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REGULAR ARTICLE

The uptake of macronutrients by an active silicon accumulator plant growing in two different substrata

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Abstract

Pennisetum clandestinum (*Graminae/Poaceae*) an active Si-accumulator, was cultivated in two different substrata, both with reduced Si solubility. Plants growing in organic-rich soils contained much less Ca, K, Na and Si, than species growing in sandy soils. Although the highest macronutrient concentrations were associated to the highest Si levels in the organs of *P. clandestinum*, the R correlation values indicate that Si does not influence the internal balance and the uptake of these elements. In *ca* 65% of the cases roots have the highest average values regardless of the type of culture, while the contents of Mg in the shoots and roots of *P. clandestinum* were generally not significantly different (P>0.05). A significant decline of the macronutrient levels associated to the shoots and roots of *P. clandestinum* was observed from the 4th to the 6th month assay, especially for Ca in both organs, while for Mg and Na the decline is focused mainly in the shoots; K and Si decline is generally below 10%. When average values of Si in shoots and roots of plants collected from organic-rich and sandy soils were plotted against the average concentrations of Ca, K, Mg and Na in the same organs, weak but positive R correlation values were obtained - the highest R values were observed for Na and K and the lowest for Ca and Mg, regardless of the culture. Exception for the high R value observed for K, although the influence of Si on the K status in the whole plant is time-depending - R values, diminished from the 4th to the 6th month, as it happens in the majority of the cases. In conclusion, *P. clandestinum* can grow well and healthily in substrata with acid pH values and high carbonate content and low solubility of Si suggesting that the definition of the essentiality of Si, even in a Si-accumulator plant is still a matter of great controversy.

Key words: Macronutrients, Organic-rich soil cultures, *Pennisetum clandestinum*, Sand cultures, Silicon

Introduction

Pennisetum clandestinum Hochst. ex Chiov (Kikuyu grass, Graminae/Poaceae) is an active Si accumulator, growing in altitude in the natural habitat in East and Central Africa, and a plant used in pastures all over the world (Fulkerson et al., 1998; Williams and Baruch, 2000). Although Si is not essential for higher plants, it improves fitness in nature significantly and it increases agricultural productivity (Raven, 2003). Its presence and availability influences many aspects of the biology of plants, particularly the mineral nutrition balance. Miyake and Takahashi (1985) observed that soybean plants grown without Si, accumulated unusually high concentrations of P, while the addition of Si in the medium increased K concentration in shoots and roots but reduced Na in salt-stressed barley (Liang, 1999), although Gunes et al. (2007) observed that different Si applications on barley growing in sodic-boron toxic soil does not influence their Na contents.

Moreover, Si is known to effectively mitigate various abiotic stresses such as aluminum, arsenic, cadmium, chromium or manganese toxicities, or salinity, drought, chilling and freezing stresses. The mechanisms of Si-mediated alleviation of metal toxicities in higher plants may include the stimulation of antioxidant systems, the complexation or co-precipitation of toxic metal ions with Si or the interference with the uptake processes (Liang et al., 2007). The Si-mediated alleviation of metals toxicity suggests that Si could be a candidate for Cd (Rizwan et al., 2012), Cr (Ali et al., 2013) or As (Tripathi et al., 2013)

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detoxification in crops under Cd, Cr or As-contaminated soils.

Different soil types may also influence the content of Si within the same plant, without promoting an imbalance in mineral content in general (Henriet et al., 2008). The uptake of Si by perennial ryegrass is influenced by the soil type, source of Si and rate of Si applications (Nanayakkara et al., 2008) and the Si content of the plants increased with increasing rates of applications.

Nevertheless, we agree with Epstein (1994) who claimed that Si in higher plants is beneficial but not essential, which is consistent with the findings of Ma et al. (2002) who observed a rice mutant defective in Si uptake, which is neither phenotypically different from the wild type nor different in terms of nutrient uptake especially P and K. Otherwise, the beneficial effects of Si are mainly associated with its high deposition in plant tissues enhancing their strength and rigidity and its capacity to overcome stresses, leading some authors to purpose transgenic crops with the genes controlling Si uptake (Richmond and Sussman, 2003; Ma and Yamaji, 2006).

Sandy soils are low in plant-available Si (Datnoff et al., 1997) as well as those with high silt and organic matter contents. Since the solubility of monosilicic acid is much reduced in the presence of Al, Ca and Fe and low pH values (Birchall, 1978), an experiment where several factors (quartz sand, high organic matter and carbonate contents and low pH) might probably affect the uptake of Si by *P. clandestinum* was undertaken, in order to evaluate the effects on growth, mineral balance and assess the extension of the beneficial effect of Si, if really exists.

Materials and Methods

Pennisetum clandestinum (Hochst. ex Chiov) plants used in soil and sand cultures were cultivated according to the previously described methods (Reboredo, 1988, 1991; Reboredo et al., 2006). Small cuttings had been in water for three-four days and were transported a posteriori to sand and soil cultures in pots with ca. 1700 cm3 volume under daylight.

Each pot contained a single cutting; 120 individuals were tested - half of them growing in sand (82.2% sand, 15.6% carbonate content, 1.0% organic matter and 1.2% silt-clay fraction; pH 6.9; water content 16%) and the other half in an organic-rich soil (38.2% coarse fraction, 12.6% carbonate content, 43.3% organic matter and 5.9% silt-clay fraction; pH 5.6; water content 48%).

Sand and organic-rich soil characterization was undertaken according to Rivière (1977). The elemental composition of both substrata is described in a previous work (Reboredo et al. 2006).

Cuttings were irrigated twice a week with 50 ml of a nutrient solution (Baumeister and Schmidt, 1962) at a final pH of 5.6. From the 2nd month until the end of the experiment – summer period, plants were supplied with a nutrient solution three times a week in order to avoid an excessive dryness of the substrata.

Five *P. clandestinum* plants from each different substrata (each pot contained a single plant) were collected 4 and 6 months after the beginning of the treatment, washed with bidistilled water and separated into shoots and roots and dried at 100ºC to constant weight. Vegetal material was digested by HNO3 according Vandecasteele and Block (1993), Ca, K, Mg, Mn, Na, and Si being determined by atomic absorption spectrometry.

N and P were also monitored in triplicate in plant samples. Nitrogen was determined according to the Kjeldahl method (Watts and Halliwell, 1996) and phosphorus, according to the method described by Watanabe and Olsen (1965). Fibre determination was achieved through the Weende method (Adrian et al., 2000).

An analysis of variance (ANOVA) was performed and average values were compared by the Tukey's test (Sokal and Rohlf, 1994). The adjustment of data through a linear regression analysis was performed as well as the R value.

Results

In what concerns Si, Ca, Mg, Na and K, roots of *Pennisetum clandestinum* have, in ca 65% of the cases, the highest average values regardless of the type of culture considered, except for K and Mg. In the latter case, however, shoots in sand cultures contained an average value of 1.0% Mg, against 0.9% Mg observed in roots ($P>0.05$) while shoots growing in organic-rich soils exhibited almost twice the average Mg value of roots (Table 1).

Table 1. *Average values of Si, Ca, Mg, Na, K and total N and P in *Pennisetum clandestinum* shoots and roots.

	Sandy soils				Organic-rich soils			
	Shoot		Root		Shoot		Root	
§Si*	1697b	± 260	2164c	± 226	788a	± 168	870a	± 243
†Si	1415b	± 134	1954c	± 173	732a	± 92.4	791a	± 143
decline (%)	*16.6*		*9.7*		*7.1*		*9.1*	
§Ca**	3.5c	± 0.54	5.3d	± 0.7	0.61a	± 0.10	1.5b	± 0.1
†Ca	2.3c	± 0.32	4.4d	± 0.69	0.48a	± 0.07	1.1b	± 0.16
decline (%)	*34.3*		*17.0*		*21.3*		*26.7*	
§Mg**	1.0bc	± 0.19	0.91b	± 0.13	1.2c	± 0.12	0.64a	± 0.07
†Mg	0.73b	± 0.11	0.78b	± 0.10	0.83b	± 0.06	0.59a	± 0.06
decline (%)	*27.0*		*14.3*		*30.8*		*7.8*	
§Na	2655b	± 364	3936d	± 606	1970a	± 320	3479c	± 450
†Na	2084b	± 304	3459c	± 474	1459a	± 291	3139c	± 259
decline (%)	*21.5*		*12.1*		*25.9*		*10.0*	
§K**	6.9c	± 1.3	4.6b	± 0.54	6.4c	± 1.0	3.4a	± 0.28
†K	6.5c	± 0.9	4.2ab	± 0.5	5.3bc	± 0.5	3.1a	± 0.6
decline (%)	*5.8*		*8.7*		*17.2*		*8.8*	
§Fibre**	25.5				25.8			
†Fibre	17				21			
decline (%)	*33.3*				*18.6*			
§Total N**	2.4b	± 0.07	1.4a	± 0.12	3.7c	± 0.3	1.1a	± 0.17
†Total N	2.0b	± 0.15	1.1a	± 0.13	3.1c	± 0.3	0.9a	± 0.15
decline (%)	*16.7*		*21.4*		*16.2*		*18.2*	
§Total P**	0.11b	± 0.03	0.07ab	± 0.01	0.34c	± 0.07	0.11b	± 0.03
†Total P	0.10b	± 0.03	0.06ab	± 0.01	0.27c	± 0.05	0.09b	± 0.03
decline (%)	*9.1*		*14.3*		*20.6*		*18.2*	
§N/P ratio	21.8				10.9			
†N/P ratio	20.0				11.5			

Mean values, in the same row, not followed by a common letter are significantly different (P<0.05);

(*) Values referred in Reboredo et al. 2006

Mean values are expressed as mg.kg-1 dry weight ± S deviation or as % dry weight (**)

Samples collected in the 4th (§) and 6th month assay (†)

The levels of Ca, K, Na and Si of *P. clandestinum* plants growing in sand were clearly higher than those observed in plants growing in organic-rich soils, with an exception for the Mg levels which were similar, regardless of the type of culture (Table 1). This fact was also confirmed at the end of the experiment – the Mg levels of plant shoots from different substrata and the levels of the roots collected from the sandy soils were not significantly different (P>0.05).

Despite the differences of both matrices, the average levels of Si in shoots and roots of plants cultivated in sand were, at the end of the experiment (6th month), 1.9 and 2.5 times higher than the average values found in the same organs, in plants growing in organic-rich soils (Table 1). These ratios were similar in the 4th month assay - 2.2 and 2.5 for shoots and roots, respectively.

When total mean values of Si in shoots and roots of plants collected from organic-rich soils and sandy soils were plotted against the average concentrations of Ca, K, Mg and Na in the same organs, R positive values were observed (Tables 2, 3, 4 and 5). Several conclusions can be enhanced such as: in general the highest R values were observed for Na and K and the lowest R values for Ca and Mg, regardless of the culture; R values decreased from the 4th month assay to the end of the experiment, in the great majority of the cases and finally the strong correlation (P<0.001) between Si and K in shoots collected from organic soils at the 4th month assay (R - 0.980).

Table 2. *Pennisetum clandestinum* R values from plants growing in organic-rich soils

	Shoots organic-rich soils 4 months					Roots organic-rich soils 4 months				
	Ca	Mg	Na	K	Si	Ca	Mg	Na	K	Si
Ca	-									
Mg	0.151	-				0.019	-			
Na	0.879**	0.103	-			0.090	0.253	-		
K	0.328	0.277	0.562	-		0.002	0.690	0.669	-	
Si	0.233	0.210	0.457	0.980***	-	0.195	0.407	0.708	0.607	-

***P<0.001; ** P < 0.01

Table 3. *Pennisetum clandestinum* R values from plants growing in organic-rich soils

	Shoots organic-rich soils 6 months					Roots organic-rich soils 6 months				
	Ca	Mg	Na	K	Si	Ca	Mg	Na	K	Si
Ca	-									
Mg	0.209	-				0.000	-			
Na	0.451	0.673	-			0.062	0.808*	-		
K	0.100	0.857**	0.307	-		0.185	0.206	0.289	-	
Si	0.057	0.560	0.176	0.568	-	0.011	0.631	0.638	0.614	-

* P < 0.05; ** P < 0.01

Table 4. *Pennisetum clandestinum* R values from plants growing in sandy soils

	Shoots sandy soils 4 months					Roots sandy soils 4 months				
	Ca	Mg	Na	K	Si	Ca	Mg	Na	K	Si
Ca	-									
Mg	0.334	-				0.112	-			
Na	0.236	0.329	-			0.794*	0.066	-		
K	0.039	0.019	0.312	-		0.195	0.065	0.338	-	
Si	0.105	0.301	0.652	0.591	-	0.107	0.040	0.438	0.730	-

* P < 0.05

Table 5. *Pennisetum clandestinum* R values from plants growing in sandy soils

	Shoots sandy soils 6 months					Roots sandy soils 6 months				
	Ca	Mg	Na	K	Si	Ca	Mg	Na	K	Si
Ca	-									
Mg	0.254	-				0.249	-			
Na	0.285	0.150	-			0.017	0.187	-		
K	0.805*	0.069	0.587	-		0.052	0.899**	0.345	-	
Si	0.489	0.207	0.468	0.514	-	0.056	0.388	0.337	0.530	-

* P < 0.05; ** P < 0.01

When average concentrations of each studied element from shoots and roots of plants collected from both substrata were plotted against the average concentrations of the remaining elements in the same organs, weak R positive values were observed, generally, although in a few cases strong correlations were noted (Tables 2, 3, 4 and 5). Nevertheless, no pattern can be established from the results here presented.

When the K, Na and Si levels at the 4th month were compared with those measured two months later, a strong decline was detected, especially for shoot Na contents – 25.9% and 21.5% for shoots growing in organic-rich soils and in sandy soils, respectively. The Si decline was high in shoots collected from sandy soils (16.6%) and low in shoots collected from organic-rich soils (7.1%), occurring the inverse for K (Table 1). The decline of K and Si at the bellow-ground organs is less 10% (Table 1).

The strong decline of Ca and Mg, from the 4th to the 6th month, was evident in shoots and roots of *Pennisetum clandestinum* collected from sandy and organic-rich soils, although the Mg decline for the roots was considerably lower, varying between 14.3% and 7.8% (Table 1).

In terms of shoot and root declines, regardless of the substrata used, we observed the following trend: Shoot decline – Ca/Mg>Na>K/Si; Root decline – Ca>Mg/Na>K/Si

Total N is high in shoots growing in organic-rich soils with percentages varying between 3.7 and 3.1% at the 4th and 6th month assay, respectively, far above the average values found in shoots growing in sandy soils. The average root values of N in the same periods, and regardless the type of cultures, were not significantly different (P>0.05) - Table 1. Plants growing in sandy soils exhibited very low amounts of total P, while those growing in organic-rich soils were not deficient in this particular element.

The fibre contents of the shoots of plants cultivated in sandy and organic rich soils were similar at the 4th month assay, while at the 6th month shoots collected from the same substrata exhibited a decline of 33.3% and 18.6%, respectively (Table 1).

Discussion

The Si levels of *Pennisetum clandestinum* were very low, especially in plants growing in organic rich soils, which is probably related with the nature of the matrices mainly quartz, high carbonate and organic matter contents, besides Al and Fe levels of the silt-clay fraction which could lower the concentration of monosilicic acid in soil solution.

Although the pH of the nutrient solution favors the uptake of micronutrients instead of macronutrients and Si, Miles (1998) observed that *P. clandestinum* is tolerant to high soil acidity without significant effects on yield, while Sidari et al. (2004) concluded that *P. clandestinum* is a grass tolerant to pH values ranging between 4.0 and 6.0, without adverse effects on biomass production and nutritive properties (amino acid content, crude protein) although the mineral balance had not been studied.

Depending on the type of soils the average leaf Si concentration ranges from 2.7 to 3.9 g kg^{-1} for bananas cropped in Eastern slopes in Guadeloupe and from 7.7 to 9.6 g kg^{-1} for those cropped in Western slopes (Henriet et al., 2008). These differences in the Si content do not interfere with the mineral content in the leaves which were very similar, in general. For example Mg ranges from 2.9 to 3.2 g kg^{-1}, K from 28.3 to 33.3 g kg^{-1}, Ca from 4.1 to 6.6 g kg^{-1} and P from 1.8 to 2.2 g kg^{-1}. The largest variation was observed for Mn – 0.37 to 1.5 g kg^{-1}.

Nanayakkara et al. (2008) also observed that the uptake of several macro and micronutrients by perennial ryegrass (*Lolium perenne* L.) was not influenced by increasing amounts of Si applied to the soil, nor the type of soil. This non-dependence of Si, as it happens in our case, raises the question why accumulate so much Si especially in above-ground organs, if the same plants can live healthily with much less amounts without decreasing yields and the resistence to diseases.

The Si accumulation by the long-lived leaves of *Sasa veitchii* was rapid during spring and summer and slow during winter (Motomura et al., 2002). The Si decrease in *P. clandestinum*, generally less than 10%, runs in parallel with the summer season and the beginning of autumn, when ends the experiment and a decline in the mineral content of kikuyu occurred (Table 1).

The Ca levels in the shoots of *Pennisetum clandestinum* growing in sandy soils were clearly higher (3.5%) than those observed by Huett and Menary (1980) in the same plant organs and disagrees with several statements that kikuyu is deficient in Na and Ca (Fulkerson, 2007) and presented several imbalances of Ca, P, K, Mg and Na deficiency (Marais, 2001).

Sodium shoot levels of kikuyu grass range between 0.2 and 0.15% for plants growing in organic soils and 0.26 and 0.21% for those growing in sand, above the 0.14% value referred by Fulkerson (2007) for summer. Our Ca levels also indicate that instead of provide supplements to dairy cows grazing kikuyu pastures, soils can be amended with calcium compounds, besides the fertilization with N.

The application of calcium carbonate linearly increased the Ca concentration of kikuyu grass Whittet cultivar, but linearly decreased the Si concentration, as well as Mg and Mn levels (Mathews et al., 2009). Thus, it seems that the choice of the type of soil and adequate management are critical while the response of kikuyu grass is enough flexible to fit the purpose of those who search a better nutritive value.

An antagonistic effect of K on Si concentrations of the grass *Paspalum vaginatum* due to the soil treatment with potassium silicate was observed by Trenholm et al. (2001). The increased K tissue concentration reduced Si concentration, indicating preferential uptake of K and exclusion of Si.

In our case, Si does not seem to influence the internal balance and the uptake of K - an exception was noted in the 4^{th} month assay, the strong correlation (P<0.001) between Si and K (R - 0.9801) in the shoots of *P. clandestinum* growing in organic soils. Also, the ionic balance between K and Na did not seem to be affected in *P.*

clandestinum plants - no significant correlations were observed between these elements in both substrata, regardless of the month of vegetal sample collection (Tables 2, 3, 4 and 5).

Broadley et al. (2004) observed that K is the dominant cation in shoot tissues of Poales under both experimental and natural conditions with an average value of 5.44% (n =18), which agrees with our results, while Mg ranges within Poales between 0.12% and 0.30%, clearly below our lower average value – 0.73%, indicating that Mg uptake by *P. clandestinum* is unaffected by the differences in the matrices.

Weak positive correlations between Mg and Ca levels of *P. clandestinum* shoots were observed, but not inverse correlations, as noted by Reboredo and Silvares (2007) studying the mineral balance of normal and abnormal stems (fasciated forms) of *Spartium junceum* - the elements were strongly inverse correlated.

The more silicon is present in the tissues the less phosphorus is detected. When the levels of P are high, as it happens for shoots growing in organic rich soils (approximately three times more than the levels observed in shoots growing in sand), the respective Si content is low, which agrees with Miyake and Takahashi (1985), who observed that soybean plants grown without Si, accumulated unusually high P concentrations. However, several authors confirmed that Si appplications can increase the phosphorus content in rice plants (Islam and Saha, 1969) while others showed that the addition of phosphate had not significant effect on Si absorption by wheat (Rains et al., 2006).

Comparatively with the levels of P measured in the 4th month assay, declines of 9.1% and 20.6% were observed at the end of the experiment, in the shoots of *P. clandestinum* growing in sand and organic-rich soils, respectively. These declines are parallel to the end of the summer season and beginning of autumn, which agrees with Fulkerson et al. (1998), who verified that in *P. clandestinum* the P levels changed significantly with season falling and the gradual increase of the dormancy.

From the nine tropical pasture grasses studied, Andrew and Robin (1971), observed that *P. clandestinum* was the least responsive and *Melinus minutiflora* the most responsive, in terms of growth and chemical composition, after phosphate addition to phosphate-deficient soils. The phosphate application also decreased the concentration of K in plants and increased the Mg contents in the majority of the species, without significant effects on Ca contents.

It seems that the percentage of the total N is independent from the Si content of the organs, whatever type of culture there is. Comparatively with the levels of N measured in the 4th month assay declines of 16.7% and 16.2% were observed at the end of the experiment, in the shoots of plants growing in sand and organic-rich soils, respectively.

The analysis of the N/P shoot concentration ratio partially agrees with the indication of a factor 10 (Tessier and Raynal, 2003), but only for shoots growing in organic-rich soils. The ratios of shoots growing in sandy soils reflect a P limitation, probably due to the Si content.

The average crude fibre contents at the 4th month assay is in agreement with the values observed by Muscolo et al. (2003) and Fulkerson (2007) although two months later these values had declined 33.3% and 18.6%, for shoots collected in sandy and organic rich soils, respectively.

Conclusions

Pennisetum clandestinum an active Si accumulator can grow well and healthily in the substrata where Si is mainly insoluble suggesting that the lack or poverty of this element is not a limiting factor. Only P seems to suffer the influence of Si in the case of plants growing in sandy soils. Even K, which seems to be strong correlated to the respective Si contents of shoots growing in organic soils (not in sandy soils), reveals, as the experiment develops, a gradually weaker correlation as assessed by the R values, enhancing in this particular case, that Si could be beneficial only at a certain stage of growth.

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