

# Effects of silicon on aluminum toxicity in upland rice plants

Lucas Barbosa de Freitas · Dirceu Maximino Fernandes ·  
Suelen Cristina Mendonça Maia · Adalton Mazetti Fernandes

Received: 17 April 2017 / Accepted: 21 August 2017 / Published online: 29 August 2017  
© Springer International Publishing AG 2017

## Abstract

**Aims** This study aimed to determine the capacity of Si to mitigate Al toxicity in upland rice plants (*Oryza sativa* L.) by evaluating plant growth and the Si and Al uptake kinetics.

**Methods** Plants were grown for 40 days, after which the Si and Al uptake kinetics ( $C_{min}$ ,  $K_m$  and  $I_{max}$ ) were analyzed. Then, the shoots and roots were separated, and the dry matter, root morphology and Si and Al concentration and accumulation in the plant were evaluated.

**Results** Aluminum decreased plant growth and the Si uptake capacity by decreasing the root growth and Si transport system efficiency in the upland rice roots ( $>$

$K_m$  and  $> C_{min}$ ). Silicon mitigated Al toxicity in the upland rice plants by decreasing Al transport to the plant shoots, although it did not reduce the Al uptake rate ( $I_{max}$ ). Si treatment increased the growth of upland rice plant shoots grown in the presence of Al without influencing the root growth. The alleviation of Al toxicity by Si is more evident in the susceptible upland rice cultivar Maravilha.

**Conclusions** Silicon mitigated Al toxicity in the upland rice plants by decreasing Al transport to the plant shoots but did not reduce the Al uptake rate by roots.

**Keywords** Uptake kinetics · Root morphology · Silicon alleviation · Silicon uptake

## Abbreviations

C	Cultivar
$C_{min}$	External concentration when net uptake is zero
DM	Dry matter
$K_m$	Michaelis-Menten constant
$I_{max}$	maximal transport rate

## Introduction

Aluminum (Al) is toxic to plant growth and becomes a problem in acid soils; it is also a limiting factor for agricultural production. Al directly affects plant roots by decreasing and/or inhibiting root cell division (Clarkson 1965; Morimura and Matsumoto 1978), interfering with mitosis (Budikova and Durcekova 2004;

---

L. B. de Freitas (✉)  
Faculdade La Salle, Universitária Avenue, 1000 W, Lucas do Rio Verde 78455-000, Brazil  
e-mail: lucasbarbosaf@yahoo.com.br

D. M. Fernandes  
College of Agricultural Sciences, Department of Soil and Environmental Resources, São Paulo State University (UNESP), José Barbosa de Barros Street, 1780, Botucatu 18610-307, Brazil

S. C. M. Maia  
Advanced Campus Cristalina, Goiano Federal Institute (IF Goiano), Araguaia Street, P.O. Box 166, Cristalina 73850-000, Brazil

A. M. Fernandes  
Center for Tropical Roots and Starches, São Paulo State University (UNESP), José Barbosa de Barros Street, 1780, Botucatu 18610-307, Brazil

Doncheva et al. 2005; Li et al. 2008; Yi et al. 2010) and with cell elongation, and decreasing cell wall plasticity and elasticity (Tabuchi and Matsumoto 2001; Ma et al. 2004; Zheng and Yang 2005; Horst et al. 2007). In addition, Al has negative effects on the plasma membrane, cytoskeleton, cell nucleus and apoplast (Horst et al. 2007; Yang et al. 2008; Khan et al. 2009; Panda et al. 2009; Rangel et al. 2009; Yang et al. 2011) and alters cellular calcium homeostasis (Huang et al. 1996; Rengel and Zhang 2003).

Aluminum-induced alterations to the plant cell cause plant roots grown under conditions of Al toxicity to become atrophied and brittle, experience fine-scale changes, and present increased cell wall rigidity and thickness, and changes in membrane transport proteins are also observed (Meharg 1993; Kochian et al. 2004; Vitorello et al. 2005; Zobel et al. 2007; Kopittke et al. 2008). Therefore, a root developed in the presence of Al experiences reduced growth and presents less efficient water and nutrient uptake, especially in the deeper soil layers (Mistro et al. 2001; Barceló and Poschenrieder 2002; Kochian et al. 2004; Mariano and Keltjens 2005; Olivares et al. 2009; Silva et al. 2010; Freitas et al. 2017). Furthermore, as a secondary effect, Al induces less chlorophyll production in the plant shoots and decreases the photosynthetic rate (Zhang et al. 2007; Ali et al. 2008; Aftab et al. 2010; Shen et al. 2014). These effects on roots impair plant shoot growth and grain production.

Upland rice plants are moderately tolerant to Al (Ma et al. 2002); therefore, Brazil cultivates this type of rice in soils with low natural fertility (“Cerrado”) that have high Al levels. Nevertheless, because the growth of these plants may be impaired by Al toxicity (Singh et al. 2011; Alvarez et al. 2012), mitigation techniques are required. One method of reducing the damage caused by Al to plants is the application of silicates; this approach is supported by studies that have demonstrated that silicon (Si) can alleviate the damage caused by Al (Hammond et al. 1995; Corrales et al. 1997; Cocker et al. 1998; Sangster and Hodson 2001; Kidd et al. 2001; Wang et al. 2004; Singh et al. 2011; Shen et al. 2014). However, the interaction between Si and Al is not well understood, and several hypotheses regarding the role of Si in the alleviation of Al toxicity remain inconclusive.

Silicon contributes to the alleviation of Al toxicity via reactions that occur in the soil solution as well as via plant internal mechanisms. The mitigating effect of Si

on Al toxicity is related to decreasing Al levels in the soil solution via Al-Si complexing (Ma et al. 1997; Liang et al. 2007); furthermore, Si may reduce Al toxicity in the plant (Hodson and Evans 1995; Corrales et al. 1997; Cocker et al. 1998; Neumam and Nieden 2001; Kidd et al. 2001; Ryder et al. 2003; Wang et al. 2004; Liang et al. 2007) because accumulations of Al and Si in the plant are mutually exclusive, causing the plant to take up Si instead of Al (Hodson and Evans 1995). Thus, the Al tolerance of certain plant species may be associated with higher Si uptake and accumulation in the plant tissues, especially in upland rice plants, which present highly efficient Si uptake and accumulation (Ma and Yamaji 2006; Tokura et al. 2011).

Thus, studies evaluating Si and Al uptake kinetics are important for understanding the interactions of these elements in the plant and nutrient solution. The uptake efficiency of any element is influenced by its kinetic parameters (Barber 1984).

Therefore, the aim of this study was to evaluate the capacity of Si to mitigate Al toxicity in upland rice plants by evaluating the plant growth and the Si and Al uptake kinetics.

## Materials and methods

The experiment was performed in a nutrient solution in a greenhouse at the Department of Soil and Environmental Resources of São Paulo State University in Botucatu, São Paulo, Brazil. The experiment was arranged in a  $2 \times 5$  factorial randomized complete block design, with five replicates. The experiments included two upland rice cultivars (ANa7007, which is Al tolerant, and Maravilha, which is Al susceptible) (Freitas et al. 2016) and four Si and Al treatments (control = without Si and Al; +Si = with Si and without Al; +Al = without Si and with Al; and +Si + Al = with Si and Al). The Si and Al concentrations in the solution were defined in preliminary studies. The Si was supplied at  $1.7 \text{ mmol L}^{-1}$ , and the Al was supplied at  $1.4 \text{ mmol L}^{-1}$ . Potassium silicate was used as the Si source, with the potassium previously removed in a cationic column. The Al source was aluminum chloride.

To obtain plants for the experiment, seeds were germinated in a germination chamber, and after the emergence of seedlings, those with a consistent and uniform shape were selected. In total, eight seedlings were transferred to individual 4 L pots filled with nutrient solution.

The nutrient solution used for plant growth contained the following (in  $\text{mmol L}^{-1}$ ): 1.42 Ca, 1.51 K, 0.33 Mg, 0.95 N-NO<sub>3</sub>, 0.41 N-NH<sub>4</sub>, 0.01 P, 0.21 S, 0.21 Cl, 0.22 Fe, 0.009 Mn, 0.008 B, 0.00076 Zn and 0.00031 Cu. Only the Si and Al elements varied between the treatments.

In the first seven days of growth, all nutrients were used in the nutrient solution at half concentration to encourage plant adaptation, and for the next 14 days, the full nutrient concentrations were used. After this period, the Si and Al treatments were added, and the plants were grown for an additional 19 days.

Throughout the experiment, the nutrient solution was aerated and the pH was monitored daily and maintained at approximately 4.0 ( $\pm 0.1$ ), and NaOH ( $0.1 \text{ mol L}^{-1}$ ) and HCl ( $0.1 \text{ mol L}^{-1}$ ) were used to adjust the pH. The nutrient solution was replaced weekly while also adding the appropriate treatments, and the amount lost to evapotranspiration was replaced daily with demineralized water.

After 40 days of growth, the Si and Al uptake kinetics of the plants were analyzed according to the Claassen and Barber (1974) method. This method allows quantification of the rate of depletion of Si and Al from solution, characterizing the Si and Al flux through the plant roots, since the plants adapt nutrient uptake kinetics to their internal nutrient status. The method uses only one plant or group of plants to obtain data over a range of Si and Al concentrations in solution and measures the concentration below which net influx of Si and Al through roots ceases ( $C_{\text{min}}$ ). This method thus allows the identification of the  $I_{\text{max}}$  of Si and Al, i.e., the maximum transport rate or maximum influx rate of Si and Al; the Michaelis-Menten constant ( $K_{\text{m}}$ ) that represents the Si and Al concentrations in solution that produce 50% of  $I_{\text{max}}$ ; and the  $C_{\text{min}}$ , which represents the Si and Al concentrations in solution at which net influx is zero.

The nutrient solution for all of the treatments was replaced by the same solution without Si and Al, and the plants remained in this solution for 48 h to increase the plant uptake ability of the studied elements. Then, the nutrient solution was replaced again, and  $0.11 \text{ mmol L}^{-1}$  Si and  $0.19 \text{ mmol L}^{-1}$  Al were added to all of the treatments. The plants remained under these conditions for one hour, until uptake was stabilized in the roots. Then, the nutrient solution for all of the treatments was replaced again with a solution identical to the previous solution with Al and Si, and sampling was initiated.

Samples (10 mL each) of the solution were collected every 30 min in the first six hours, every 60 min in the six subsequent hours, and once in the final 24 h. Then, four additional samples were collected every 12 h to obtain the  $C_{\text{min}}$ . Throughout the sampling period, the pot volume was kept constant by the addition of demineralized water. The temperature of the nutrient solution throughout the sampling averaged  $22.6 \text{ }^{\circ}\text{C}$ , and the solution pH was monitored every 60 min and maintained at approximately 4.0 ( $\pm 0.1$ ).

The Si and Al concentrations in the collected samples were determined by Inductively Coupled Plasma (ICP). The  $K_{\text{m}}$  and  $I_{\text{max}}$  values were estimated based on the Si and Al concentrations in the samples and the root dry matter values, using the software CinéticaWin – the Windows version of Cinética 1.2 (Ruiz and Fernandes Filho 1992). In all treatments, the  $C_{\text{min}}$  values for Si and Al were obtained when the Si and Al concentrations in the solution remained constant (external concentration when net uptake is zero). Thus, in all treatments, the Al  $C_{\text{min}}$  was considered to be the value obtained at 24 h. The values of Si  $C_{\text{min}}$  in the control and +Si treatments were obtained at 24 h, but in the treatments +Al and +Si + Al, the Si  $C_{\text{min}}$  was obtained at 48 h.

After the exhaust solution was collected, the plant shoots and roots were separated. The length, surface area and diameter of the roots were determined using a scanner linked to a desktop computer running WinRhizo 3.8b software (Regent Instruments, Inc., Quebec, Canada) following the methods of Tennant (1975). The root length was also quantified separately for the fine roots (diameter < 0.5 mm), medium roots (diameter between 0.5 to 1.00 mm) and thick roots (diameter > 1.00 mm). Then, the shoot and root samples were dried in a forced-air circulation oven ( $65 \text{ }^{\circ}\text{C}$ ) to a constant weight, and the dry matter (DM) content was determined. The samples were ground and the Si and Al concentrations were determined according to the method of Elliott and Snyder (1991) as adapted by Korndörfer et al. (1999) and Malavolta et al. (1997), respectively. The DM and the Si and Al concentrations in both parts of the plant were used to calculate the accumulated Si and Al quantities. The whole-plant accumulated Si and Al quantities were obtained from the sum of the root and shoot accumulations.

The data were subjected to analysis of variance. The treatment averages were obtained by comparing the t-test results (LSD) at the 5% probability level.

## Results

The shoot, root and whole plant DM of the upland rice plants were affected by the treatments and by the interactions between the cultivar (C) and the Si and Al supply (Si-Al) (Table 1). The shoot DM of the cultivar ANa7007 (Al tolerant) was higher than that of the cultivar Maravilha only in the treatment that received Al and Si. For both cultivars, the Si treatments with and without Al provided shoot DM similar to that in the control treatment (without Si and Al); however, in the treatment without Si, Al reduced the shoot DM by 13%

and 10% for ANa7007 and Maravilha, respectively (Table 1).

In the isolated Si treatment, the root DM of the cultivar ANa7007 (Al tolerant) was higher than that of Maravilha (Al susceptible), whereas in the treatments with Al, the root DM of ANa7007 was lower than that of Maravilha, independent of the Si supply (Table 1). However, in both cultivars, the root DM did not increase under the Si treatments (Table 1).

The whole-plant DM was only higher in ANa7007 than in Maravilha in the isolated Si treatment (Table 1). However, although plant growth decreased in both

**Table 1** Dry matter accumulation in the plant tissues and root system parameters of upland rice cultivars grown under different conditions of silicon (Si) and aluminum (Al) inclusion in a nutrient solution. The results of an analysis of variance are shown

Cultivar	Si and Al conditions				Source of variation		
	Control	+Si	+Al	+Si + Al	C <sup>(1)</sup>	Si-Al	C × Si-Al
Shoot dry matter (g pot <sup>-1</sup> )							
Maravilha	11.1ab	11.7a	10.2b	11.3 <sup>†</sup> a	<0.001	<0.001	0.008
ANa7007	11.7bc	12.5ab	11.02c	12.6a			
Root dry matter (g pot <sup>-1</sup> )							
Maravilha	5.8a	5.6 <sup>†</sup> a	3.9 <sup>†</sup> b	3.9 <sup>†</sup> b	<0.001	<0.001	<0.001
ANa7007	5.9a	6.2a	2.9b	2.7b			
Whole-plant dry matter (g pot <sup>-1</sup> )							
Maravilha	16.9a	17.3 <sup>†</sup> a	14.2b	15.2b	0.086	<0.001	0.018
ANa7007	17.6a	18.8a	13.9c	15.4b			
Root length (m pot <sup>-1</sup> )							
Maravilha	1090a	1068 <sup>†</sup> a	375b	325b	<0.001	<0.001	0.002
ANa7007	1187b	1334a	360c	354c			
Root surface (cm <sup>2</sup> pot <sup>-1</sup> )							
Maravilha	9395a	8935 <sup>†</sup> a	3916 <sup>†</sup> b	3422b	0.598	<0.001	0.001
ANa7007	9799a	9706a	2872b	2947b			
Root diameter (mm)							
Maravilha	0.28b	0.27b	0.33 <sup>†</sup> a	0.35 <sup>†</sup> a	<0.001	<0.001	0.008
ANa7007	0.26a	0.24a	0.27a	0.28a			
Root length (<0.5 mm) (m pot <sup>-1</sup> )							
Maravilha	960a	909 <sup>†</sup> a	278b	259b	<0.001	<0.001	<0.001
ANa7007	1012b	1165a	300c	275c			
Root length (0.5–1.0 mm) (m pot <sup>-1</sup> )							
Maravilha	83 <sup>†</sup> a	82 <sup>†</sup> a	58b	50b	<0.001	<0.001	<0.001
ANa7007	116a	112a	51b	53b			
Root length (>1.0 mm) (m pot <sup>-1</sup> )							
Maravilha	46 <sup>†</sup> a	47 <sup>†</sup> a	14.0 <sup>†</sup> b	16.4 <sup>†</sup> b	0.013	<0.001	<0.001
ANa7007	58a	57a	9.1b	8.8b			

<sup>†</sup> Significant difference between the upland rice cultivars under the same Si and Al supply condition; mean values followed by the same letters in the rows are not significantly different at  $P \leq 0.05$  according to the LSD test

<sup>(1)</sup> C, cultivar; Si-Al, Si and Al supply conditions; C × Si-Al, interactions of cultivar × Si and Al supply conditions

cultivars with the addition of Al, in the treatment with the combination of Al and Si, the whole-plant DM of ANa7007 was higher than was observed with the Al-only treatment.

The root morphology parameters were influenced by the main treatment factors and the C x Si-Al interactions (Table 1). In the Si-only treatment, the cultivar ANa7007 (Al tolerant) showed a greater root length and surface area than the Al-susceptible cultivar. However, the root surface area of the cultivar Maravilha (Al susceptible) under the Al treatment was greater than that of ANa7007 (Al tolerant). The root length and surface area of both cultivars decreased in the presence of Al, independent of the presence of Si (Table 1). Moreover, Al increased the root diameter only in the cultivar Maravilha, which is susceptible to Al toxicity.

In the Si-only treatment, the lengths of the fine and medium roots were greater in ANa7007 than in Maravilha, whereas no differences in the lengths of the fine and medium roots were observed between the cultivars in the Al treatments (Table 1). The root diameter of ANa7007 was not significantly affected by Al, and because this cultivar is Al tolerant, it exhibited shorter thick roots than did the cultivar Maravilha in the Al treatments (Table 1).

Silicon accumulated in the upland rice plant shoots to higher levels in the treatments that received Si, regardless of the presence of Al in the solution (Table 2). In the roots, the Si concentration and accumulation were affected by the C x Si-Al interactions. In both cultivars, the root Si concentrations were higher when Si and Al were supplied together. In the Si and Al treatments, root accumulation of Si was lower in ANa7007 than in Maravilha; however, in both cultivars, root Si accumulation in the presence of Al was lower than in the control treatment. In the whole plant, Si accumulation did not differ between the cultivars, with more Si accumulating in the treatments that included Si, regardless of the presence of Al in the solution.

The Al concentrations in both the shoots and roots and Al accumulation in the roots were affected by the C x Si-Al interactions; however, Al accumulation in the shoots was only affected by the different Si and Al treatments (Table 2). In the Al-only treatments, the Al-tolerant cultivar (ANa7007) showed lower Al concentrations in the shoots than the susceptible cultivar (Maravilha) but did not exhibit lower Al accumulation. However, in both cultivars, the Al concentrations in the shoots were only higher under treatment with Al alone,

whereas in the combined Si and Al treatments, the shoot Al concentration decreased. Although Si decreased the shoot Al concentrations in both cultivars, only Maravilha exhibited decreased Al accumulation in the shoots under the Al and Si treatments.

Independent of the Si supply, the presence of Al in the solution caused ANa7007 (Al tolerant) to exhibit higher root Al concentrations, although it accumulated less Al in the roots than the susceptible cultivar because of its lower root DM production (Tables 1 and 2).

In the whole plant, the accumulation of Al was influenced by the C x Si-Al interactions (Table 2). The Al-tolerant cultivar (ANa7007) only accumulated less Al than the susceptible cultivar (Maravilha) under treatment with Al alone, whereas supplying Si in the solution only decreased the accumulation of Al in the susceptible cultivar. In the Al-tolerant cultivar, the presence of Si in the solution did not decrease the accumulation of Al in the shoots, roots or whole plant. However, in the presence of Al, the addition of Si increased the shoot DM of this cultivar (Tables 1 and 2).

In both cultivars, Si was taken up from the solution at a higher rate in the treatments without Al, and after 10–12 h, the Si uptake rate remained constant, with Si concentrations below  $20 \mu\text{mol L}^{-1}$  being observed in the solution (Fig. 1a and b). By contrast, in the treatments with Al, although the rate of Si uptake was reduced, after 10 h, the concentration in the solution was higher than  $60 \mu\text{mol L}^{-1}$ .

The kinetic parameters of Si uptake were affected by the C x Si-Al interactions (Table 3). In the control and combined Si-Al treatments, ANa7007 exhibited higher Si  $I_{\text{max}}$  values than Maravilha. For both cultivars, the Si  $I_{\text{max}}$  in the control treatment was 1.5 times higher on average than in the Si-only treatment and 2.2 times higher than in the treatments with Al.

In the presence of Al, the Si  $K_{\text{m}}$  and  $C_{\text{min}}$  values differed between the cultivars, with higher values being observed in ANa7007 under the Al-only treatment and in Maravilha under combined Si and Al treatment (Table 3).

The rate of Al uptake from the solution was low in the first 10 h and then remained relatively stable (Fig. 1). The kinetic parameters of Al uptake were affected by the C x Si-Al interactions (Table 3). The cultivar Maravilha (Al susceptible) exhibited a higher Al  $I_{\text{max}}$  than ANa7007 in the treatments without Al during the initial plant growth stage. However, in the Al-susceptible cultivar, Al  $I_{\text{max}}$  was lower in the control treatment and in

**Table 2** Concentration and accumulation of silicon (Si) and aluminum (Al) in plant tissues and whole plants of upland rice cultivars grown under different conditions of silicon (Si) and aluminum (Al) inclusion in a nutrient solution. The results of an analysis of variance are shown

Cultivar	Si and Al conditions				Source of variation		
	Control	+Si	+Al	+Si + Al	C <sup>(1)</sup>	Si-Al	C × Si-Al
Shoot Si concentration (g kg <sup>-1</sup> )							
Maravilha	8.9b	36.9a	9.3b	38.1a	0.862	<0.001	0.996
ANa7007	8.9b	37.0a	9.0b	37.7a			
Root Si concentration (g kg <sup>-1</sup> )							
Maravilha	4.7 <sup>†</sup> b	5.0 <sup>†</sup> b	4.3b	6.2 <sup>†</sup> a	0.017	<0.001	0.008
ANa7007	4.0b	4.2b	5.0a	5.3a			
Shoot Si accumulation (mg pot <sup>-1</sup> )							
Maravilha	102b	435a	94b	444a	0.041	<0.001	0.537
ANa7007	112b	472a	101b	493a			
Root Si accumulation (mg pot <sup>-1</sup> )							
Maravilha	29a	28ab	17c	25 <sup>†</sup> b	<0.001	<0.001	0.008
ANa7007	26a	27a	15b	15b			
Whole-plant Si accum. (mg pot <sup>-1</sup> )							
Maravilha	132b	462a	112b	469a	0.076	<0.001	0.603
ANa7007	138b	499a	116b	508a			
Shoot Al concentration (g kg <sup>-1</sup> )							
Maravilha	0.06c	0.08c	0.41 <sup>†</sup> a	0.29b	0.013	<0.001	0.024
ANa7007	0.07c	0.05c	0.34a	0.28b			
Root Al concentration (g kg <sup>-1</sup> )							
Maravilha	0.26b	0.28b	2.06 <sup>†</sup> a	1.92 <sup>†</sup> a	0.002	<0.001	0.006
ANa7007	0.28b	0.25b	2.28a	2.43a			
Shoot Al accumulation (mg pot <sup>-1</sup> )							
Maravilha	0.72c	0.98c	4.22a	3.46b	0.812	<0.001	0.214
ANa7007	0.97b	0.67b	3.86a	3.74a			
Root Al accumulation (mg pot <sup>-1</sup> )							
Maravilha	1.70b	1.58b	8.21 <sup>†</sup> a	7.86 <sup>†</sup> a	0.001	<0.001	0.003
ANa7007	1.84b	1.62b	6.61a	6.85a			
Whole-plant Al accum. (mg pot <sup>-1</sup> )							
Maravilha	2.42c	2.56c	12.44 <sup>†</sup> a	11.33b	0.003	<0.001	0.002
ANa7007	2.81b	2.30b	10.48a	10.59a			

<sup>†</sup> Significant difference between the upland rice cultivars under the same Si and Al supply condition; mean values followed by the same letters in the rows are not significantly different at  $P \leq 0.05$  according to the LSD test

<sup>(1)</sup> C, cultivar; Si-Al, Si and Al supply conditions; C × Si-Al, interactions of cultivar × Si and Al supply conditions

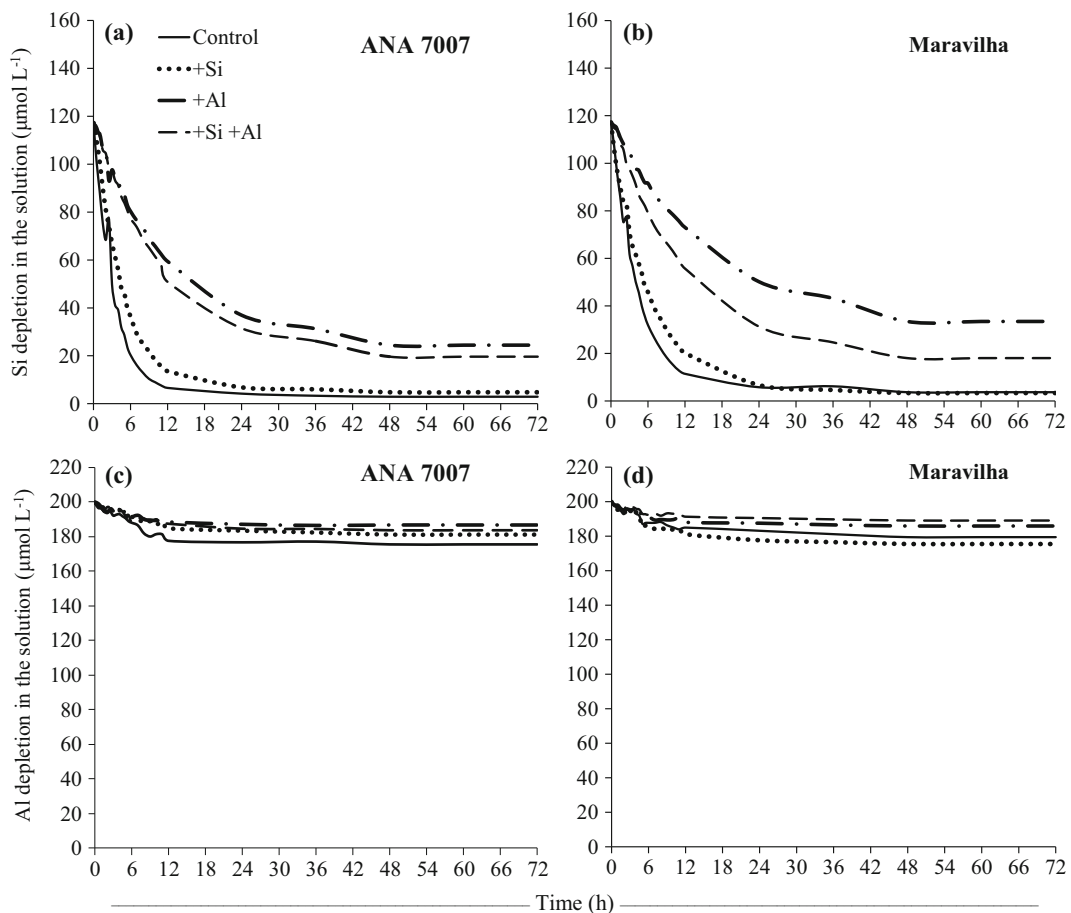
the treatments with Al than in the Si-only treatment, regardless of the presence of Si in the combined Si-Al treatment. In the Al-tolerant cultivar, the Al I<sub>max</sub> was only reduced in the control treatment.

In the control treatment, the Al K<sub>m</sub> and C<sub>min</sub> values were lower in ANa7007 than in Maravilha. Under treatment with Si or Al alone or with the combination of Si and Al, the K<sub>m</sub> values did not differ markedly between the cultivars, and in the Al-tolerant cultivar, the Al K<sub>m</sub> was lower in the control treatment than in the Si-only or combined Si and Al treatments. In the susceptible

cultivar Maravilha, the C<sub>min</sub> was lower in the Si-only treatment and higher in the Al-only and combined Si-Al treatments; however, both cultivars showed increased Al C<sub>min</sub> in the treatments that included Al during the initial growth stage.

## Discussion

The higher shoot DM production observed in the Si-Al treatment compared with the treatment with Al alone



**Fig. 1** Si and Al depletion in nutrient solution by upland rice cultivars ANA7007 (a and c) and Maravilha (b and d) grown under different conditions of silicon (Si) and aluminum (Al) inclusion in a nutrient solution

(without Si) and the similar DM production between the Si-Al and control treatments indicate that Si mitigated Al toxicity and increased and/or maintained shoot DM production. Regarding root DM, the higher value recorded in the Al-susceptible cultivar than in the Al-tolerant cultivar occurred due to greater root damage in the Al-susceptible cultivar, which presented thicker, heavier roots (Table 1) because Al toxicity induces an increase in root thickness (Zobel et al. 2007). In general, Si promoted increased growth only in the shoots of the plants, especially under Al stress conditions, resulting in higher whole-plant DM production. Other studies (e.g., in peanut (Shen et al. 2014) and rice plants (Singh et al. 2011)) also demonstrated that for plants grown in the presence of Al, Si increases the shoot growth.

The decrease in the DM shoot and root production in the Al treatments, in addition to being directly influenced by the Al toxic activity, can also suffer

from the influence of interactions of Al and P in the nutrient solution and inside the plant, decreasing the use of this nutrient by the plant (Gaume et al. 2001; Liao et al. 2006).

The greater root length and surface area observed in the Si-only treatment of the Al-tolerant cultivar occurred because there is an increase in root production (root DM) (Table 1). On the other hand, the root surface area of the Al-susceptible cultivar was greater than that of the Al-tolerant cultivar because the roots of the susceptible cultivar, Maravilha, increased in diameter under Al toxicity, whereas this did not occur in the Al-tolerant cultivar (Table 1).

The decreases in the root length and surface area of both cultivars in the presence of Al demonstrate that Si did not decrease the stress caused by Al in the roots, where the primary toxic action of Al occurs (Zhang et al. 2007). Furthermore, Al increased root diameter only in

**Table 3** Kinetic parameters of silicon (Si) and aluminum (Al) uptake by upland rice cultivars grown under different conditions of silicon (Si) and aluminum (Al) inclusion in a nutrient solution. The results of an analysis of variance are shown

Cultivar	Si and Al conditions				Source of variation		
	Control	+Si	+Al	+Si + Al	C <sup>(1)</sup>	Si-Al	C × Si-Al
Si - I <sub>max</sub> (μmol cm <sup>-2</sup> h <sup>-1</sup> 10 <sup>-3</sup> )							
Maravilha	13.7 <sup>†</sup> a	10.9b	7.1c	4.6 <sup>†</sup> d	<0.001	<0.001	0.019
ANa7007	18.1a	10.7b	8.8bc	8.2c			
Si - K <sub>m</sub> (μmol L <sup>-1</sup> )							
Maravilha	40c	39c	53 <sup>†</sup> b	63 <sup>†</sup> a	0.143	<0.001	<0.001
ANa7007	37c	40c	58a	52b			
Si - C <sub>min</sub> (μmol L <sup>-1</sup> )							
Maravilha	5.2c	4.9c	24.6 <sup>†</sup> b	41.8 <sup>†</sup> a	0.002	<0.001	<0.001
ANa7007	3.4d	5.8c	34.9a	25.7b			
Al - I <sub>max</sub> (μmol cm <sup>-2</sup> h <sup>-1</sup> 10 <sup>-3</sup> )							
Maravilha	3.0 <sup>†</sup> b	3.9 <sup>†</sup> a	2.8b	2.6b	0.040	0.007	0.002
ANa7007	1.5b	2.8a	3.0a	3.2a			
Al - K <sub>m</sub> (μmol L <sup>-1</sup> )							
Maravilha	188 <sup>†</sup> a	189a	192a	189a	0.180	0.021	0.017
ANa7007	180b	192a	186ab	192a			
Al - C <sub>min</sub> (μmol L <sup>-1</sup> )							
Maravilha	181 <sup>†</sup> b	176 <sup>†</sup> c	189 <sup>†</sup> a	186a	0.344	<0.001	0.002
ANa7007	176c	182b	184ab	187a			

<sup>†</sup> Significant difference between the upland rice cultivars under the same Si and Al supply condition; mean values followed by the same letters in the rows are not significantly different at  $P \leq 0.05$  according to the LSD test

<sup>(1)</sup> C, cultivar; Si-Al, Si and Al supply conditions; C × Si-Al, interactions of cultivar × Si and Al supply conditions

the cultivar Maravilha, demonstrating that upland rice cultivars that are tolerant to Al (such as ANa7007) continue to produce fine roots even under conditions of Al toxicity. Although Si did not mitigate the toxic effects of Al on root growth in the upland rice plants in this study, research has shown that Si may increase root growth under conditions of Al toxicity in rice plants (Rahman et al. 1998; Giongo and Bohnen 2011; Singh et al. 2011) and corn (Wang et al. 2004), and it may even decrease the root diameter of peanut plants grown under Al stress (Shen et al. 2014).

The results demonstrate that the cultivar ANa7007 produced greater quantities of fine roots when grown in the presence of Si without Al. Si is known to have a more pronounced effect on plants under stress (Ma and Takahashi 2002), and it primarily accumulates in the plant shoots, where it exerts its effect (Ma and Yamaji 2006). Moreover, the effects of Si on root growth are poorly understood; however, our results indicate that even in the absence of abiotic stress, Si may have a beneficial influence on the root growth of upland rice plants. The results also demonstrate that in the cultivar

Maravilha (Al susceptible), the Al supply promoted greater damage to the root system, thereby causing an increase in the length of thick roots. Thicker roots show a reduced capacity for water and nutrient uptake from the soil compared with medium and fine roots (Taiz and Zeiger 2013).

The finding of greater Si accumulation in the shoots even in the treatments that received Al indicates that Al did not decrease the transport of Si to plant shoots. In the whole plant, the observation that more Si accumulated in the treatments that included Si, regardless of the presence of Al, demonstrates that Al did not alter the uptake of Si or significantly affect the quantity of Si that accumulated in the shoots and the whole plant (Table 2).

The finding that the decrease in the shoot Al concentration was mediated by Si demonstrates that the presence of Si in the solution decreased Al translocation to the shoots, which contributed to the increase in plant shoot DM compared with that in the Al treatment (Table 1). According to Cocker et al. (1998) and Vázquez et al. (1999), the Si added to the solution may interact with Al, make it non-toxic to the plant and



decrease Al translocation to the shoot, thereby alleviating its toxicity in the plant shoots, which was confirmed in our study.

The increased concentration of Al in the roots of tolerant cultivars (e.g., ANa7007) is a strategy exhibited by the plant to inactivate or store the Al in a non-toxic form in the roots and to translocate less Al to the shoots, thereby decreasing the Al toxicity to the plant (Kochian 1995; Matsumoto 2000; Barceló and Poschenrieder 2002; Ma and Furukawa 2003). The presence of Si in the solution did not reduce the root Al concentration and accumulation in the treatments in which Al was present, and similar results were observed for the root DM (Tables 1 and 2).

In the whole plant, the Si decreased Al accumulation only in the susceptible cultivar, indicating that the Si-induced mitigation of Al toxicity was more evident in the Al-susceptible cultivar and that the main effect of Si was related to a reduction of Al transport and shoot accumulation (Singh et al. 2011; Shen et al. 2014).

The higher Si uptake observed in the treatments without Al demonstrates a lower capacity for Si uptake in the plants grown under Al toxicity.

Our findings indicate that Al decreased Si uptake by negatively affecting root morphology and physiology (Tables 1 and 3). Aluminum toxicity alters the plasma membrane permeability (Kochian 1995; Ahn et al. 2001; Yamamoto et al. 2001), thereby modifying the fluidity of lipids because of the electrostatic connection, which is induced by Al in the polar regions of phosphatidylcholine (Rengel 1996; Justino et al. 2006). Because Al toxicity affects the root growth, it also affects the nutrient uptake. These effects were also observed in sorghum plants in which Al modified the kinetic constants of root P uptake, thereby decreasing the uptake of P (Pereira et al. 2008).

The reduced  $I_{max}$  values caused by Al must be related to damage to the Si transporters and less activity of the genes responsible for Si signaling (*Lsi1*) (Ma et al. 2004, 2006, 2007) because these genes act in the root exodermis and endoderm, where Al produces the most damage. Because rice is a Si-accumulating plant, Si plays an important role in its growth (Ma and Takahashi 2002). Thus, the higher Si  $I_{max}$  value in the control plants indicates that plants grown without Si that were subsequently supplied with this element (Table 3) increase their  $I_{max}$  to maintain their internal balance of Si.

Both cultivars experienced increased Si  $K_m$  and  $C_{min}$  values in the presence of Al, demonstrating that Al in the solution decreased the affinity of the Si transporter system in the roots ( $K_m$ ) as well as the plant Si uptake capacity, since in the presence of Al in the solution, the plants ceased the Si uptake despite high Si availability in the solution ( $>C_{min}$ ) (Table 3). This result was likely caused by Al-induced structural damage to the roots (Kochian et al. 2004). Moreover, these findings demonstrate that for a plant to maintain Si uptake in the presence of Al, the Si availability in the solution must be approximately 6.6 times higher than in the absence of Al, since in the treatments without Al (control and +Si), the  $C_{min}$  of both cultivars averaged 4.8, whereas in the treatments with Al (+Al and +Si + Al) the  $C_{min}$  values averaged 31.8 (Table 3). The Al-induced structural damage to the roots also negatively affects water and nutrient uptake by the plants (Mistro et al. 2001; Mendonça et al. 2003), as observed in this study, in which Al increased the Si  $C_{min}$ , thereby reducing the plants Si uptake capacity.

The finding that the Al-tolerant cultivar showed lower Si  $K_m$  and  $C_{min}$  values in the treatments involving Si than in the Al-only treatments indicates that in this cultivar, the supply of Si in the solution alleviated Al toxicity in the roots, maintained a higher Si transporter affinity and supported the Si uptake capacity.

Aluminum uptake was irregular in both cultivars (Fig. 1c and d), indicating that during growth, the upland rice plants utilize protection mechanisms to prevent the uptake of Al from the nutrient solution (Kochian et al. 2005). The rate of Al uptake from the solution was low in the first 10 h and then remained relatively constant; therefore, the rate of Al depletion from the solution was always lower in the treatments with Al because these treatments promoted restricted root growth.

Our results indicate that in both cultivars, the supply of Si did not reduce the Al uptake rate ( $I_{max}$ ) in the plants, although Si mediated a significant reduction of Al transport to the plant shoots in the Al-susceptible cultivar (Maravilha), thereby promoting lower Al accumulation in the shoots and the whole plant (Tables 2 and 3). In the literature, two hypotheses have been postulated regarding the mediation of Al toxicity by Si. The first is related to interactions that occur inside the plant (Hodson and Evans 1995; Corrales et al. 1997; Cocker et al. 1998; Neumam and Nieden 2001; Kidd et al. 2001; Liang et al. 2007), such as that shown in this work. The second hypothesis is related to interactions between Si

and Al in the soil solution (Ma et al. 1997) and the complexing of Al into non-toxic forms, which was not observed in this study because the Al-tolerant cultivar accumulated the same quantities of Al in the treatments with and without Si (Table 2).

The lower values of Al Km and Cmin observed in the cultivar ANa7007 than in the cultivar Maravilha in the control treatment show that although the Al-tolerant cultivar may exhibit a higher efficiency of Al transporters in its roots (lower Km and Cmin), it has a low Al I<sub>max</sub>, indicating that the Al transport system in the roots is efficient but that the Al uptake rate is low due to the lower number of specific transporters for Al uptake in the roots (Table 3), resulting in a slight Al depletion in the nutrient solution (Fig. 1). In rice plants, these Al transporters in the root system have been identified (e.g., Nr1h1 - Nramp aluminum transporter), and it has been observed that in root tips of Al-tolerant rice accessions, the level of Nr1h1 expression and the levels of Al in the cell sap were higher, whereas the Al levels in the cell wall were lower (Li et al. 2014) as well as the reports of Simões et al. (2012) and Xia et al. (2010). Negishi et al. (2012) reported that the expression level of PM Al transporter (PALT1) and the vacuolar Al transporter (VALT) regulate Al tolerance and sensitivity in Arabidopsis. Those findings obtained led to the suggestion that Nr1h1 plays a role in partitioning Al between the rice root cell wall and symplasm as an Al resistance mechanism (Li et al. 2014).

The reduced Al Cmin in the Al treatments indicates that this ion toxicity reduced the root growth and also reduced the root uptake surface area, which also reduced the capacity of the plants to take up Al from the solution.

## Conclusions

Aluminum decreased plant growth and the Si uptake capacity by decreasing the root growth and Si transport system efficiency in the upland rice roots (> Km and > Cmin). The addition of Si mitigated the Al toxicity in upland rice plants by decreasing the Al transport to the plant shoots, although it did not reduce the Al uptake rate (I<sub>max</sub>). The addition of Si increased the growth of the upland rice plant shoots grown in the presence of Al but did not influence the root growth. The alleviation of Al toxicity by Si was more evident in the susceptible cultivar Maravilha.

**Acknowledgements** We are grateful to the São Paulo Research Foundation (FAPESP) for supporting this research (grant #2011/22182-8) and for providing a scholarship to the first author (grant #2011/09283-0) and to The National Council for Scientific and Technological Development (CNPq) for providing a research grant to the second author. We would also like to thank the Federal Institute Goiano for providing a research grant to the third author and for supporting this study.

## Compliance with ethical standards

**Conflict of interest** The authors affirm that there are no conflicts of interest regarding this manuscript.

## References

- Aftab T, Khan MMA, Idrees M, Moinuddin NM (2010) Effects of aluminium exposures on growth, photosynthetic efficiency, lipid peroxidation, antioxidant enzymes and artemisinin content of *Artemisia Annuua* L. *J Phytology* 2:23–37
- Ahn SJ, Sivaguru M, Osawa H, Chung GC, Matsumoto H (2001) Aluminum inhibits the H<sup>+</sup>-ATPase activity by permanently altering the plasma membrane surface potentials in squash roots. *Plant Physiol* 126:1381–1390
- Ali B, Hasan SA, Hayat S, Hayat Q, Yadav S, Fariduddin Q, Ahmad A (2008) A role for brassinosteroids in the amelioration of aluminium stress through antioxidant system in mung bean (*Vigna radiata* L. Wilczek). *Environ Exp Bot* 62:153–159. <https://doi.org/10.1016/j.envexpbot.2007.07.014>
- Alvarez I, Reynaldo OS, Testillano P, Risueño C, Arias M (2012) Morphological and cellular changes in rice roots (*Oryza sativa* L.) caused by Al stress. *Bot Stud* 53:67–73
- Barber SA (1984) Soil nutrient bioavailability: a mechanistic approach. John Wiley, New York
- Barceló J, Poschenrieder C (2002) Fast root growth responses, root exudates and internal detoxification as clues to the mechanisms of aluminum toxicity and resistance. *Environ Exp Bot* 48:75–92. [https://doi.org/10.1016/S0098-8472\(02\)00013-8](https://doi.org/10.1016/S0098-8472(02)00013-8)
- Budikova S, Durcekova K (2004) Aluminium accumulation in roots of Al-sensitive barley cultivar changes root cell structure and induces callose synthesis. *Biologia* 59:215–220
- Claassen N, Barber SAA (1974) Method for characterizing the relation between nutrient concentration and flux into roots of intact plants. *Plant Physiol* 54:564–568. <https://doi.org/10.1104/pp.54.4.564>
- Clarkson DT (1965) The effect of aluminium and some other trivalent metal cations on cell division in the root apices of *Allium cepa*. *Ann Bot* 29:309–315. <https://doi.org/10.1093/oxfordjournals.aob.a083953>
- Cocker KM, Evans DE, Hodson MJ (1998) The amelioration of aluminium toxicity by silicon in higher plants: solution chemistry or an in planta mechanism. *Physiol Plant* 104:608–614. <https://doi.org/10.1034/j.1399-3054.1998.1040413.x>
- Corrales I, Poschenrieder C, Barceló J (1997) Influence of silicon pretreatment on aluminum toxicity in maize roots. *Plant Soil* 190:203–209. <https://doi.org/10.1023/A:1004209828791>

- Doncheva S, Amenós M, Poschenrieder C, Barceló J (2005) Root cell patterning: a primary target for aluminium toxicity in maize. *J Exp Bot* 56:1213–1220. <https://doi.org/10.1093/jxb/eri115>
- Elliott CL, Snyder GH (1991) Autoclave-induced digestion for the colorimetric determination of silicon in rice straw. *J Agric Food Chem* 39:1118–1119. <https://doi.org/10.1021/jf00006a024>
- Freitas LB, Fernandes DM, Pivetta LA, Maia SCMM (2016) Tolerance of upland rice cultivars to aluminum and acidic pH. *Rev Bras Eng Agric Ambient* 20:886–614. <https://doi.org/10.1590/1807-1929/agriambi.v20n10p886-890>
- Freitas LB, Fernandes DM, Maia SCMM, Mazziero BG (2017) Aluminum in mineral nutrition of upland rice plants. *Agrária* 12:26–34. <https://doi.org/10.5039/agraria.v12i1a5414>
- Gaume A, Mächler F, Frossard E (2001) Aluminum resistance in two cultivars of *Zea mays* L.: root exudation of organic acids and influence of phosphorous nutrition. *Plant Soil* 234:73–81. <https://doi.org/10.1023/A:1010535132296>
- Giongo V, Bohnen H (2011) Relation between aluminum and silicon in maize genotypes resistant and sensitive at aluminum toxicity. (In Portuguese, with English abstract.) *Biosci J* 27:348–356
- Hammond KE, Evans DE, Hodson MJ (1995) Aluminum/silicon interactions in barley (*Hordeum vulgare* L.) seedlings. *Plant Soil* 173:89–95. <https://doi.org/10.1007/BF00155521>
- Hodson MJ, Evans DE (1995) Aluminium/silicon interactions in higher plants. *J Exp Bot* 46:161–171. <https://doi.org/10.1093/jxb/46.2.161>
- Horst WJ, Kollmeier M, Schmohl N, Sivaguru M, Wang Y, Felle HH, Hedrich R, Schröder W, Staß A (2007) Significance of the root apoplast for aluminium toxicity and resistance of maize. In: Sattelmacher B, Horst WJ (eds) The apoplast of higher plants compartment of storage, transport, and reactions. Springer Verlag, Dordrecht, pp 49–66
- Huang JW, Pellet DM, Papernik LA, Kochian LV (1996) Aluminum interactions with voltage-dependent calcium transport in plasma membrane vesicles isolated from roots of aluminum-sensitive and -resistant wheat cultivars. *Plant Physiol* 110:561–569
- Justino GC, Cambraia J, Oliva MA, Oliveira JA (2006) Uptake and reduction of nitrate in two rice cultivars in the presence of aluminum. (In Portuguese, with English abstract.) *Pesq Agrop Brasileira* 41:1285–1290. <https://doi.org/10.1590/S0100-204X2006000800011>
- Khan MS, Tawaraya K, Sekimoto K, Koyama H, Kobayashi Y, Murayama T, Chuba M, Kambayashi M, Shiono Y, Uemura M, Ishikawa S, Wagatsuma T (2009) Relative abundance of delta5-sterols in plasma membrane lipids of root-tip cells correlates with aluminum tolerance of rice. *Physiol Plant* 135:73–83. <https://doi.org/10.1111/j.1399-3054.2008.01175.x>
- Kidd PS, Llugany M, Poschenrieder C, Günsé B, Barceló J (2001) The role of root exudates in aluminum resistance and silicon induced amelioration of aluminum toxicity in three varieties of maize (*Zea mays* L.) *J Exp Bot* 52:1339–1352. <https://doi.org/10.1093/jexbot/52.359.1339>
- Kochian LV (1995) Cellular mechanisms of aluminum toxicity and resistance in plants. *Annu Rev Plant Physiol Plant Mol Biol* 46:237–260. <https://doi.org/10.1146/annurev.pp.46.060195.001321>
- Kochian LV, Hoekenga OA, Piñeros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. *Annu Rev Plant Biol* 55:459–493. <https://doi.org/10.1146/annurev.arplant.55.031903.141655>
- Kochian LV, Piñeros MA, Hoekenga OA (2005) The physiology, genetics and molecular biology of plant aluminum resistance and toxicity. *Plant Soil* 274:175–195. <https://doi.org/10.1007/s11104-004-1158-7>
- Kopittke PM, Blamey FPC, Menzies NW (2008) Toxicities of soluble Al, Cu, and La include ruptures to rhizodermal and root cortical cells of cowpea. *Plant Soil* 303:217–227. <https://doi.org/10.1007/s11104-007-9500-5>
- Komdörfer GH, Coelho NM, Snyder GH, Myzutan CT (1999) Avaliação de métodos de extração de silício em solos cultivados com arroz de sequeiro. (In Portuguese, with English abstract.) *Rev Bras Ciênc Solo* 23:101–106. <https://doi.org/10.1590/S0100-06831999000100013>
- Li Y, Yang GX, Luo LT, Ke T, Zhang JR, Li KX, He GY (2008) Aluminium sensitivity and tolerance in model and elite wheat varieties. *Cereal Res Commun* 36:257–267. <https://doi.org/10.1556/CRC.36.2008.2.6>
- Li JY, Liu J, Dong D, Jia X, McCouch SR, Kochian LV (2014) Natural variation underlies alterations in Nramp aluminum transporter (NRAT1) expression and function that play a key role in rice aluminum tolerance. *Proc Natl Acad Sci U S A* 111:6503–6508. <https://doi.org/10.1073/pnas.1318975111>
- Liang Y, Sun W, Zhu Y, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. *Environ Pollut* 147:422–428. <https://doi.org/10.1016/j.envpol.2006.06.008>
- Liao H, Wan H, Shaff J, Wang X, Yan X, Kochian L (2006) Phosphorus and aluminum interactions in soybean in relation to aluminum tolerance. Exudation of specific organic acids from different regions of the intact root system. *Plant Physiol* 141:674–684. <https://doi.org/10.1104/pp.105.076497>
- Ma JF, Furukawa J (2003) Recent progress in the research of external Al detoxification in higher plants: a mini review. *J Inorg Biochem* 97:46–51. [https://doi.org/10.1016/S0162-0134\(03\)00245-9](https://doi.org/10.1016/S0162-0134(03)00245-9)
- Ma JF, Takahashi E (2002) Soil, fertilizer, and plant silicon research in Japan. Elsevier Science, Amsterdam
- Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. *Trends Plant Sci* 11:392–397. <https://doi.org/10.1016/j.tplants.2006.06.007>
- Ma JF, Sasaki M, Matsumoto H (1997) Al-induced inhibition of root elongation in corn, *Zea mays* L. is overcome by Si addition. *Plant Soil* 188:171–176. <https://doi.org/10.1023/A:1004274223516>
- Ma JF, Shen R, Zhao Z, Wissuwa M, Takeuchi Y, Ebitani T, Yano M (2002) Response of rice to Al stress and identification of quantitative trait loci for Al tolerance. *Plant Cell Physiol* 43:652–659. <https://doi.org/10.1093/pcp/pcf081>
- Ma JF, Mitani N, Nagao S, Konishi S, Tamai K, Iwashita T, Yano M (2004) Characterization of the silicon uptake and molecular mapping of the silicon transporter gene in rice. *Plant Physiol* 136:3284–3289. <https://doi.org/10.1104/pp.104.047365>
- Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M (2006) A silicon transporter in rice. *Nature* 440:688–691. <https://doi.org/10.1038/nature04590>

- Ma JF, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M (2007) An efflux transporter of silicon in rice. *Nature* 448:209–211. <https://doi.org/10.1038/nature05964>
- Malavolta E, Vitti GC, Oliveira SA (1997) Evaluation of nutritional status of plants: principles and applications 2nd edn. (In Portuguese.) Potafos, Piracicaba
- Mariano ED, Keltjens WG (2005) Long-term effects of aluminum exposure on nutrient uptake by maize genotypes differing in aluminum resistance. *J Plant Nutr* 28:323–333. <https://doi.org/10.1081/PLN-200047625>
- Matsumoto H (2000) Cell biology of aluminum toxicity and tolerance in higher plants. *Int Rev Cytol* 200:1–46. [https://doi.org/10.1016/S0074-7696\(00\)00001-2](https://doi.org/10.1016/S0074-7696(00)00001-2)
- Meharg AA (1993) The role of the plasmalemma in metal tolerance in angiosperms. *Physiol Plant* 88:191–198. <https://doi.org/10.1111/j.1399-3054.1993.tb01777.x>
- Mendonça RJ, Cambraia J, Oliveira JA, Oliva MA (2003) Aluminum effects on the uptake and utilization of macronutrients in two rice cultivars. (In Portuguese, with English abstract.) *Pesq Agrop Brasileira* 38:843–846. <https://doi.org/10.1590/S0100-204X2003000700008>
- Mistro JC, Camargo CEO, Pettinelli-Júnior A (2001) Evaluation of wheat genotypes from different origins in relation to aluminum toxicity. (In Portuguese, with English abstract.) *Bragantia* 60:1–9. <https://doi.org/10.1590/S0006-87052001000300004>
- Morimura S, Matsumoto H (1978) Effect of aluminum on some properties and template activity of purified pea DNA. *Plant Cell Physiol* 19:429–436. <https://doi.org/10.1093/oxfordjournals.pcp.a075611>
- Negishi T, Oshima K, Hattori M, Kanai M, Mano S, Nishimura M, Yoshida K (2012) Tonoplast- and plasma membrane-localized aquaporin-family transporters in blue hydrangea sepals of aluminum hyperaccumulating plant. *PLoS One* 7:e4389. <https://doi.org/10.1371/journal.pone.0043189>
- Neumam D, Nieden U (2001) Silicon and heavy metal tolerance of higher plants. *Phytochemistry* 56:685–692. [https://doi.org/10.1016/S0031-9422\(00\)00472-6](https://doi.org/10.1016/S0031-9422(00)00472-6)
- Olivares E, Peña E, Marcano E, Mostacero J, Aguiar G, Benítez M, Rengifo E (2009) Aluminum accumulation and its relationship with mineral plant nutrients in 12 pteridophytes from Venezuela. *Environ Exp Bot* 65:132–141. <https://doi.org/10.1016/j.envexpbot.2008.04.002>
- Panda SK, Baluska F, Matsumoto H (2009) Aluminum stress signaling in plants. *Plant Signal Behav* 7:592–597. <https://doi.org/10.4161/psb.4.7.8903>
- Pereira JM, Cambraia J, Fonseca Júnior ÉM, Ribeiro C (2008) Aluminum effect on uptake, accumulation and fractionation of phosphorus in sorghum. (In Portuguese, with English abstract.) *Bragantia* 67:961–967. <https://doi.org/10.1590/S0006-87052008000400019>
- Rahman MT, Kawamura K, Koyama H, Hara T (1998) Varietal differences in the growth of rice plants in response to aluminum and silicon. *Soil Sci Plant Nutr* 44:423–431. <https://doi.org/10.1080/00380768.1998.10414464>
- Rangel AF, Rao IM, Horst WJ (2009) Intracellular distribution and binding state of aluminum in root apices of two common bean (*Phaseolus vulgaris*) genotypes in relation to Al toxicity. *Physiol Plant* 135:162–173. <https://doi.org/10.1111/j.1399-3054.2008.01183.x>
- Rengel Z (1996) Uptake of aluminum by plant cells. *New Phytol* 134:389–406. <https://doi.org/10.1111/j.1469-8137.1996.tb04356.x>
- Rengel Z, Zhang W (2003) Role of dynamics of intracellular calcium in aluminium-toxicity syndrome. *New Phytol* 159:295–314. <https://doi.org/10.1046/j.1469-8137.2003.00821.x>
- Ruiz HA, Fernandes Filho EI (1992). Cinética: software to estimate the  $I_{max}$  and  $K_m$  constants of Michaelis-Menten equation. In: 20 Brazilian meeting of soil fertility and plant nutrition. (In Portuguese.) Piracicaba, pp 124–125
- Ryder M, Gérard F, Evans DE, Hodson MJ (2003) The use of root growth and modelling data to investigate amelioration of aluminium toxicity by silicon in *Picea abies* seedlings. *J Inorg Biochem* 97:52–58. [https://doi.org/10.1016/S0162-0134\(03\)00181-8](https://doi.org/10.1016/S0162-0134(03)00181-8)
- Sangster AG, Hodson ML (2001) Silicon and aluminium deposition in the cell wall phytoliths of gymnosperm leaves. In: Meunier JD, Colin FAA (eds) *Phytoliths: applications in earth science and human history*. A A Balkema, Rotterdam, pp 343–355
- Shen X, Xiao X, Dong Z, Chen Y (2014) Silicon effects on antioxidative enzymes and lipid peroxidation in leaves and roots of peanut under aluminum stress. *Acta Physiol Plant* 36:3063–3069. <https://doi.org/10.1007/s11738-014-1676-8>
- Silva S, Pinto-Carnide O, Martins-Lopes P, Matos M, Guedes-Pinto H, Santos C (2010) Differential aluminium changes on nutrient accumulation and root differentiation in an Al sensitive vs. tolerant wheat. *Environ Exp Bot* 68:91–98. <https://doi.org/10.1016/j.envexpbot.2009.10.005>
- Simões CC, Melo JO, Magalhaes JV, Guimaraes CT (2012) Genetic and molecular mechanisms of aluminium tolerance in plants. *Genet Mol Res* 11:1949–1957. <https://doi.org/10.4238/2012.July.19.14>
- Singh VP, Tripathi DK, Kumar D, Chauhan DK (2011) Influence of exogenous silicon addition on aluminium tolerance in rice seedlings. *Biol Trace Elem Res* 144:1260–1274. <https://doi.org/10.1007/s12011-011-9118-6>
- Tabuchi A, Matsumoto H (2001) Changes in cell-wall properties of wheat (*Triticum aestivum*) roots during aluminum-induced growth inhibition. *Physiol Plant* 112:353–358. <https://doi.org/10.1034/j.1399-3054.2001.1120308.x>
- Taiz L, Zeiger E (2013) *Plant physiology*, 5rd edn. Sinauer, England
- Tennant DA (1975) A test of a modified line intersect method of estimating rootlength. *J Ecol* 63:995–1001. <https://doi.org/10.2307/2258617>
- Tokura AM, Furtini Neto AE, Carneiro LF, Curi N, Santos JZL, Alovisei AA (2011) Dynamics of phosphorus forms in soils with contrasting texture and mineralogy cultivated with rice. (In Portuguese, with English abstract.) *Acta Sci Agron* 33:171–179. <https://doi.org/10.4025/actasciagron.v33i1.1435>
- Vázquez MD, Poschenrieder C, Corrales I, Barceló (1999) Changes in apoplastic Al during the initial growth response to Al by roots of a resistant maize variety. *Plant Physiol* 119:435–444. doi: <https://doi.org/10.1104/pp.119.2.435>
- Vitarello VA, Capaldi FR, Stefanuto VA (2005) Recent advances in aluminium toxicity and resistance in higher plants. *Braz J Plant Physiol* 17:129–143. <https://doi.org/10.1590/S1677-04202005000100011>
- Wang Y, Stass A, Horst WJ (2004) Apoplastic binding of aluminium is involved in silicon-induced amelioration of

- aluminum toxicity in maize. *Plant Physiol* 136:3762–3770. <https://doi.org/10.1104/pp.104.045005>
- Xia J, Yamaji N, Kasai T, Ma JF (2010) Plasma membrane-localized transporter for aluminum in rice. *Proc Natl Acad Sci U S A* 107:18381–18385. <https://doi.org/10.1073/pnas.1004949107>
- Yamamoto Y, Hobayashi Y, Matsumoto H (2001) Lipid peroxidation is an early symptom triggered by aluminum, but not the primary cause of elongation inhibition in pea roots. *Plant Physiol* 125:199–208. <https://doi.org/10.1104/pp.125.1.199>
- Yang JL, Li YY, Zhang YJ, Zhang SS, Wu YR, Wu P, Zheng SJ (2008) Cell wall polysaccharides are specifically involved in the exclusion of aluminum from the rice root apex. *Plant Physiol* 146:602–611. <https://doi.org/10.1104/pp.107.111989>
- Yang JL, Zhu XF, Peng YZ, Zheng C, Li GX, Liu Y, Shi YZ, Zheng SJ (2011) Cell wall hemicelluloses contributes significantly to aluminum adsorption and root growth in *Arabidopsis*. *Plant Physiol* 155:1885–1892. <https://doi.org/10.1104/pp.111.172221>
- Yi M, Yi H, Li H, Wu L (2010) Aluminum induces chromosome aberrations, micronuclei, and cell cycle dysfunction in root cells of *Vicia faba*. *Environ Toxicol* 25:124–129. <https://doi.org/10.1002/tox.20482>
- Zhang XB, Liu P, Yang YS, Xu GD (2007) Effect of Al in soil on photosynthesis and related morphological and physiological characteristics of two soybean genotypes. *Bot Stud* 48:435–444
- Zheng SJ, Yang JL (2005) Target sites of aluminum phytotoxicity. *Biol Plant* 49:321–331. <https://doi.org/10.1007/s10535-005-0001-1>
- Zobel RW, Kinraide TB, Baligar VC (2007) Fine root diameters can change in response to changes in nutrient concentrations. *Plant Soil* 297:243–254. <https://doi.org/10.1007/s11104-007-9341-2>