be efficient to predict final crop yield.

4.2 Materials and Methods

Culture solution

Three upland rice varieties identified as Al tolerant (BB), Al moderately tolerant (BM) and Al sensitive (PA) varieties (from Chapter 2 and 3), and KDML105 were used in this experiment. Five days after germination, four plants of each variety were transplanted to 10 L plastic pot containing nutrient solution in a completely randomized design, with three replicates. The composition of nutrient solution was the same as described in the Experiment 3.2.1.2. There were four levels of Al [added as $Al_2(SO_4)_3.18H_2O$]: 0, 10, 20 and 30 mg L^{-1} (designated as Al_0, Al_{10}, Al_{20} and Al_{30}, respectively). The solution was renewed every week and the pH value adjusted daily to 4.0 ± 0.05 with 1N HCl or 1N NaOH. There were separated pots for two harvests at 30 and 45 days after treatments.

Sampling and measurement

At harvest, maximum root length, maximum shoot length, root number, root and shoot dry weights were determined. Maximum root length was measured in the longest root. Maximum shoot length was measured from base of stem to the tip of the terminal leaf. Root number was counted on individual plants. Root and shoot dry weights were measured after oven drying at 70°C for 48 hours. Relative value of root length (RRL) was calculated by dividing the root length of seedling grown with Al (Al_{10}, Al_{20} or Al_{30}) that grown without Al (Al_0). Relative value of shoot length (RSL), root number (RRN), root dry weight (RRW), shoot dry weight (RSW) and total dry weight (RTW) were computed in the similar way.

Plant analysis

Plant samples of root, shoot and flag leaf were kept separately, oven-dried at 80 °C for 48 hours, ground to pass a 1 mm mesh. One set of the plant samples were digested in sulfuric acid and analyzed by the Kjeldahl method for N. Another set of samples were dry-ashed at 500°C for 8 hours and dissolved in 0.1 N HCl; P was determined by using a colorimetric assay (molybdovanado-phosphoric acid method) and a spectrophotometer (Murphy and Riley, 1962); K, Ca, Mg and Al by atomic absorption spectrophotometer. Nutrient content, relative nutrient content and nutrient uptake efficiency (nutrient uptake per unit root weight) were calculated as follow:

$$\text{Nutrient content} = \text{\% concentration of element x plant dry weight}$$

$$\text{Relative nutrient content} = \frac{\text{Nutrient content in whole plant with Al}}{\text{Nutrient content in whole plant without Al}} \text{ x 100}$$

$$\text{Nutrient uptake efficiency} = \frac{\text{Nutrient content in whole plant}}{\text{Root dry weight}}$$

Statistical analysis

Analysis of variance was conducted using a factorial treatment combination arranged in Completely Randomized Design (CRD). Data were analyzed using analysis of variance (ANOVA) to determine the effects of variety, Al level and interaction between variety and Al level. Means were compared by least significant difference (LSD) at $P < 0.05$. Some data were transformed by log10 before statistical analysis.

4.3 Results

Effect of Al on plant growth

Root length

Comparative response to Al in three upland rice varieties; BB, BM and PA, and KDML105 found in the Experiment 3.2.1.2 was confirmed in this study with four Al levels. In absence of Al, root length of BB and BM was faster elongation than in PA and KDML105 at 30 days, but the different among varieties were disappeared at 45 days. Increasing of Al levels above Al_{10} depressed root length of all varieties, but more in Al sensitive PA and KDML105 than in BB and BM. At 30 days, root length of all varieties was not inhibited at Al_{10}. With increasing Al, root length of PA and KDML105 was depressed 43% and 60% at Al_{20} and 62% and 72% at Al_{30} as compared with Al_0, respectively. In contrast, BB and BM were less inhibited by increasing of Al; their root lengths were about the same at Al_{20} but became clearly differentiated at Al_{30}, showing BB to be less inhibited than BM, by depressing 29% and 47% as compared with Al_0, respectively (Table 4.1).

These results were confirmed at 45 days after treatment; root length of the upland rice varieties was not inhibited at Al_{10} but not in KDML105 which was depressed by 20%. Above Al_{10}, root length of KDML105 was more severely inhibited than PA; KDML105 was depressed 70% and 82% but only 45% and 66% of PA at Al_{20} and Al_{30} compared with Al_0, respectively (Table 4.1).

Differential response to Al among the varieties became more obvious in the change in root length between 30 and 45 days. At control (Al_0), root length of PA and KDML105 was more increased 38% and 48%, respectively, whereas BB and BM were not much difference from 30 days. With increasing Al to Al_{20} and Al_{30}, root length of BM and BB grew about 30% more in the intervening 15 days whereas PA and KDML105 almost stopped growing after 30 days at Al_{30} (Table 4.1).

Shoot length

At 30 days after treatment, shoot length of all varieties was not inhibited at Al_{10}. With increasing Al levels above Al_{10}, shoot length of Al sensitive PA and KDML105 was depressed 15% and 32% at Al_{20}, and 35% and 44% at Al_{30}, respectively. In contrast, both BB and BM were unaffected at Al_{20} and inhibited 20% less at Al_{30} (Table 4.2).

The difference in effects of Al on shoot length was more obvious at 45 days after treatment, particularly Al sensitive varieties. Shoot length of PA was less inhibited than KDML105, by depressing 21% and 41% at Al_{20} and more severe to 39% and 58% at Al_{30}, respectively. There was no difference between BB and BM which had twice as long shoot as KDML105 at Al_{30} (Table 4.2).

Comparing between 30 and 45 days, the varieties were different in shoot growth as affected by Al. At control (Al_0), shoot length of KDML105 was increased 78% more whereas BB was increased only 49% between15 days. However, the growth of KDML105 was linearly depressed with increasing of Al levels, by increasing only 33% at Al_{30}. While shoot length of BB and BM still grew at higher Al levels, by increasing 45% and 59% more at Al_{30} in the intervening 15 days, respectively (Table 4.2).

Root number

Levels of Al toxicity in nutrient solution affected to plant root numbers of all varieties without significant interaction between Al levels and varieties. At 30 days after treatment, root numbers of KDML105 was lower than others varieties, irrespective of Al levels. Root numbers of all varieties were highest at Al_{10} and then linearly depressed with increasing Al to Al_{20} and Al_{30}, respectively (Table 4.3).

The response of root numbers at 45 days was different from 30 days after treatment; root numbers of all varieties was the highest in absence of Al. Root numbers were linearly depressed with increasing Al levels, irrespective of varieties, by depressing about 50% at Al_{30} as compared with Al_0. Both BB and BM were higher to produce root numbers than that in Al sensitive PA and KDML105, 28% and 55%, respectively (Table 4.3).

Comparing between 30 and 45 days, root numbers of BB, BM and KDML105 were increased more than three times, but only two times in PA in absence of Al. However, the growth of new roots in the intervening 15 days was depressed differently in different varieties at higher Al levels. Root numbers of BB and BM were about doubled in 15 days in Al_{30} whereas in KDML105 there was almost no new roots growth after 30 days (Table 4.3).

Root dry weight

At 30 days after treatment, there was differently response to Al among varieties in root dry weight. In Al_0, root dry weight of the upland rice varieties was similar and 40% higher than KDML105. Root dry weight of all varieties was not inhibited with increasing to Al_{10}, except KDML105 which was depressed 50% more as compared with Al_0. Root dry weight of BB was not inhibited at higher Al levels whereas BM was depressed 44% and 48% at Al_{20} and Al_{30} as compared with Al_0, respectively. However, both of them became almost the same at Al_{30}, and several times higher than Al sensitive PA and KDML105. On the other hand, root dry weight of Al sensitive PA and KDML105 was depressed 78% and 87% at Al_{30} compared with Al_0, respectively (Table 4.4).

Root dry weight at 45 days responded somewhat differently to Al from the responses at 30 days. At 45 days, there was clearly differentiation between varieties at Al_0; BB was the highest followed by BM and PA, and KDML105 was the lowest. Although root dry weight of BB was not inhibited by Al at 30 days, at 45 days it was depressed 44% at Al_{20} and 56% at Al_{30} compared with Al_0. BM showed the same effect of Al on root dry weight as BB, the root dry weight of these two varieties at Al_{20} and Al_{30} were about half of those in Al_0. In contrast, the root dry weight of PA and KDML105 were more severely depressed by increasing Al levels, with root dry weight in Al_{30} being only 17% of that in Al_0 for PA and only 7% for KDML105 (Table 4.4).

Comparing between 30 and 45 days, there was different effects of Al on the increment of root dry weight of the different varieties. In absence of Al, root dry weight of BB and BM was increased about four times in the 15 days, and they still grew by more than three times at Al_{20} and Al_{30}. On the other hand, the growth rate of PA and KDML105 was lower than in BB and BM at all Al levels, but with the biggest difference in root dry weight incremental at higher Al levels. In the intervening 15 days, root dry weight of Al sensitive PA and KDML105 were about the same and three times increasing at Al_0, but with less growth in root dry weight in Al_{20} and Al_{30}, especially in KDML105. At these higher Al levels, the root dry weight of PA in Al_{30} was about doubled in the 15 days, but root dry weight of KDML105 was almost unchanged after 30 days (Table 4.4).

Shoot dry weight

There was differential response in shoot dry weight between varieties in their response to Al. At 30 days, shoot dry weight of BB and BM was almost similar at all Al levels which were clearly higher than Al sensitive PA and KDML105. BB and BM were not inhibited at Al_{10}, and depressed 50% and 60% at Al_{20} and Al_{30} as compared to Al_0, respectively. In contrast, although shoot dry weight of PA had higher than in KDML105 in presence of Al, both of them were depressed in the same level. They were more severe at lower Al level, by depressing about half at Al_{10} and then falling to 80% at Al_{30} (Table 4.5).

The response of shoot dry weight at 45 days showed the same trend as in 30 days. Both BB and BM were several times higher than PA and KDML105, respectively, particularly at higher Al levels. At Al_{30} as compared to Al_0, shoot dry weight of BB and BM was depressed about 60% whereas the growth of PA and KDML105 was more severe, by depressing 90% (Table 4.5).

Comparing between 30 and 45 days, shoot dry weight of all varieties was increased more than 4 times at Al_0. The differential response between Al tolerant and sensitive was more obvious at higher Al levels. At Al_{30}, shoot dry weight of BB and BM was increased about five times in the intervening 15 days whereas PA and KDML105 were slightly increased (Table 4.5).

Relative response to Al

Comparison of the varieties in their response to Al can be made with relative values of root length (RRL, root length in Al relative to that without Al) and total dry weight (RTW, total dry weight in Al relative to that without Al), which could be used as indicator for tolerance to Al toxicity. The values of RRL and RTW of the rice varieties were differently depressed by increasing Al (Figure 4.1 and Figure 4.2). At 30 days, the RRL of all varieties did not show the inhibiting effect of Al at Al_{10}, indeed some stimulating effect of Al was seen in PA and KDML105. With increasing Al, the RRL of PA and KDML105 was depressed to 57% and 40% in Al_{20} and to 38% and 28% at Al_{30}, respectively. In contrast, BB and BM was much less inhibited at higher Al levels; their RRL was about the same at Al_{20} but became clearly differentiated at Al_{30}, showing BB to be more tolerant (RRL 71%) than BM (53%) (Figure 4.1A). These results were confirmed at 45 days after treatments. The RRL was clearly different among varieties at Al_{20} and Al_{30}. The RRL of PA and KDML105 also showed inhibiting effect of Al at Al_{10}. There was some difference between PA and KDML105, which can be considered Al sensitive. The RRL of PA was twice as much as KDML105 at higher Al levels. Similarly, differentiation between the Al tolerant BB and BM was clearly seen in the RRL of BB, which was significantly higher than that BM, by 15% in Al_{20} and by 30% in Al_{30} (Figure 4.1B).

The varieties also responded differently to Al in their RTW, but differentiation among the varieties were somewhat different from those measured with the RRL, especially between the Al sensitive PA and KDML105 and between the Al tolerant BB and BM. At 30 days RTW was differently inhibited among varieties at Al_{10}; BB was higher than BM and PA whereas KDML105 was the lowest by only half of BB.

With increasing Al, PA and KDML105 were highly depressed, RTW was 30% and 15% at Al_{20} and only 18% and 12% at Al_{30}, respectively. The difference between BB and BM disappeared at higher Al levels, their RTW were 55% and 45% at Al_{20} and Al_{30}, respectively (Figure 4.2A). In addition, RTW at 45 days also showed the same trend in response to Al as in 30 days. The RTW of BB and BM were double to triple that in PA and KDML105 at the higher Al levels (Figure 4.2B).

To evaluated Al tolerance among rice varieties, parameter of RRL was correlated well with other growth parameters, particularly at higher levels of Al. The result showed that at 30 days, RRL at Al_{30} relative to Al_0 was closely related to their RRW (r = 0.975***; $P < 0.001$) and RSW (r = 0.949***; $P < 0.001$), correlation of those at 45 days also showed the similar way. However, there was less correlation between RRL and RRN that may not be an effective parameter for Al screening (Table 4.6).

Table 4.1 Root length of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	41.7 aA	41.3 aA	33.3 abA	29.6 bA
BM	40.0 aA	40.6 aA	28.7 bA	21.1 cB
PA	29.3 aB	33.7 aAB	16.8 bB	11.2 cC
KDML105	27.4 aB	30.0 aB	11.0 bC	7.7 cD
F-test	V*	Al*	V x Al*	
45 days				
BB	45.1 aA	46.0 aA	43.0 aA	38.6 aA
BM	44.6 abA	49.3 aA	36.2 bA	27.2 cB
PA	40.5 aA	34.2 aB	22.3 bB	13.9 cC
KDML105	40.6 aA	32.3 bB	12.1 cC	7.3 dD
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicated F-test for variety, Al level and variety and Al level interaction effects, respectively. The difference between varieties in the same column is indicated by upper case letters. The difference between Al levels in the same row is indicated by lower case letters.

Table 4.2 Shoot length of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	53.4 aA	53.1 aAB	46.8 abA	43.8 bA
BM	51.7 aA	55.3 aA	47.9 abA	42.2 bA
PA	48.0 aA	49.9 aAB	40.9 bA	31.2 cB
KDML105	37.4 aB	43.4 aB	25.3 bB	20.8 cC
F-test	V*	Al*	V x Al*	
45 days				
BB	77.9 aAB	79.4 aA	71.8 abAB	63.8 bA
BM	82.9 aA	79.8 abA	76.7 abA	67.4 bA
PA	74.7 aAB	70.3 abAB	59.2 bB	45.6 cB
KDML105	66.2 aB	60.9 aB	39.3 bC	27.5 cC
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicated F-test for variety, Al level and variety and Al level interaction effects, respectively. The difference between varieties in the same column is indicated by upper case letters. The difference between Al levels in the same row is indicated by lower case letters.

Table 4.3 Root number of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})				Mean
	0	10	20	30	
30 days					
BB	34.8	41.3	26.4	24.5	31.7 A
BM	29.1	40.9	26.8	20.9	29.4 A
PA	30.6	36.9	28.5	19.6	28.9 A
KDML105	15.5	27.4	12.1	12.4	16.9 B
Mean	27.5 b	36.6 a	23.5 bc	19.3 c	
F-test	V*		Al*		V x Al^{ns}
$LSD_{0.05}$	4.7		4.7		-
45 days					
BB	91.3	91.6	60.7	55.6	74.8 A
BM	91.4	64.7	61.8	49.6	66.9 A
PA	73.8	54.8	38.1	35.6	50.6 B
KDML105	49.8	43.4	18.2	17.2	32.2 C
Mean	76.5 a	63.6 b	44.7 c	39.5 c	56.1
F-test	V*		Al*		V x Al^{ns}
$LSD_{0.05}$	10.9		10.9		-

ns and * non significant and significant at $P < 0.05$, respectively. V, Al and V x Al indicated F-test for variety, Al level and variety and Al level interaction effects, respectively. The difference between varieties in the same column is indicated by upper case letters. The difference between Al levels in the same row is indicated by lower case letters.

Table 4.4 Root dry weight (mg plant^{-1}) of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	194.5 aA	197.6 aA	138.9 aA	131.2 aA
BM	212.6 aA	157.8 abA	119.3 bAB	109.7 bA
PA	183.5 aAB	134.6 aA	80.7 bB	40.4 cB
KDML105	118.7 aB	53.7 bB	20.6 cC	14.8 cC
F-test	V*	Al*	V x Al*	
45 days				
BB	889.3 aA	864.0 aA	499.0 bA	392.3 cA
BM	723.9 aB	611.3 aB	426.4 bA	376.7 bA
PA	546.4 aC	363.7 bC	176.3 cB	93.0 dB
KDML105	309.0 aD	165.0 bD	43.0 cC	20.3 dC
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicated F-test for variety, Al level and variety and Al level interaction effects, respectively. The difference between varieties in the same column is indicated by upper case letters. The difference between Al levels in the same row is indicated by lower case letters.

Table 4.5 Shoot dry weight (mg plant^{-1}) of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	721 aA	611 aA	394 bA	322 bA
BM	682 aA	462 aAB	309 bA	245 bA
PA	554 aAB	316 bB	171 cB	89 dB
KDML105	419 aB	180 bC	57 cC	50 cC
F-test	V*	Al*	V x Al*	
45 days				
BB	3701 aA	3349 aA	1987 bA	1446 cA
BM	3168 aA	2477 bA	1761 cA	1366 dA
PA	2129 aB	1283 bB	566 cB	252 dB
KDML105	1625 aC	944 bC	310 cC	154 dC
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicated F-test for variety, Al level and variety and Al level interaction effects, respectively. The difference between varieties in the same column is indicated by upper case letters. The difference between Al levels in the same row is indicated by lower case letters.

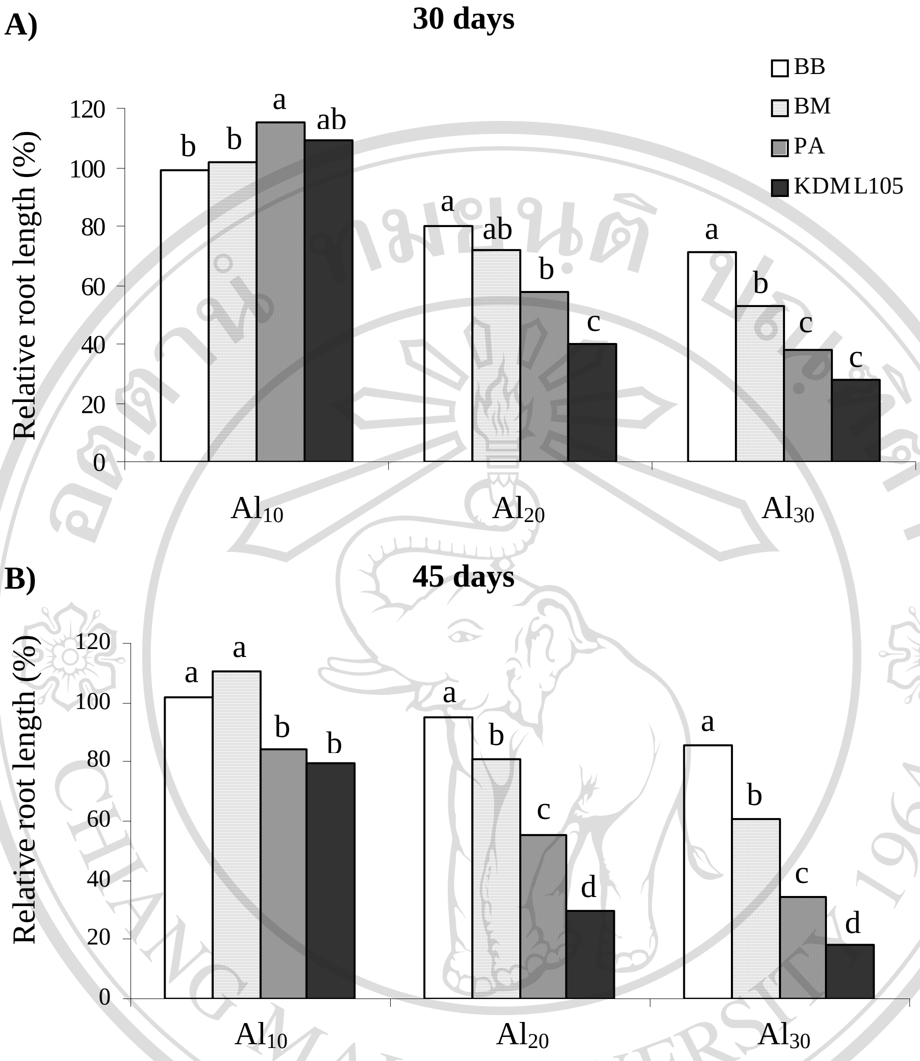

Figure 4.1 Relative root length (RRL) of four rice varieties at Al_{10}, Al_{20} and Al_{30} compared with Al_0 in nutrient solution at 30 (A) and 45 (B) days after treatments. The different between varieties in the same Al level is indicated by lower case letters by LSD at $P < 0.05$.

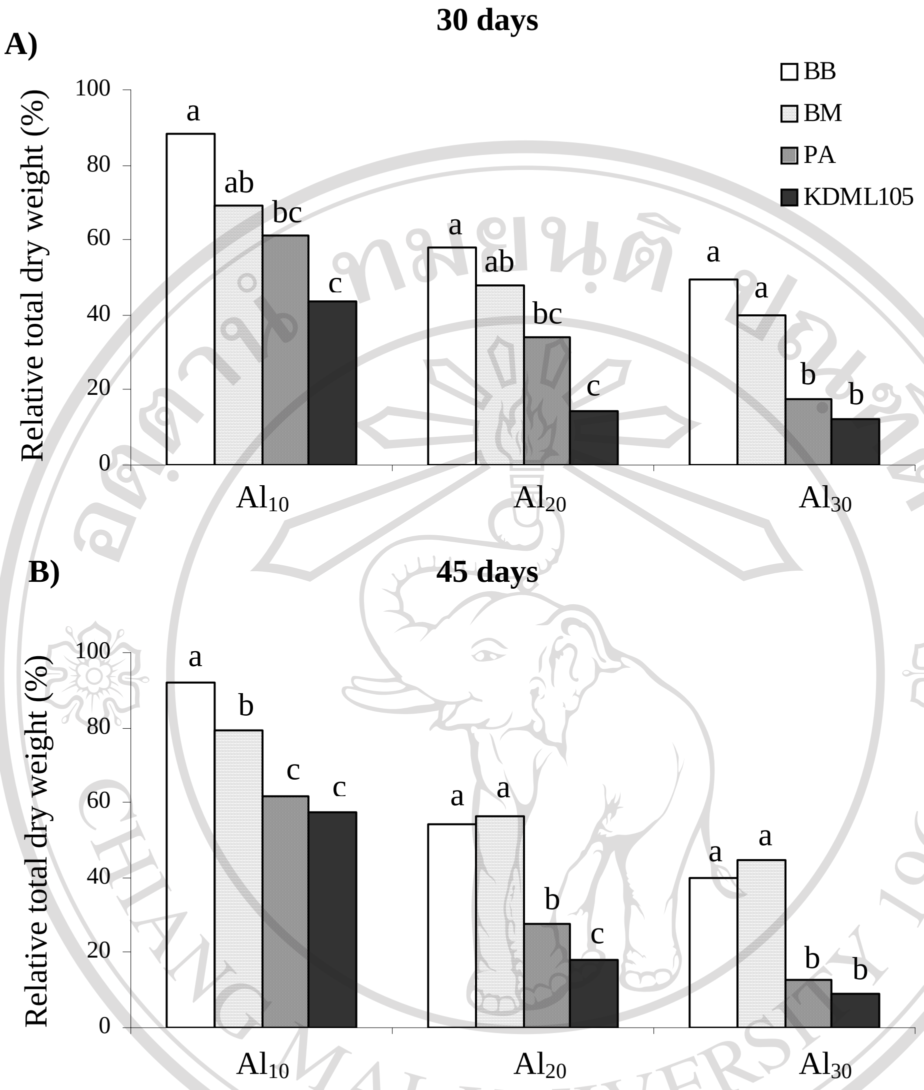

Figure 4.2 Relative total dry weight of four rice varieties at Al_{10}, Al_{20} and Al_{30} compared with Al_0 in nutrient solution at 30 (A) and 45 (B) days after treatments. The different between varieties in the same Al level is indicated by lower case letters by LSD at $P < 0.05$.

Table 4.6 Correlation coefficients between relative root length (RRL) with relative values of shoot length (RSL), root number (RRN), root dry weight (RRW), shoot dry weight (RSW) and total dry weight (RTW) at Al_{10}, Al_{20} and Al_{30} relative to Al_0 at 30 and 45 days after treatments.

Characters	RRL		
	Al_{10}	Al_{20}	Al_{30}
30 days			
RSL	0.493^{ns}	0.787**	0.877***
RRN	0.457^{ns}	0.253^{ns}	-0.027^{ns}
RRW	-0.303^{ns}	0.957***	0.975***
RSW	-0.410^{ns}	0.937***	0.949***
RTW	-0.380^{ns}	0.945***	0.958***
45 days			
RSL	0.443^{ns}	0.896***	0.870***
RRN	-0.113^{ns}	0.742**	0.649*
RRW	0.725**	0.937***	0.866***
RSW	0.811**	0.904***	0.878***
RTW	0.806**	0.915***	0.879***

ns, *, ** and *** non significant at $P < 0.05$, significant at $P < 0.05$, 0.01 and 0.001, respectively.

Al concentration in plant

Al concentration in the rice plant was increased in the presence of Al in both BB and KDML105, with Al concentration in the root was several times that in the shoot. The Al concentration in root at Al_{30} was not different between varieties and was 13 times higher than Al_0 control. However, the varieties showed differentiation in shoot at Al_{30}, Al concentration of Al sensitive variety KDML105 was twice as much as in Al tolerant varieties BB (Table 4.7).

Table 4.7 Aluminum concentration in root and shoot of BB and KDML105 with comparing at Al_0 and Al_{30} in nutrient solution at 45 days after treatment. The values represent Mean ± SE (n = 3).

Variety	Al concentration (mg/kg)	
	Al_0	Al_{30}
Root		
BB	161 ± 17	2120 ± 102
KDML105	134 ± 5	2028 ± 113
Shoot		
BB	31 ± 2	140 ± 7
KDML105	29 ± 2	279 ± 14

Nutrient accumulation in plant

Nitrogen

In the absence of Al, N accumulation in whole plant of KDML105 was 50% lower than others varieties. The content of N was depressed differently among varieties with increasing of Al levels. Nitrogen content of BB and BM was not different in each Al level and clearly higher than Al sensitive PA and KDML105. At 30 days, although PA had higher N content than KDML105 at Al_{20}, the N content of these two varieties became similar at Al_{30}, which was only about a quarter of that in BB and BM (Table 4.8).

At 45 days, there was different N content between varieties in absence of Al, BB and BM accumulated more N than in PA and KDML105 30% and 60% at Al_0, respectively. The difference response to Al between BB and BM on the one hand and PA and KDML105 on the other was clear in their N content in the presence of Al (Table 4.8). In Al_{10}, the N content of BB and BM was not depressed, where as that of PA and KDML105 was about half that in Al_0. The difference between the Al sensitive (PA and KDML105) and tolerant group (BB and BM) was even more distinct as Al increased. By Al_{30}, the N content of PA and KDML105 were only about one tenth of that in Al_0, where as BB and BM were able to accumulate almost half of the N that they did in Al_0.

Comparing the N accumulation in the time between 30 and 45 days, BB and BM accumulated three to four times N at all Al levels in the intervening 15 days. While PA and KDML105 more than tripled their N content in the same period at Al_0, at higher Al levels the N content of PA was increased significantly less where as the N content in KDML105 was almost constant after 30 days (Table 4.8).

Phosphorus

Phosphorus accumulation in whole plant was depressed with increasing of Al levels, but with different effects on different varieties. At 30 days, P content of three upland rice varieties were twice as much as KDML105 in Al_0, but those of them were linearly depressed with increasing of Al from Al_{10} to Al_{30}. At Al_{20}, P content of PA was depressed to the same level as KDML105 and more severe that KDML105 at Al_{30}. While P content of BB and BM were decreased about the same at all Al toxic, both of them were several times higher than Al sensitive varieties at Al_{20} and further more at Al_{30} (Table 4.9).

At 45 days, P content of BB and BM was much higher than PA and KDML105 in absence of Al. By effect of Al, both BB and BM were depressed about 50% and 60% at Al_{20} and Al_{30}, respectively, whereas the effect on PA and KDML105 were much more severe, by depressing 70% and 90% at Al_{20}, and up to 90% and 95% at Al_{30}, respectively (Table 4.9).

Comparing P accumulation between 30 and 45 days, the P content of BB and BM was increased about four to five times at all Al levels. For the Al sensitive PA and KDML105, PA accumulated slightly more P in the intervening 15 days than KDML105, which almost stopped taking up more P after 30 days (Table 4.9).

Potassium

At 30 days, K accumulation of KDML105 was lower than others varieties in absence of Al that was the same as in N and P. PA accumulated more K than in KDML105 at Al_0, but differentiation in K content was disappeared in presence of Al which about two and three times lower than Al tolerant varieties BB and BM at Al_{20}

and Al_{30}, respectively. The content of BB and BM was depressed about 60% at Al_{30} while PA and KDML105 were more severe by depressing 80% (Table 4.10).

In addition, even K content of PA was significantly higher than KDML105 at Al_{10} and Al_{20}, these two varieties had the same K content at Al_{30} by 45 days. The content of Al tolerant varieties BB and BM were depressed from 10% to 60% at Al_{10} to Al_{30}, but PA and KDML105 were highly depressed from 40% to 90%. Moreover, K content of BB and BM were 6 to10 times higher than PA and KDML105 at Al_{30} (Table 4.10).

While Al inhibited K accumulation in whole plants of all varieties, BB and BM continued to accumulate several times more K at all Al levels between 30 to 45 days. The Al sensitive PA and KDML105 showed different effect of Al on K accumulation in the period between 30 and 45 days. In Al_{20} and Al_{30} PA tripled its K content in this period while KDML105 took up hardly any more K after 30 days (Table 4.10).

Calcium

At 30 days, Ca accumulation was not significantly different among varieties in absence of Al, however, the differentiation between Al tolerant BB and BM, and Al sensitive PA and KDML105 was found in presence of Al. BB and BM accumulated more Ca than in PA and KDML105 by about twice to three times at Al_{20} and Al_{30}, respectively. The K content of PA and KDML105 was severely depressed at higher of Al, by depressing 70% and up to 90% at Al_{20} and Al_{30}, respectively, whereas the effect of Al on Ca content was much less in BB and BM (Table 4.11).

By 45 days, at Al_0 Ca content of BB and BM was double that in PA and KDML105. The differentiation was more obvious in presence of Al, BB and BM were three and up to five times higher than PA and KDML105 at Al_{20} and Al_{30}, respectively. The Ca content of all varieties at 45 days was depressed in the same rates as in 30 days with increasing of Al levels (Table 4.11).

In the 15 days period between 30 and 45 days, Al tolerant BB and BM accumulated more Ca than Al sensitive PA and KDML105, but with much larger difference in the presence of Al. In the intervening 15 days, Ca content of PA and KDML105 was increased about three times whereas BB and BM were up to five times at all Al levels. In Al_{30} PA accumulated the same amount of Ca as KDML105, which is different from the case of N, P and K, which PA tended to accumulate more than KDML105 in Al_{30}(Table 4.11).

Magnesium

The varieties were not different in their Mg content in Al_0 at 30 days. However, K content of BB and BM was higher than PA and KDML105 in presence of Al, particularly in higher Al levels. With increasing Al, Mg content of BB and BM was depressed by 60% and 70% at Al_{20} and Al_{30}, respectively, but in PA and KDML105 the depression was 80% at Al_{20} and 90% at Al_{30} (Table 4.12). At 45 days, BB had twice as much as Mg as PA and KDML105 in Al_0. The Mg accumulation of all varieties was inhibited at Al_{10}, by depressing 30% and 40% of BB and BM, respectively, and more severely by 60% in PA and KDML105. All of them were depressed more severe at Al_{30}, by 80% in BB and BM, and more than 90% in PA and KDML105. However, Al tolerant BB and BM clearly had higher in Mg content than

Al sensitive PA and KDML105 at higher Al levels, by accumulated four times more at Al_{20} and up to seven times at Al_{30}, respectively (Table 4.12).

In the period between 30 and 45 days, in Al_0, Al tolerant BB and BM accumulated more Mg than Al sensitive PA and KDML105. The difference between the two groups became even larger at higher levels of Al. In this 15 days period, Mg accumulation of BB and BM was increased by more than 5 times at Al_{20} and Al_{30}, while at the same Al levels PA and KDML105 accumulated only three and two times Mg, respectively (Table 4.12).

Relative nutrient uptakes

The contents of N, P, K, Ca and Mg at Al_{10}, Al_{20} and Al_{30} relative to Al_0 were difference among the varieties (Figure 4.3 to Figure 4.7). At 30 days, the relative nutrient contents of BB were higher than BM at Al_{10} and $Al_{20,}$ but the difference between these two varieties disappeared at Al_{30}. Although all relative nutrient contents except P of KDML105 were higher than PA and almost the same level as BB at Al_{10}, those of KDML105 were depressed more than half and grouped to the same level as PA at Al_{20} and Al_{30}. At Al $_{30}$ relative to Al_0, all nutrient contents of Al tolerant BB and BM were twice as much as Al sensitive PA and KDML105 (Figure 4.3 to Figure 4.7).

At 45 days, the relative nutrient contents showed clear differentiation between Al tolerant BB and BM and Al sensitive PA and KDML105 at Al_{10}, Al_{20} and Al_{30} relative to Al_0. All nutrient contents of PA and KDML105 were not different at all Al levels except P which PA was higher than KDML105 in the medium ranges of Al and became the similar at Al_{30} relative to Al_0 (Figure 4.3 to Figure 4.7).

In addition, the relative content of N, P, K, Ca and Mg was positively correlated with RRL at Al_{20} and Al_{30} relative to Al_0 but not in Al_{10} at 30 days (Table 4.13).

Nutrient uptake efficiency

The nutrient uptake efficiency (nutrient content per g root dry weight) of upland rice varieties was linearly depressed with increasing of Al levels but not in KDML105 (Figure 4.8). In Al_0, N uptake efficiency of BB was the highest followed by BM and PA but the lowest in KDML105 which was 40% less than BB. While N uptake efficiency of three upland rice varieties were linearly depressed 20% and 30% at Al_{20} and Al_{30}, respectively, KDML105 showed the opposite trend, by being higher by 30% in Al_{20} and 40% at Al_{30}. In addition, at Al_{30} N uptake efficiency of KDML105 was 40% and 80% greater than BB and PA, respectively (Figure 4.8A).

At Al_0, uptake efficiency of P was about the same between Al tolerant BB and BM which were higher than PA whereas KDML105 was the lowest. P uptake efficiency of three upland rice varieties dropped sharply with increasing Al, by depressing 60% of BB and BM, and 80% of PA at Al_{30} compared with Al_0. In contrast, the effect of Al on P uptake efficiency of KDML105 was somewhat less, by being depressed by only 30% at Al_{30}. Moreover, KDML105 was more efficient than PA in presence of Al and grouped in the same as BB and BM at Al_{20} and Al_{30} (Figure 4.8B).

The uptake efficiency of K was not different among four varieties at Al_0. However, K uptake efficiency in the three upland rice varieties was slightly depressed with increasing Al but not in KDML105. In Al_{10}, Al_{20} and Al_{30} KDML105 was more efficient in K uptake than that in Al_0, and in Al_{30} the K uptake efficiency of KDML105 was about twice as much as that in the three upland rice varieties (Figure 4.8C).

The varieties showed the same trend in uptake efficiency of Ca and Mg. The upland rice varieties were almost the same in the uptake efficiency of these nutrients in Al_0. Although PA was more depressed than BB and BM at medium ranged of Al, they became the same at Al_{30} which were depressed from Al_0 50% and 60% of Ca and Mg uptake efficiency, respectively (Figure 4.8D and 4.7E). However, the upland rice varieties were less efficient in Ca and Mg than KDML105 at all Al levels. The Ca uptake efficiency of KDML105 was almost constant at all Al levels, which was twice as much as the upland rice varieties at higher Al levels (Figure 4.8D). The Mg uptake efficiency of KDML105 was highly depressed with higher than Al_{10}, by depressing 40% at Al_{30} compared to Al_0. This result suggested that the efficiency of Mg was highly differentiation among varieties at Al_{10} and Al_{20} than that in Al_{30} (Figure 4.7E).

Table 4.8 Nitrogen content (mg plant^{-1}) in whole plant of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	46.4 aA	39.1 aA	25.3 bA	21.1 bA
BM	43.5 aA	29.0 aA	19.1 bA	15.2 bA
PA	34.6 aA	19.6 bB	11.0 cB	4.6 dB
KDML105	18.5 aB	15.5 aB	7.2 bC	4.4 cB
F-test	V*	Al*	V x Al*	
45 days				
BB	169.5 aA	161.2 aA	108.8 bA	79.5 bA
BM	157.5 aA	125.3 abA	93.7 bA	73.4 cA
PA	110.9 aB	66.8 bB	29.7 cB	13.3 dB
KDML105	63.5 aC	38.2 bC	11.1 cC	5.3 dC
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicates F-test for variety, Al level and variety and Al levels interaction effects. The difference between Al levels in the same row is indicated by lower case letters. The different between varieties in the same column is indicated by upper case letters.

Table 4.9 Phosphorus content (mg plant^{-1}) in whole plant of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	6.83 aA	5.69 aA	2.85 bA	1.96 cA
BM	6.99 aA	4.53 bA	2.28 cA	1.46 dA
PA	5.40 aA	2.83 bB	0.76 cB	0.24 dC
KDML105	2.96 aB	1.83 bC	0.65 cB	0.34 dB
F-test	V*	Al*	V x Al*	
45 days				
BB	26.80 aA	20.86 bA	13.44 cA	10.46 dA
BM	24.71 aB	18.49 bB	13.65 cA	10.61 dA
PA	15.54 aC	9.98 bC	4.52 cB	1.50 dB
KDML105	9.46 aD	4.29 bD	0.89 cB	0.47 dB
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicates F-test for variety, Al level and variety and Al levels interaction effects. The difference between Al levels in the same row is indicated by lower case letters. The different between varieties in the same column is indicated by upper case letters.

Table 4.10 Potassium content (mg plant^{-1}) in whole plant of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	48.10 aA	43.33 aA	27.95 bA	20.49 bA
BM	47.95 aA	32.35 bAB	20.29 cA	15.88 cA
PA	39.49 aA	25.02 bB	11.32 cB	4.53 bD
KDML105	24.99 aB	21.72 aB	9.56 bB	4.86 bC
F-test	V*	Al*	V x Al*	
45 days				
BB	203.9 aA	187.6 aA	120.4 bA	77.4 cA
BM	189.6 aA	164.0 bB	111.3 cA	68.5 dA
PA	147.8 aB	94.9 bC	34.3 cB	11.6 dB
KDML105	88.0 aC	51.0 bD	13.3 cC	6.3 cB
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicates F-test for variety, Al level and variety and Al levels interaction effects. The difference between Al levels in the same row is indicated by lower case letters. The different between varieties in the same column is indicated by upper case letters.

Table 4.11 Calcium content (mg plant^{-1}) in whole plant of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	1.91 aA	1.46 aA	0.81 bA	0.62 bA
BM	1.99 aA	1.22 bA	0.73 cA	0.55 cA
PA	1.53 aA	0.81 bB	0.35 cB	0.17 dB
KDML105	1.37 aA	0.93 bB	0.37 cB	0.20 dB
F-test	V*	Al*	V x Al*	
45 days				
BB	10.30 aA	7.35 bA	3.83 cA	2.87 dA
BM	9.47 aB	6.02 bB	3.76 cA	2.79 dA
PA	5.56 aC	2.92 bC	1.20 cB	0.53 cB
KDML105	5.30 aC	2.82 bC	0.92 cB	0.41 cB
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicates F-test for variety, Al level and variety and Al levels interaction effects. The difference between Al levels in the same row is indicated by lower case letters. The different between varieties in the same column is indicated by upper case letters.

Table 4.12 Magnesium content (mg plant^{-1}) in whole plant of four rice varieties when grown in nutrient solution with four Al levels for 30 and 45 days.

Variety	Al level (mg L^{-1})			
	0	10	20	30
30 days				
BB	2.95 aA	2.30 aA	1.18 bA	0.76 cA
BM	2.90 aA	1.81 bAB	0.98 cA	0.60 dA
PA	2.44 aA	1.11 bC	0.40 cB	0.19 dB
KDML105	2.12 aA	1.45 bBC	0.52 cB	0.20 dB
F-test	V*	Al*	V x Al*	
45 days				
BB	18.79 aA	13.30 bA	5.80 cA	3.81 dA
BM	15.76 aB	9.90 bB	5.49 cA	3.53 dA
PA	10.04 aC	4.32 bC	1.39 cB	0.59 cB
KDML105	9.00 aC	3.81 bC	1.05 cB	0.41 cB
F-test	V*	Al*	V x Al*	

Data were transformed for statistical analysis by log10.

* Significant at $P < 0.05$. V, Al and V x Al indicates F-test for variety, Al level and variety and Al levels interaction effects. The difference between Al levels in the same row is indicated by lower case letters. The different between varieties in the same column is indicated by upper case letters.

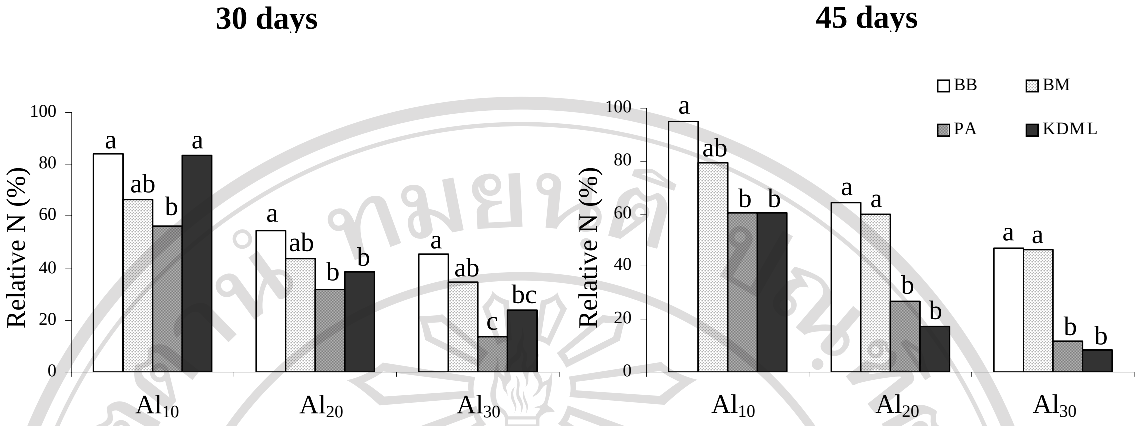

Figure 4.3 Relative nutrient uptake of nitrogen of four rice varieties at Al$_{10}$, Al$_{20}$ and Al$_{30}$ compared with Al$_0$ in nutrient solution at 30 and 45 days after treatments. The different between varieties in the same Al levels is indicated by lower case letters by LSD at $P < 0.05$.

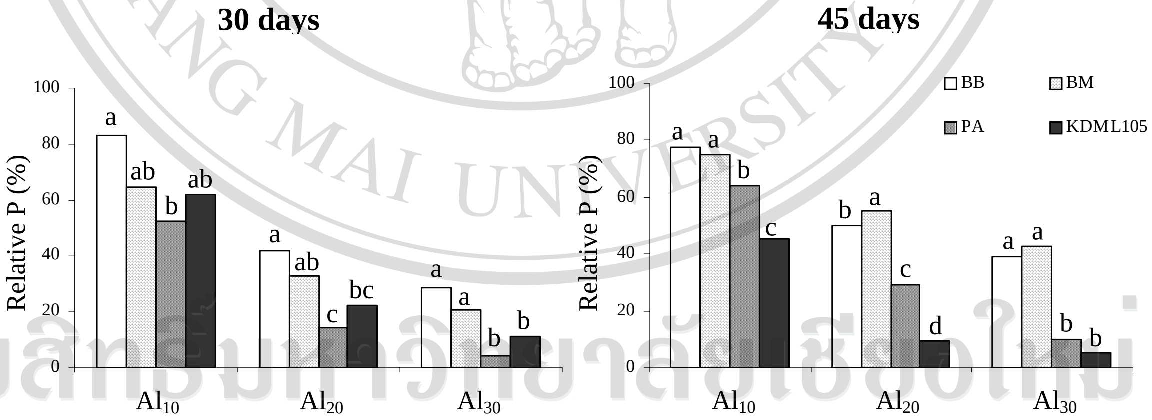

Figure 4.4 Relative nutrient uptake of phosphorus of four rice varieties at Al$_{10}$, Al$_{20}$ and Al$_{30}$ compared with Al$_0$ in nutrient solution at 30 and 45 days after treatments. The different between varieties in the same Al levels is indicated by lower case letters by LSD at $P < 0.05$.

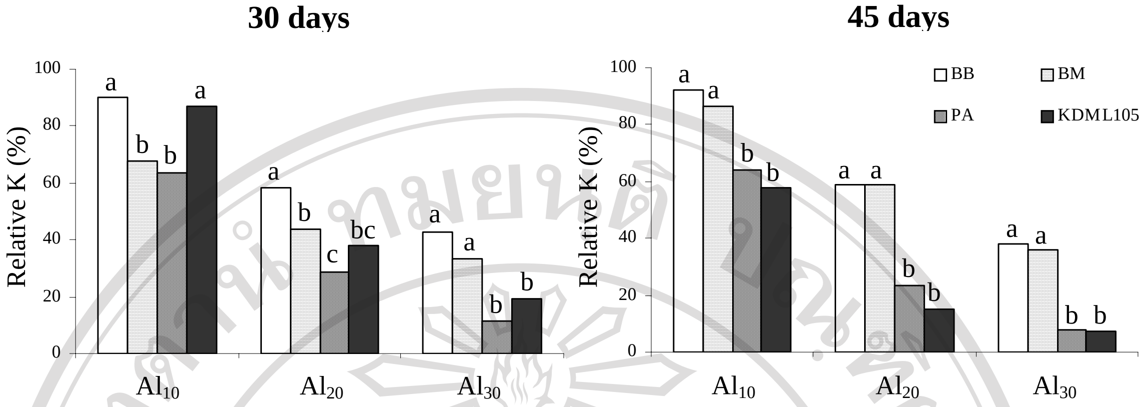

Figure 4.5 Relative nutrient uptake of potassium of four rice varieties at Al_{10}, Al_{20} and Al_{30} compared with Al_0 in nutrient solution at 30 and 45 days after treatments. The different between varieties in the same Al levels is indicated by lower case letters by LSD at $P < 0.05$.

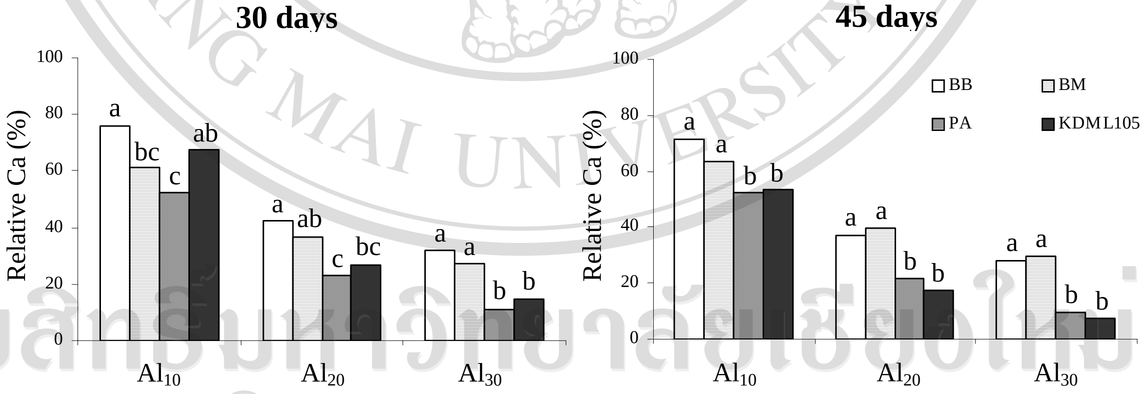

Figure 4.6 Relative nutrient uptake of calcium of four rice varieties at Al_{10}, Al_{20} and Al_{30} compared with Al_0 in nutrient solution at 30 and 45 days after treatments. The different between varieties in the same Al levels is indicated by lower case letters by LSD at $P < 0.05$.

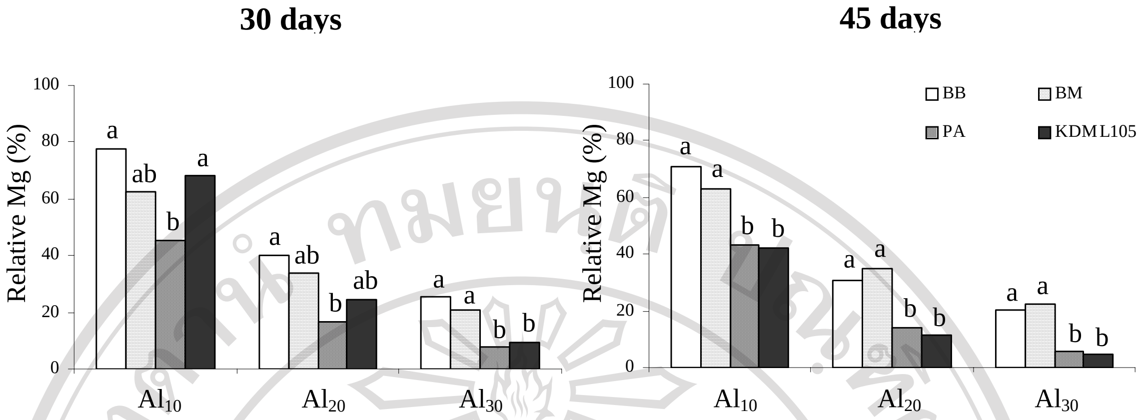

Figure 4.7 Relative nutrient uptake of magnesium of four rice varieties at Al_{10}, Al_{20} and Al_{30} compared with Al_0 in nutrient solution at 30 and 45 days after treatments. The different between varieties in the same Al levels is indicated by lower case letters by LSD at $P < 0.05$.

Table 4.13 Correlation coefficient between RRL with relative nutrient contents of N, P, K, Ca and Mg at Al_{10}, Al_{20} and Al_{30} relative to Al_0 at 30 days after treatments.

Relative of nutrient element	Relative root length		
	Al_{10}	Al_{20}	Al_{30}
Nitrogen	-0.319^{ns}	0.647*	0.772**
Phosphorus	-0.473^{ns}	0.711**	0.792**
Potassium	-0.247^{ns}	0.640*	0.803**
Calcium	-0.519^{ns}	0.725**	0.852***
Magnesium	-0.429^{ns}	0.665*	0.877***

ns, *, ** and *** non significant at $P < 0.05$, significant at $P < 0.05$, 0.01 and 0.001 respectively.

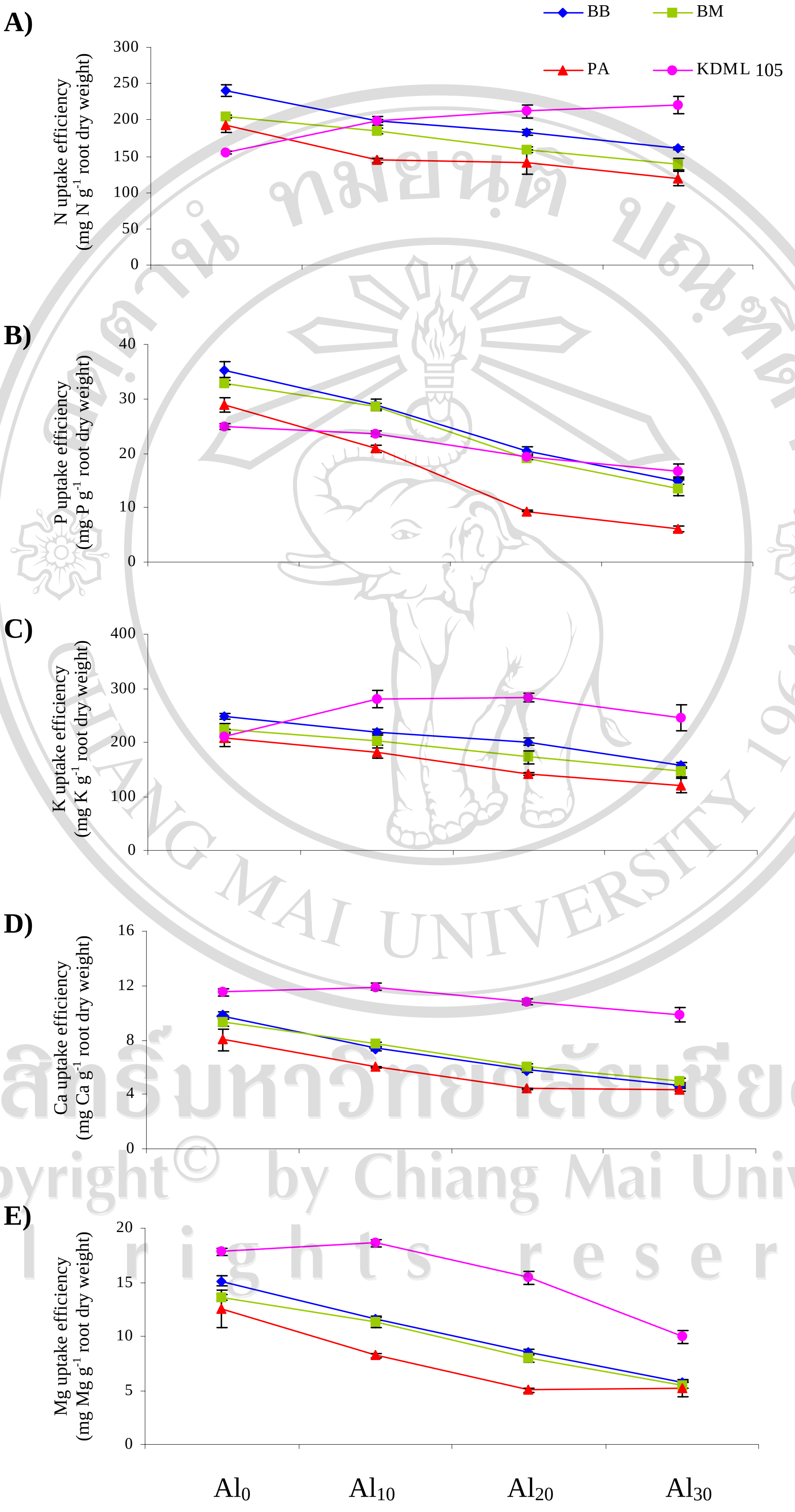
A)
BB
BM
PA
KDML 105
N uptake efficiency
(mg N g^{-1} root dry weight)
0
50
100
150
200
250
300
B)
P uptake efficiency
(mg P g^{-1} root dry weight)
0
10
20
30
40
C)
K uptake efficiency
(mg K g^{-1} root dry weight)
0
100
200
300
400
D)
Ca uptake efficiency
(mg Ca g^{-1} root dry weight)
0
4
8
12
16
E)
Mg uptake efficiency
(mg Mg g^{-1} root dry weight)
0
5
10
15
20
Al_0
Al_{10}
Al_{20}
Al_{30}

Figure 4.8 Nutrient uptake efficiency of N, P, K, Ca and Mg (A, B, C, D, E) of four rice varieties in culture solution at four Al levels at 30 days after treatments. The error bar represented Mean ± SE.

4.4 Discussion

The previous study in Chapter 3 suggested that the screening for Al tolerance in upland rice varieties in nutrient solution was effectively measured by RRL at Al_{30} relative to Al_0. This chapter used three of those varieties that difference in Al tolerance based on their RRL for clearly understanding in responses for Al tolerance mechanisms in rice. The results suggested that low Al level at Al_{10} was sometimes beneficial effect on root length, root length of all rice varieties were uninhibited and some of those were higher root length than in Al_0 which supported by previous studies (Clark, 1977; Howeler and Cadavid, 1976; Jan and Pettersson, 1993). However, a longer period at 45 days did not show a positive effect in root length like as 30 days, the toxic at Al_{10} inhibited root length particularly in Al sensitive varieties, PA and KDML105. Suggesting that root tips and root elongation zones may be more suffering by Al after 30 days, cell expansion and cell division were disturbed, particularly elongation of new roots are easier suffering by Al.

After Al_{10}, the differences between varieties in tolerance to Al toxicity were revealed. Plant growth of PA was the most sensitivity to Al as compared with other upland rice varieties, which was similar to improved variety KDML105 as shown in Chapter3. Although BB and BM were classified to the different Al tolerant groups based on their RRL in Al_{30}, they produced similar dry matter and nutrient uptake at this Al toxic, and they also grew in the same rate from 30 to 45 days of the treatment. Thus, different RRL in Al_{30} between BM and BB was not reflected in differential tolerance because the shorter root length in BM appeared to have been compensated by root dry weight and presumably surface area to take up water and essential nutrients. Costa de Macedo *et al.* (1997) suggested that dry weight parameter appeared better than length parameter, two tolerant rice varieties that much more different on their root length responded similarly in shoot dry weight. These results should be noted that not only focus on root length, root or shoot weight may be a better indicator or closely agreement to nutrient uptake to produce more growth or tolerate to Al toxicity in rice.

In addition to the response on root growth, the mechanisms of efficiency in uptake and accumulation of essential nutrients in plants should be clearly understood between different Al tolerant rice varieties that lead to improve crop yield under Al stress or acidic soil. In the present study, growth of upland rice varieties in the presence of Al was found to correlate with nutrient accumulation. The depression of nutrient uptake was accentuated at higher Al levels, more so in Al sensitive than Al tolerant varieties. Rengel and Jurkic (1992) noted that the decreased uptake of essential nutrients in plants may be the result of either reduced root growth (and thus reduced root surface available for nutrient absorption) brought about by Al or direct interference of Al with nutrient accumulation in roots and with nutrient transport to shoots. Some Al tolerant varieties (e. g. rice, wheat, barley and pea) increased the pH of nutrient solution in which they grew and thus decreased the solubility and toxicity of Al by precipitation (Foy, 1984). The increase in rhizosphere pH not only decreases Al^{3+} and H^+ concentration and their toxicity but can also increase the binding of Ca^{2+} and Mg^{2+} in the root apoplasm (Marschner, 1995).

In the present study the negative effects of Al were more pronounced on the uptakes of P, Mg and Ca than other elements. The uptakes of these elements at Al_{30} were reduced 80% of the control, when averaged across four rice varieties. Inhibition of P uptake occurred due to precipitation of P with Al at the root outer surface and Al bound at cell wall in the root apoplast. After P precipitated with Al, it is not absorbed or used in the plant metabolism (Foy et al., 1978). Some reports suggested that Al tend to increased P concentration in rice roots and decreased those in shoots (Fageria *et al.*, 1988b; Jan and Pettersson, 1993). The precipitation of Al-phosphate complexes in the free space in roots may inactivate part of the available P and lead to less P being available for metabolic reactions and transport to the shoots (Jan and Pettersson, 1995). Accumulation of P in plants were reduced by Al application, but the inhibition was different depend on varieties. Phosphorus accumulation of Al tolerant BB and BM were 5-6 folds higher than Al sensitive PA and KDML105 at Al_{30}. Jemo *et al.* (2007) suggested that Al tolerant varieties not only accumulated higher P in the plants but also more adapted to soil P deficiency than Al sensitive varieties.

Generally, Al toxicity appears as induced Ca and Mg deficiency in plants. In the root apoplast, Al competed with nutrient cations, such as Ca and Mg, for binding sites on the root cortical cell walls and on the outer surface of the plasma membrane, decreasing the concentration of these nutrients due partly to Al may displace Ca^{2+} and Mg^{2+} from critical sites in the root apoplast (Marschner, 1995; Rengel, 1992), or Al may be blocking Ca^{2+} channels in the plasma membrane (Kochian, 1995). At Al_{10} or Al_{20} relative to Al_0, the genotypic variation in response to Ca and Mg uptakes were still unclear, but different between varieties was much clearer at Al_{30}. At Al_{30}, the uptakes of these elements were reduced 70% of Al tolerant and 90% of Al sensitive varieties as compared with control. Calcium accumulation in rice was agreement by previous study, suggesting that acid-soil sensitive variety was found to be depressed Ca much further at higher Al levels than in tolerant variety (Okada *et al.*, 2003).

Relative nutrient uptakes particularly in Al sensitive varieties were more serious in longer period at 45 days. At Al_{30}, Al sensitive varieties accumulated P, K, Ca and Mg less than 10% of the control, whereas the accumulation of those elements were two to three times higher in Al tolerant varieties. Aluminum tolerant varieties maintained higher dry matter under Al stress, which contributed the capacity to keep their nutrient uptakes in higher rates than in sensitive varieties for long term. Mariano and Keltjens (2005) suggested that the ability to maintain a less disturbed nutrient uptake under Al stress could be an important component in tolerance to Al.

The effect of Al sensitive KDML105 is noteworthy for an exception to this generalization. While increasing Al depressed nutrient uptake efficiency of three upland rice varieties, it had much less effect on the nutrient accumulated per g root dry weight in KDML105. This may explain the trend for nutrient uptake in KDML105 to be depressed less by increasing Al than in PA, the other Al sensitive variety, although root growth in KDML105 was slightly more sensitive to Al. However, it should also be noted that this Al tolerance in root function to take up nutrients in KDML105 was insufficient to bring it to the same level of overall tolerance as BB or BM.

Aluminum tolerant plants may be grouped according to where Al accumulated within plant tissues. One of Al tolerant mechanisms is associated with less Al in shoot, accumulation of more Al in roots (Foy, 1984). Our result suggested that partitioning and translocation of Al to the shoot may play a key role in Al tolerance in rice. While Al tolerant BB and sensitive KDML105 had about the same Al concentration in their roots, BB appeared to have transported less Al to the shoots than KDML105. The critical concentration for Al toxicity varied considerably in the literatures. It ranges from 100 mg Al kg^{-1} dry weight (Doberman and Fairhurst, 2000) to 300 mg Al kg^{-1} dry weight (FFTC, 2001) in the rice shoot at the tillering stage is generally considered toxic. The present study showed that Al sensitive KDML105 with 280 mg Al kg^{-1} in shoot in Al_{30} was very close to this toxic level, while Al tolerant BB had only half the Al concentration. Therefore, efficient retention of Al in roots is one of the characteristics of Al tolerance in rice which was also involved to internal Al tolerant mechanism (Howeler, 1991; Jan and Pettersson, 1995). By contrast, some evidences showed that Al tolerant rice varieties accumulated less Al in root than in Al sensitive varieties (Ma *et al.*, 2002; Xu *et al.*, 2004). Limited root accumulation of Al is generally attributed to a mechanism that excludes Al from the root of Al tolerant varieties (Kochian *et al.*, 2005; Ma *et al.*, 2001). However, no correlation between Al tolerance and the amount of organic acid exudation was found in rice genotypes (Ishikawa *et al.*, 2000; Ma *et al.*, 2002).

In this study, the tolerance to Al toxicity of upland rice BB, BM and PA in nutrient solution was in close agreement with their performance on acid soils in farmers' fields (see in Chapter2). In acid soil, plant growth, nutrient uptake and grain yield of Al tolerant BB and BM were similarly responses and much higher than Al sensitive PA. These results confirmed that short-term responses for Al toxicity in nutrient solution could predict final crop yield in acid soils.

The description of rice in tolerance to Al should be associated with ability to grow more roots that are able to take up more nutrients in the presence of Al. Aluminum tolerant variety may also retain more Al in the roots, and so prevent Al to accumulate in the shoots. Although, relative of root and shoot dry weight is a better parameter in nutrient uptakes than RRL, the screening for Al tolerance in large germplasm including segregated populations for rice breeding can be carried out by RRL because of easy measurement and non-destructive. In this case, upland rice varieties BB and BM were similar in tolerance to Al in nutrient solution as well as in acid soils. However, BB may be more useful to farmers in Tee Cha village who must grow their rice on soil with extreme acidity, and also as a donor of Al tolerance trait in rice breeding than BM. Because the longer root of BB may be a better characteristic for rice adapted to drought stress and infertile soils to absorb water and essential nutrients in the deeper soils, particularly in upland rice areas.