Growth Response and Nutrient Concentrations of Sago Palm under Aluminum Stress

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Abstract

The growth response, nutrient concentrations in different plant parts and some physiological features under Al treatment were investigated to evaluate the Al resistance of sago palm under acidic conditions. Seedlings at the 7th leaf stage were used for the treatment of 0, 10, 20, 100 and 200 ppm Al in culture solution at pH 3.6 for 4.5 months. The study revealed that the growth of sago palm increased at low Al concentrations in the growth media under acidic conditions. This result might be attributed to a positive effect on the uptake of major nutrients, such as P, N and Ca^{2+}. Nevertheless, the total dry weight and leaflet area significantly decreased under the 200 ppm Al treatment. This result might be associated with a significant decrease of the Ca^{2+} and Mg^{2+} uptake. The critical value at which the growth of sago palm was inhibited is considered to be approximately 200 ppm Al in the growth media. In addition, sago palm maintains a low Al^{3+} concentration in the leaflets by storing Al^{3+} mainly in the roots, especially in the lateral roots, and the Al^{3+} concentration in the whole plant did not increase significantly even under the 200 ppm Al treatment. We conclude that Al resistance of sago palm might be due to the avoidance mechanism via the Al exclusion ability under acidic condition.

Keywords: acidic condition; aluminum resistance; nutrient accumulation; physiological characteristic; sago palm.

1. Introduction

Aluminum (Al) toxicity is considered to be a serious factor limiting crop production in acid soil. The problem in acidic areas is generally severe when soil pH drops below 5 [1]. According to Kochian et al. [2], Al^{3+}, the toxic trivalent cation, is the most abundant mononuclear the most important effects of Al on plant growth is the inhibition of nutrient uptake Al ion causing rhizotoxicity in plants and is generally believed to be the most toxic form of the metal. The most common symptom of Al toxicity is stunting of the root system with lateral root shortening and root tips turning brown [3]. Root growth inhibition by Al toxicity has been found in rice [4], maize [5] and wheat [6]. However, one of [7]. An inhibition of the nutrient uptake caused by Al has been reported for several

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essential elements including Ca, Mg, K [8] and Cu [9]. The uptake of these elements was affected directly through antagonistic inhibition or precipitation and indirectly through phenomena such as membrane function disorders [10]. In addition, common responses of shoots to Al include a reduction of stomatal aperture, a decrease in photosynthetic activity leading to chlorosis and necrosis of leaves, a decrease in leaf numbers and a decrease in shoot biomass [11]. However, there are several reports that some plant species have adapted and grow well under acid soil condition with no apparent symptoms of the Al toxicity. It might be that Al can stimulate plant growth or ion uptake [12, 13].

Sago palm, a starch producing plant, is one of the very few crops that can grow in a natural deep peat swamp with minimal drainage. By cultivating of sago palm, it is possible to convert vast areas of peat swamp into productive agricultural land without sophisticated and expensive soil modification such as drainage or compaction [14]. However, deep peat soils in swampy areas are usually characterized by low pH values, a deficiency in mineral elements and a high rate of exchangeable Al [15]. Foy and Fleming [16] suggest that there is a good correlation between Al-resistant plants in nutrient solution and resistance to low pH conditions. It is therefore assumed that sago palm may be resistant to acidic pH and Al toxicity. However, few studies have examined the Al-induced changes on the growth responses of sago palm. The objective of the present study was to investigate the effect of Al concentration on growth and nutrient absorption as well as some physiological characteristics of sago palm, to elucidate Al resistance under acidic conditions.

2. Materials and methods

2.1 Plant materials and Al treatment

Sago palm fruits were collected in the swampy areas of Rattapum, Songkhla, Thailand. Fertilized and well-developed fruits were selected and treated physically to remove seed coat tissues. The cleaned seeds were placed in a plastic tray filled with tap water and then kept in a dark room at 30ºC in Thammasat University, Patumtanee, Thailand, as reported by Ehara et al. [17]. The germinated seeds were brought to Mie, Japan and transplanted to a 1/5000a Wagner pot filled with vermiculite and Kimura B culture solution containing (μM) 36.5 $(NH_4)_2SO_4$, 9.1 K_2SO_4, 54.7 $MgSO_4$, 18.3 KNO_3, 36.5 Ca $(NO_3)_2$, 18.2 KH_2PO_4 and 3.9 FeO_3 [18]. The culture solution was adjusted to an initial pH of 5.5 using 1.0N HCl before being transferred into pots, as reported by Ehara et al. [19]. The pots were placed in a greenhouse under natural sunlight and maintained at over 15ºC, even at night, at Mie University. The culture solution was replenished daily in an amount equal to that consumed.

Three seedlings at the 7th leaf stage, with the 8th leaf emerging and the mean plant length of all plant materials at 39 cm, were cultured in Kimura B culture solution without Al (hereafter referred to as control) or containing different levels of $AlCl_3 \cdot 6H_2O$ corresponding to 10, 20, 100 and 200 ppm Al for 4.5 months. The pH of the culture solution was adjusted to 3.6 using 1N HCl as required. The pots were placed in the same greenhouse under natural sunlight. An air pump was connected to the pots to provide air to the roots. The culture solution was replenished daily in an amount equal to that consumed, and the entire culture solution was renewed twice weekly to avoid accumulation of excess Al.

2.2 Photosynthetic rate, transpiration rate and stomatal conductance

Eighteen weeks after the start of culture, the leaflets of the most active leaves or the 4th leaf position from the top were selected for measurement of the net photosynthetic rate, transpiration rate and stomatal conductance using a portable

active radiation (PAR) of 800-1,000 μmol m^{-2} s^{-1}. As a light source, a halogen lamp was used. The appropriate PAR was obtained by changing the distance between the projector and the leaves.

2.3 Chlorophyll content in the leaflets

After harvesting, the chlorophyll content of the leaflets at each leaf position was measured using the method of Mackinney [20]. An area of 0.25 cm^2 was punched out and soaked in 10 ml of 80% (v/v) acetone to extract chlorophyll. The chlorophyll content was expressed as the content per unit surface area.

2.4 Sampling and nutrient concentrations in plants

The treated plants were sampled and washed thoroughly in distilled water. The plants were separated into three parts: leaflets, petioles including rachis and roots. The fresh weight of each part was recorded. The leaflet areas were measured using an automatic area meter (AAM-9, Hayashi-Denko, Japan). The roots were divided into lateral roots and adventitious roots. Adventitious and lateral roots were classified according to the method of Nitta et al. [21] as follows. The adventitious roots were 6 to 11 mm in diameter and lateral roots were less than 6 mm in diameter. The adventitious roots were divided into the stele and the cortex (epidermis, exodermis, suberized sclerenchyma cell).

All samples were dried in an oven at 80ºC for 72 hours to measure the dry weight and then ground into powder in order to analyze the nutrient concentrations. The ground samples were reduced to ash in a furnace and extracted with 1.0N HNO_3, and the K^+, Ca^{2+} and Mg^{2+} concentrations were determined using a high-performance liquid chromatograph (HPLC) with a conductivity detector (IC-C3, CDD-6A, Shimadzu, Japan). The concentration of P was evaluated by atomic absorption spectrophotometry. The total N concentration was determined by the semi-micro Kjeldahl method while the Al^{3+} concentration was determined calorimetrically by the aluminon method.

2.5 Statistical analysis

Data were analyzed using NCSS 2001 (Number Cruncher Statistical Systems). The effects of treatments were determined by one-way ANOVA (analysis of variance), and the differences among the mean values of treatment were compared using the Tukey-Kramer test with significance determined at the 5% level of probability.

3. Results and discussion

3.1 Plant growth

Table 1 shows the number of emerged leaves, live leaves and dead leaves throughout the Al treatments. The new leaves emerged even at the higher levels of Al concentration in the growth media. However, the number of emerged leaves in the 200 ppm Al treatment (5 leaves) was significantly lower than that in all other treatments (7-8 leaves). The number of live leaves during the experiment was 11, 10, 8, 8 and 6 under the control, 10 ppm Al, 20 ppm Al, 100 ppm Al and 200 ppm Al treatments, respectively. A significant difference in the number of live leaves was also observed in the 200 ppm Al treatment compared with the control. Contrarily, the number of dead leaves was significantly increased with the rise of the Al concentration in the media. It thus appears that the delay of new leaf emergence and the acceleration of leaf senescence of sago palm occurred at the higher Al treatments.

The effects of the Al concentration on the increment of plant length, total leaflet area and dry weight of sago palm grown under the Al treatments for 4.5 months are shown in Table 2. There were no significant differences in the increment of plant length,

Table 1. The number of emerged, live and dead leaves under different Al treatments.

Al concentration (ppm)	Emerged leaves	Live leaves	Dead leaves
Control	7.0 ± 0.0 a	10.7 ± 2.1 a	3.0 ± 0.6 b
10	7.7 ± 0.6 a	10.0 ± 1.0 a	3.7 ± 0.6.b
20	7.0 ± 0.0 a	8.3 ± 2.3 ab	4.7 ± 0.6 ab
100	6.7 ± 0.6 a	7.7 ± 0.6 ab	5.7 ± 0.6 a
200	5.3 ± 0.6 b	6.0 ± 0.0 b	6.0 ± 0.0 a

Mean ± SD followed by different letters within a column are significantly different at the 0.05 level by the Tukey-Kramer test (n=3).

total leaflet area and dry weight of all plant parts among the Al treatments even at the 100 ppm Al in the culture solution. However, on all the measurements, there were significant differences between the 200 ppm Al treatment and the control. According to Zhang et al. [22], Al toxicity was identified as a critical value of the Al concentration for crop management. The critical value of the Al concentration for plants grown in hydroponic systems were evaluated for many plant species, such as 1.5 mg l^{-1} Al for oat (*Avena sativa*), 0.8 mg l^{-1} Al for barley (*Hordeum vulgare*) and 8.9 mg l^{-1} Al for maize (*Zea mays*) [23]. In the current experiment, the adventitious and lateral roots of sago palm seedlings under the 200 ppm Al treatment were stunted, brownish and thick, and the root dry weight was 58% smaller than that in the control, representing a significant difference. Consequently, the critical value to inhibit the growth of sago palm was considered to be approximately 200 ppm Al in the growth media. According to Jong and Flach [14], the Al concentration in the peat soil of sago palm cultivation in Sarawak, Malaysia, was in the range of 5 to 14 ppm Al. In addition, from our field study of the sago palm grown at different levels of soil pH in Southern, Thailand, the Al concentration in these soils was in the range of 4.5 to 145 ppm Al [24].

In fact, it is well known that aluminum toxicity had many effects on the growth of various plant species [25-27].

However, the current experiment showed a stimulus effect at lower Al concentration on the sago palm growth. In the 10 ppm Al treatment, the total leaflet area and total dry weight tended to be higher than that in the control although the difference in these growth characteristics was not significant between the control and the 10 ppm Al treatment. A similar tendency was found in the tea plant [28] and some native plants [13]. Baker and Walker [29] suggest that the metal resistant plants could demonstrate an increased need for the metals to which they are resistant. As a result, resistant plants grow less well in a growth media with low ion levels.

3.2 Physiological characteristics

The chlorophyll content per unit leaflet area at almost all leaf positions slightly decreased with higher levels of Al concentration in the growth media. However, significant differences between treatments were found only at the higher leaf positions (Fig. 1). In addition, the differences in the mean values of the chlorophyll content per unit leaflet area among the Al treatments were small. This outcome corresponds to observations in other plant species such as a certain type of soybean [30] and *Quercus glauca* Thumb [31].

Table 3 shows the net photosynthetic rate, transpiration rate and stomatal conductance of the 4th leaf position from the top, which was considered

to be the most active physiologically based on leaf development and chlorophyll content. The net photosynthetic rate and transpiration rate decreased with the rise of Al concentrations in the growth media. The net photosynthetic rate in 200 ppm Al treatment was 33% smaller than that in the control significantly at the 0.05 level. These results indicate that high Al concentration in the culture solution directly inhibits the photosynthetic process. The difference in the stomatal conductance between the control and the 10 ppm Al treatment was not significant, but thereafter the stomatal conductance significantly decreased with further rises of Al concentrations in the growth media. At higher Al concentrations, the decrease in the net photosynthetic rate was attributed to a decrease of stomatal conductance (Table 3), inhibition in photochemical capacity (data not shown), reduction of the chlorophyll content (Fig. 1) or a combination of these factors.

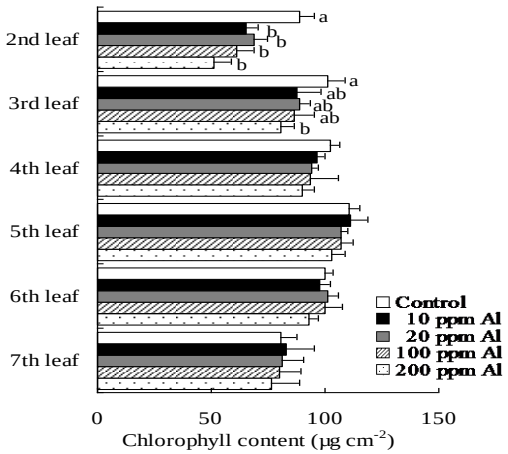

Fig. 1. Chlorophyll content per unit leaflet area at different leaf positions under different Al treatments. Horizontal bars represent the standard deviation (n=3). Different letters indicate a significant difference among the Al treatments at the 0.05 level by the Tukey-Kramer test.

Fig. 2 shows the net photosynthetic rate expressed on a chlorophyll content basis under different Al treatments. Although the net photosynthetic rate significantly decreased and the chlorophyll content slightly decreased with the rise of Al concentrations in the growth media, there was no significant decrease in the net photosynthesis rate (expressed on a chlorophyll content basis) between the control and other Al treatments up to the 100 ppm Al level. These results indicate that sago palm can maintain CO_2 fixation in chlorophyll up to 100 ppm Al, while chlorophyll production is depressed at higher levels of Al. In the 200 ppm Al treatment, however, the net photosynthetic rate expressed on a chlorophyll content basis was significant lower than that in the control. These results may account for the observation that the decrease in the net photosynthetic rate was larger than the decrease in the chlorophyll content. CO_2 fixation in chlorophyll was affected by the 200 ppm Al treatment more than chlorophyll production.

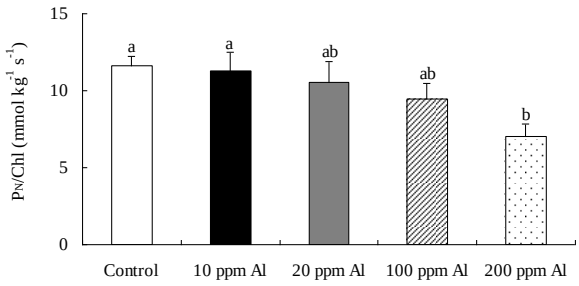

Fig. 2. Photosynthetic rate per chlorophyll content (P_N/Chl) of the 4th leaf position from the top under different Al treatments. Vertical bars represent the standard deviation (n=3). Different letters indicate a significant difference among the Al treatments at the 0.05 level by the Tukey-Kramer test.

Table 2. Effect of Al concentration on increment of plant length, leaflet area per plant and dry weight.

Al concentration (ppm)	Increment of plant length (cm)	Leaflet area per plant (cm^2)	Dry weight per plant (g)			
			Leaflet	Petiole	Root	Whole
Control	38.2 ± 4.0 ab	2,418.8 ± 228.0 ab	17.3 ± 5.9 ab	20.1 ± 4.9 ab	9.0 ± 5.1 ab	46.4 ± 15.8 ab
10	42.1 ± 3.1 a	3,008.6 ± 222.8 a	23.0 ± 1.3 a	27.1 ± 2.5 a	13.6 ± 0.8 a	63.7 ± 4.3 a
20	37.5 ± 7.6 ab	2,092.0 ± 206.3 b	15.7 ± 6.9 bc	16.3 ± 6.1 b	6.7 ± 1.9 b	38.7 ± 14.8 bc
100	37.2 ± 5.4 ab	2,151.7 ± 150.5 b	15.1 ± 0.5 bc	18.0 ± 2.9 b	6.6 ± 0.9 b	39.7 ± 5.3 bc
200	26.3 ± 4.9 b	1,153.4 ± 163.8 c	8.0 ± 1.7 c	11.2 ± 2.7 c	3.8 ± 1.7 c	22.9 ± 6.0 c

Mean ± SD followed by different letters within a column are significantly different at the 0.05 level by the Tukey-Kramer test (n=3).

3.3 Nutrient concentrations in different plant parts

3.3.1 Leaflets, petioles, roots and whole plants

The concentrations of Al^{3+}, N, P, K^{+}, Ca^{2+} and Mg^{2+} in the leaflets, petioles, roots and whole plants under the Al treatments are shown in Table 4. The Al^{3+} concentration in all plant parts increased with the rise of Al concentrations. The Al^{3+} concentration in the leaflets was lower than that in the petioles, and tended to be significantly higher in the roots than the top parts (leaflets and petiole) across all Al treatments. Our current results in sago palm strongly support the assumption that Al^{3+} has a high binding ability with cellular components of the root, and usually shows little translocation to the upper parts of the plant [32]. Although, the difference of Al^{3+} concentrations among the leaf positions of sago palm under the Al treatments was not distinct, the Al^{3+} concentrations in the petioles tended to be higher at lower leaf positions (old leaves) than at higher leaf positions (new leaves) in all the Al treatments. This result suggests that the Al translocation from the lower leaf positions to the higher leaf positions was restricted (Fig. 3).

In general, there are two main distinct classes of Al-resistant mechanisms. One class of mechanisms allows the plant to tolerate the Al accumulation in the root and shoot symplasm. The other class operates on the ability to exclude Al from the root apex, which is often related to the Al-triggered exudation of organic acids [4]. Chenery [33] classified thousands of the plant species according to their Al concentration in plant tissues, as Al-accumulators (≥ 1,000 mg Al kg^{-1} dry weight) or Al excluders (< 1,000 mg Al kg^{-1} dry weight). Most plants contain no more than 300 mg Al kg^{-1} dry weight, whereas plant species known as the Al accumulators may contain more than 10 times this Al level without injury. For example, the Al content in the tea plants that are well-known as typical Al accumulators can reach as high as 30,000 mg kg^{-1} dry weight in old leaves [34]. In the current study, the range of Al^{3+} concentration in whole plants was from 254 to 420 mg kg^{-1} dry weight (9.4 to 15.6 μmol g^{-1} dry weight) even under the 200 ppm Al treatment (Table 4). Considering the result of the Al^{3+} concentration in the current experiment, sago palm is considered to have the Al exclusion ability under acidic conditions. However, further studies on the mechanism of Al resistance under natural adverse condition should be carried out.

The total N and P concentrations in the leaflets and petioles under the 10 ppm Al treatment were higher than those in the other Al treatments. In addition, the N concentration in the whole plants tended to increase under Al treatments up to 100 ppm Al and decreased under the higher 200 ppm Al treatment, compared with the control. The P concentration tended to increase under the Al treatments up to the 10 ppm Al treatment, but thereafter decreased (Table 4). These results indicate that Al was unlikely to have induced the P and N deficiency in plant tissues but the uptake of these nutrients was higher under a lower Al condition. Such evidence was also found in sorghum [35], rice [36], and some native plants [13].

The accumulation of N concentration in the leaflets was significantly higher than that in the petioles and roots. A tendency toward a higher N concentration in leaflets than in other parts is found in various plant species, such as winged and velvet beans [37]. However, there were no distinctive differences in the N concentration in whole plants between treatments, with all values in the range 12.6 to 14.8 mg g^{-1}. It appears that the Al treatments did not significantly depress the absorption and translocation of N in plant tissues of sago palm even under the 200 ppm Al treatment (Table 4).

The difference in the P accumulation among the plant parts was clearly exposed in the higher Al treatments. Effects of the higher Al treatment (200 ppm Al) on the P concentration in plant tissues was not observed in the leaflets, in contrast to the case of the petioles and roots, where P concentrations were significantly decreased by the higher Al treatment. These results may attribute to the lower P concentration in the whole plants under the 200 ppm Al treatment. It is likely that sago palm could maintain the accumulation and translocation of P to the leaflets even under the 200 ppm Al treatment, although the P absorption in the petioles and roots was rather restricted (Table 4).

The K^+ concentration in the roots and petioles tended to be higher than that in the leaflets in all the Al treatments (Table 4). This tendency was also observed in the winged and velvet beans reported by Anugroho et al. [37]. The Ca^{2+} concentration in different plant parts under each Al treatment tended to be stored in the petioles rather than in the leaflets and roots. In addition, the Ca^{2+} concentration in the leaflets, petioles and whole plants significantly decreased under the higher Al treatment, compared with the control. However, no significant difference was observed in the Ca^{2+} concentration in the roots between the control and other Al treatments. The Mg^{2+} concentration was higher in the roots than that in other parts, such as the leaflets and petioles. It seems that the effect of the Al treatments on the Mg^{2+} concentration in plant tissues was similar to that observed in the Ca^{2+} concentration in all plant parts, where a significant difference was observed in the 200 ppm Al-treated plants (Table 4). Considering the current results, decreases in the Ca^{2+} and Mg^{2+} concentrations in all plant parts seem to be a result of the increase of the Al concentrations in the growth media.

One interesting feature of these results is that Al^{3+} inhibited Ca^{2+} and Mg^{2+} absorption more than K^+ absorption in all plant parts under the higher Al treatment. Similar results have been reported for barley, in which Al^{3+} inhibited divalent cation influxes more than those of monovalent cations [38]. According to Huang et al. [39], the fact that Al^{3+} induced the inhibition of the ion fluxes, particularly Ca^{2+}, may play an important role in the mechanisms of $A1^{3+}$ toxicity in higher plants. A possible mechanism to explain the differential effects on cations is that the Al^{3+} toxicity is ameliorated by cations in the following order, H^+ approximately = $C^{3+} > C^{2+} > C^+$, and the

amelioration is due to their binding to or screening the negative charges on the plasma membrane [40].

Table 3. Net photosynthetic rate, transpiration rate and stomatal conductance under different Al treatments.

Al concentration (ppm)	Net photosynthetic rate (μmol m^{-2} s^{-1})	Transpiration rate (mmol m^{-2} s^{-1})	Stomatal conductance (mol m^{-2} s^{-1})
Control	10.222 ± 0.295 a	2.205 ± 0.018 a	0.111 ± 0.004 a
10	9.106 ± 0.182 b	1.783 ± 0.012 b	0.087 ± 0.017 ab
20	8.925 ± 0.435 b	1.675 ± 0.016 b	0.071 ± 0.000 b
100	7.932 ± 0.264 c	1.547 ± 0.029 c	0.063 ± 0.000 c
200	6.858 ± 0.057 d	1.108 ± 0.016 d	0.033 ± 0.000 d

Mean ± SD followed by different letters within a column are significantly different at the 0.05 level by the Tukey-Kramer test (n=3).

3.3.2 Different parts of roots

The Al^{3+}, N, P, K^+, Ca^{2+} and Mg^{2+} concentrations in the roots were measured in three parts: adventitious roots divided into stele and cortex, and lateral roots (Fig. 4). The Al^{3+} concentration in all root parts tended to increase with the rise of Al concentrations. However, a significant difference in the Al^{3+} concentration in the root parts was observed merely in the lateral roots. In addition, the Al^{3+} accumulation was significantly higher in the lateral roots than that in the stele or cortex of the adventitious roots in all the Al treatments. This result may be attributed to the expansion of the lateral roots rather than the adventitious roots. In the adventitious roots, the Al^{3+} concentration tended to be lower in the stele than that in the cortex across all Al treatments. The difference in the Al^{3+} concentration between the stele and cortex of the adventitious roots is clearly exposed in the highest Al treatment. It is likely that the cortex layer (including the epidermis, exodermis and suberized sclerenchyma cells) of the sago palm root in the current experiment has some anatomical function for preventing excess influx of Al^{3+} ions from the cortex into the stele. This was also observed in the roots of sago palm and its related species for preventing excess Na^+ influx under salt stress [41].

The P concentration in each part of the roots increased in the 10 ppm Al treatment and decreased with further increases of Al concentration in the growth media. This is a tendency similar to that observed in the leaves and petioles (Fig. 4). However, there was no significant difference in the P concentration in any root parts compared with the control. Generally, Al plays an important role in the absorption and utilization of P [12]. According to Foy and Fleming [16], Al and P in the solution easily precipitate on the root surface or inside the root, and a high Al concentration may induce P deficiency as the precipitate of $AlPO_4$ on the root surface. They also suggest that both the uptake and translocation of P from the root to the shoot can be negatively affected by Al, an effect that was also observed in rice [36] and barley [42]. In the current experiment, the increase of the P concentration in the roots of the 10 ppm Al-treated plants may result

in the binding of P and Al. Sago palm that showed growth enhancement by lower Al concentration may contain some physiological mechanisms related to its greater ability to use the precipitated P. The mechanisms to detoxify Al both externally and internally in sago palm roots under Al stress should be examined in further studies.

The N concentration in adventitious root parts decreased with 10 ppm Al treatment and increased with further rises of Al concentration although there was no significant difference in the N concentration in any root parts compared with the control (Fig. 4). According to Nichol et al. [38], Al inhibits the influx of NH_4^+ but enhances the influx of NO_3^-, an observation that is consistent with a mechanism whereby Al binds to the plasma membrane phospholipids and forms a positively charged layer that influences the ion movement to the binding sites of the transport proteins. A positive charge layer will retard the movement of cations and increase the movement of anions in proportion to the charge carried by these ions. These effects may inhibit the influx of cations but may stimulate the influx of anions. Sago palm may uptake NO_3^- in preference to NH_4^+ from the culture solution under Al stress to maintain the N concentration in the whole plants.

The K^+ concentration in different root parts decreased under the 10 ppm Al treatment and increased with further rises of Al concentration. Moreover, the difference in the K^+ accumulation among the Al treatments was clearly exposed in the stele of the adventitious roots. However, there was no significant difference in the K^+ concentration in any root parts compared with the control. This result suggests that the K uptake is independent of the increase of Al concentrations in the growth media (Fig. 4). In the case of the Ca^{2+} and Mg^{2+} concentrations, no change in ion concentrations in the stele of the adventitious roots was observed, while the concentrations in the cortex of the adventitious roots and the lateral roots significantly decreased in the 200 ppm Al treatment (Fig. 4). A decrease of Ca^{2+} and Mg^{2+} concentrations in the roots was also observed in upland rice [43] and *Betula pendula* Roth. [44]. According to Marschner [45], Al may inhibit the Ca uptake by blocking the Ca^{2+} channels in the plasma membrane and inhibit the uptake of Mg^{2+} by blocking the binding sites of the transport proteins. Akeson and Munns [46] reported that Al has a more than 500-fold greater affinity for the choline head of phosphatidylcholine, a-lipid constituent of the plasma membrane, than other cations such as Ca^{2+}. For this reason, Al can displace other cations that may form the bridges between the phospholipid head groups of the membrane bilayer. It has long been accepted that Al also directly blocks the ion transport proteins on the plasma membrane of the root cells [39]. From the observable roots under the Al treatments, the root system under the 200 ppm Al treatment was obviously damaged and apparently differentiated from the other Al treatments. This result may account for the decrease of the Ca^{2+} and Mg^{2+} concentrations in the lateral roots and the cortex of the adventitious roots.

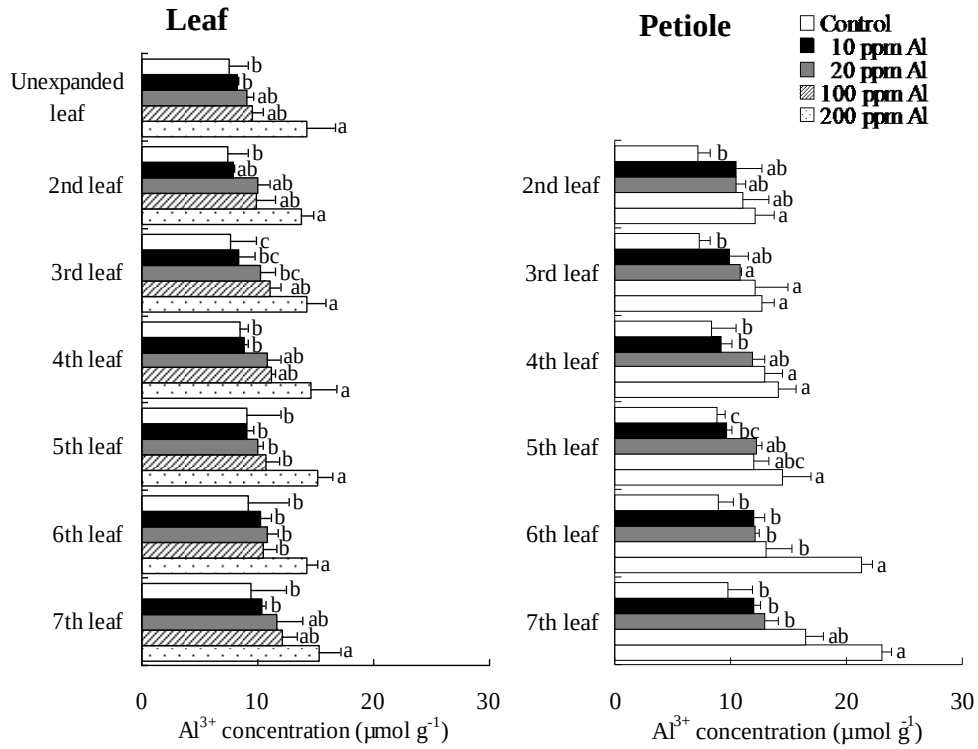

Fig. 3. Al^{3+} concentration in leaflets and petioles at different leaf positions under different Al treatments. Horizontal bars represent the standard deviation (n=3). Different letters indicate a significant difference among the Al treatments at the 0.05 level by the Tukey-Kramer test.

Table 4. Nutrient concentrations in leaflets, petioles, roots and whole plants under different Al treatments.

Nutrient concentration	Plant part	Al concentration (ppm)				
		Control	10	20	100	200
Al^{3+} ($\mu mol\ g^{-1}$)	Leaflet	8.7 ± 4.2 cB	9.5 ± 3.8 bcB	10.3 ± 0.3 bB	10.2 ± 0.2 bcB	14.3 ± 0.9 aB
	Petiole	8.9 ± 0.3 bB	10.7 ± 0.6 abB	11.6 ± 3.9 abB	13.1 ± 2.0 abB	15.1 ± 1.3 aB
	Root	12.1 ± 1.0 cA	15.1 ± 1.7 bcA	16.3 ± 1.4 abA	17.7 ± 2.3 abA	19.8 ± 0.7 aA
	Whole	9.4 ± 1.6 b	11.2 ± 1.9 b	11.9 ± 1.6 ab	12.7 ± 1.0 ab	15.6 ± 1.1 a
N ($mg\ g^{-1}$)	Leaflet	20.9 ± 2.5 aA	24.6 ± 0.8 aA	23.0 ± 1.4 aA	22.6 ± 2.0 aA	21.0 ± 6.4 aA
	Petiole	8.8 ± 0.6 aB	9.1 ± 1.8 aB	8.7 ± 0.4 aB	7.7 ± 1.5 aB	6.3 ± 0.6 aB
	Root	10.8 ± 2.5 aB	9.9 ± 0.4 aB	9.8 ± 0.8 aB	10.2 ± 2.1 aB	11.3 ± 1.5 aB
	Whole	13.6 ± 1.2 a	14.8 ± 1.1 a	14.6 ± 0.6 a	14.1 ± 1.9 a	12.6 ± 2.8 a
P ($mg\ g^{-1}$)	Leaflet	1.8 ± 0.4 aA	1.9 ± 0.2 aA	1.8 ± 0.3 aAB	1.7 ± 0.1 aAB	1.6 ± 0.1 aAB
	Petiole	2.2 ± 0.3 aA	2.3 ± 0.6 aA	2.2 ± 0.2 aA	1.9 ± 0.4 aA	1.4 ± 0.3 aA
	Root	1.6 ± 0.7 abA	1.8 ± 0.3 aA	1.4 ± 0.3 abB	1.1 ± 0.3 bcB	0.9 ± 0.3 cB
	Whole	1.9 ± 0.2 ab	2.0 ± 0.4 a	1.9 ± 0.1 ab	1.7 ± 0.3 ab	1.4 ± 0.2 b
K^{+} ($\mu mol\ g^{-1}$)	Leaflet	93.5 ± 7.4 aB	92.6 ± 7.6 aB	97.8 ± 4.8 aB	93.4 ± 13.5 aB	98.5 ± 6.3 aB
	Petiole	219.6 ± 8.4 bA	199.5 ± 39.9 bA	215.4 ± 5.2 bA	220.0 ± 27.5 bA	250.7 ± 43.7 aA
	Root	253.4 ± 23.8 aA	209.3 ± 16.5 bA	226.7 ± 1.7 abA	250.7 ± 13.3 aA	267.0 ± 11.3 aA
	Whole	178.2 ± 4.2 b	162.8 ± 21.6 b	170.7 ± 3.1 b	173.9 ± 13.4 b	200.0 ± 23.1 a
Ca^{2+} ($\mu mol\ g^{-1}$)	Leaflet	42.4 ± 7.7 aB	45.3 ± 6.0 aB	42.6 ± 5.7 aB	32.8 ± 2.1 abB	25.5 ± 3.3 bA
	Petiole	55.7 ± 13.6 abA	64.4 ± 8.2 aA	65.2 ± 7.2 aA	47.7 ± 5.9 bA	28.9 ± 9.3 cA
	Root	28.8 ± 5.3 abB	36.1 ± 0.8 aB	36.8 ± 6.9 aB	30.5 ± 3.3 abB	21.7 ± 2.0 bA
	Whole	45.7 ± 9.3 ab	51.4 ± 5.5 a	51.3 ± 3.4 a	39.2 ± 2.8 b	26.7 ± 5.7 c
Mg^{2+} ($\mu mol\ g^{-1}$)	Leaflet	41.1 ± 4.3 aB	40.3 ± 5.9 aB	40.9 ± 2.4 aB	34.8 ± 2.9 abC	29.0 ± 3.4 bA
	Petiole	56.7 ± 2.6 abAB	60.4 ± 1.8 aA	63.0 ± 5.3 aA	46.6 ± 5.3 bB	29.5 ± 7.2 cA
	Root	63.9 ± 12.4 aA	65.1 ± 7.0 aA	67.4 ± 9.2 aA	66.8 ± 4.4 aA	36.2 ± 2.5 bA
	Whole	52.1 ± 5.2 ab	54.1 ± 3.8 a	55.1 ± 3.6 a	45.5 ± 4.1 b	30.5 ± 4.3 c

Means followed by different letters are significantly different at the 0.05 level by the Tukey-Kramer test (n=3). Lowercase letters indicate a comparison among the Al treatments in each plant part. Capital letters indicate a comparison among the plant parts within each Al treatment.

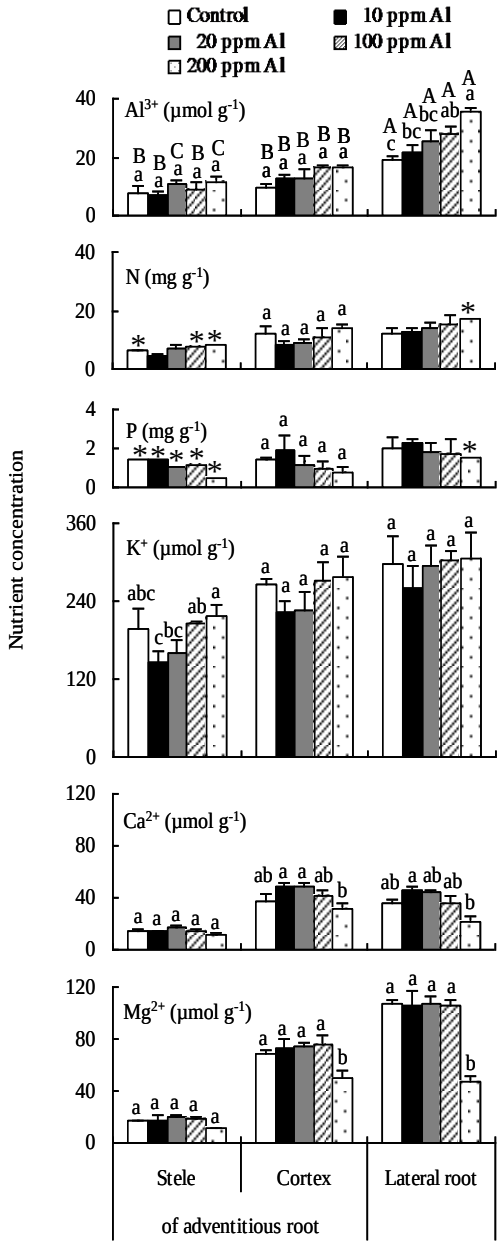

Fig. 4. Nutrient concentrations in different parts of roots (stele and cortex of adventitious roots and lateral roots) under different Al treatments. Vertical bars represent the standard deviation (n=3). Asterisks indicated the data from two plant samples (n=2). Different letters indicate a significant difference among treatments at the 0.05 level by the Tukey-Kramer test. Lowercase letters indicate a comparison among the Al treatments in each plant part. Capital letters indicate a comparison among the plant parts within each Al treatment.

4. Conclusion

The growth response of sago palm to Al stress under low pH conditions can be summarized as follows: 1) new leaf emergence is delayed and acceleration of leaf senescence occurs, 2) the photosynthetic rate is depressed although the difference in the chlorophyll content under Al stress was not significant, 3) the uptake of Ca^{2+} and Mg^{2+} is restricted while the effect of Al on the accumulation of N, P and K^{+} is negligible. Furthermore, sago palm is able to prevent the excess influx of Al^{3+} ion from the cortex to the stele in the roots, in order to maintain a low Al concentration in the top parts, such as the leaflets, even under the highest Al concentration in the growth media. It is, therefore, considered that Al resistance of sago palm might be due to the avoidance mechanism via the Al exclusion ability under acidic conditions.

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