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Effects of silicon (Si) fertilization on gas exchange and production in *Brachiaria*

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Abstract

Calcium silicate ($CaSiO_3$) applied to the soil may increase Si content in the soil and plants, as well as reduce sweating and increase water use efficiency. In this study, we aimed to investigate whether the application of $CaSiO_3$ increased Si content in plants and interfered with gas exchange and production components in *Brachiaria*. The experiment was performed using 8-L plastic pots in a greenhouse. Treatments were arranged in a randomized block design in a 3 × 5 factorial: three soils (Rhodic Acrudox, Rhodic Hapludox, and Arenic Hapludult) and five silicate rates (0, 1, 2, 4, and 6 t ha^{-1} of $CaSiO_3$/$MgSiO_3$) were used; four replications were performed. $CaSiO_3$ application to the soil increases Si concentration in the leaves. Si in plants reduces internal CO_2 concentration and increases the efficiency of water use and instantaneous carboxylation efficiency. In soils with low pH and a high Al^{+3} level, which is toxic, reduction in plant sweating increases the intrinsic efficiency of water use in *Brachiaria*. Si helped to alleviate the toxic effects of Al^{+3}.

Keywords: calcium silicate; intercellular CO_2 concentration; transpiration; efficient use of water.
Abbreviations: *A*_carbon assimilation rate, C_i_internal concentration CO_2, *E*_transpiration, *gs*_stomatal conductance, *WUE*_water use efficiency.

Introduction

Brazil has about 100 million hectares of cultivated pastures, and many of them have already undergone 10 years of grazing; approximately 60% of the areas are in a state of advanced degradation (Barducci et al., 2009). On a short- and mid-term basis, more than 30 million hectares are going to be recovered, to be degraded or sharp production decline process (Sano et al., 2008). A reason for the resistance of *Brachiaria* grass in Cerrado soil may be its ability to absorb and accumulate Si in the epidermis of leaves, thereby reducing the toxic effects of aluminum (Al), manganese (Mn), and iron (Fe) and increasing phosphorus (P) availability (Cocker et al., 1998; Korndörfer et al., 2001). Tropical soils are highly weathered, acidic, and low in Si availability for plants. Limestone has been predominantly used to correct soil acidity; however, alternate corrective materials such as silicates are available, which increase soil pH, provide Ca and Mg, and neutralize toxic Al and available Si (Korndörfer et al., 2001; Sarto et al., 2014a; Sarto et al., 2015). Si has been considered an essential nutrient for mainly grasses, and Zn concentration is higher in monocots than in dicots (van Raij, 1991). This results in several benefits for plants, especially greater tolerance to insect attack (Epstein, 2001) and diseases (Marschner, 1995), reduced sweating (Datnoff et al., 2001; Marschner, 1995), and a higher photosynthetic rate due to improvement in leaf architecture (Deren, 2001). However, Si is still relatively unknown and rarely applied in agriculture.

In many cases, increase in Si availability has increased crop development and yield, and this nutrient can indirectly influence some photosynthetic and biochemical aspects, especially in plants under biotic or abiotic stress conditions (Ma and Yamaji, 2006). Maximum growth and biomass accumulation in plants that received Si application are associated with changes in plant architectures, making them more erect, improving the angle of the leaves and light interception, avoiding excessive self-shading, delaying senescence, increasing the structural rigidity of tissues, and improving photosynthesis and reducing lodging (Gong and Chen, 2012; Ma and Yamaji, 2008). These beneficial effects are attributable to Si deposited in the cell wall of various plant organs (Ma and Yamaji, 2006) and other mechanisms. High deposition of Si in tissues results in a physical barrier that enhances the strength and rigidity of the tissues. There are few studies on the effect of Si on plant nutrition, and most of the studies have reported aspects of wheat growth and the beneficial role of Si in resistance to biotic and abiotic stresses (Rizwan et al., 2012). In addition to this aspect, the beneficial effects of Si are not always observed (Dann and Muir, 2002). There is evidence that Si has no effect on dry matter yield in *Brachiaria* grasses under conditions of water stress (Melo et al., 2003). Increased photosynthetic capacity in plants may be related to the presence of Si in the system, which causes better arrangement of leaves, makes them upright and resistant to possible damage, and reduces evapotranspiration (Agarie et al., 1998). Studies on Si absorption and gas exchange are largely restricted to crops such as rice, wheat, sugarcane, and cucumber, but few studies have investigated the importance of Si in natural vegetation and pastures.

Considering that the use of silicate tends to be the most common agricultural practice in Brazil, improved understanding of the effect of Si on crops is essential for adopting management strategies for improving crop production. In this context, the purpose of this study was to investigate whether the application of calcium silicate ($CaSiO_3$) in the soil may increase Si content in *Brachiaria* and interfere with gas exchange and production components.

Results and Discussion

Si absorption

Si content in the leaves increased with the application of $CaSiO_3$ to the soil (Fig 1). Si absorption capacity is the primary determinant of whether Si cell uptake may be improved by transpiration. This is consistent with the results of Korndörfer et al. (2010), who observed higher absorption of Si in both *Brachiaria brizanta* 'Marandu' and *Brachiaria brizanta* 'Mombasa' because of silicate application. Pereira et al. (2004) highlighted the existence of close links between foliar concentrations and the Si dose applied. This increase may be related to the higher nutrient content in the soil (Fonseca et al., 2009; Sarto et al., 2014b; Sarto et al., 2015), and grasses such as *Brachiaria* and *Panicum* are classified as accumulators because of their high capacity for accumulating Si (Ma et al., 2001).

Gas exchange

Carbon assimilation rate (A) and stomatal conductance (gs)
A and *gs* of *Brachiaria* were not influenced statistically ($p \leq 0.05$) because of $CaSiO_3$ application to the soil (Figure 1). Average values of net carbon assimilation were 27.99, 28.61, and 29.93 µmol CO_2 m^{-2} s^{-1} and those of stomatal conductance were 0.2081, 0.2101, and 0.2533 mmol H_2O m^{-2} s^{-1} in Rhodic Acrudox (Ox1), Arenic Hapludult (Ult), and Rhodic Hapludox (Ox2) soils, respectively. This was consistent with the results obtained by Braga et al. (2009). Dias-Filho (2002) observed maximum gross leaf photosynthetic rates of 30 µmol CO_2 m^{-2} s^{-1} for the grass 'Marandu' in a greenhouse.

Internal CO_2 concentration (C_i CO_2)

A quadratic response to internal C_i within a substomatic chamber was observed, with the minimum value at 2.64, 2.86, and 2.65 t ha^{-1} and 78.37, 63.13, and 95.50 ppm in Ox1, Ult, and Ox2 soils, respectively. The results are consistent with those obtained by Ferraz et al. (2014), who found a reduction in C_i CO_2 in two cotton cultivars as a function of Si foliar application. In situations where C_i is lower, the photosynthetic rate tends to be higher, and there is an inverse relationship between C_i and photosynthetic rate (Concenço et al., 2008). However, this was not observed, and despite the reduction in C_i, there was no increase in the photosynthetic rate.

Transpiration (E)* and *intrinsic water use efficiency (A/gs)

In Ox2 soil, Si fertilization reduced the rate of E and increased A/gs, (a maximum value of 146.32 A/g_s at 2.9 t ha^{-1}); however, similar findings were not obtained for Ox1 and Ult soils. Higher sweating was observed in Ox2, probably due to the low pH and high soil content of toxic Al^{+3}, Al^{+3} decreases the total concentration of chlorophyll, but the decline in rate and is even more severe (Vitorello et al., 2005; Wang et al., 2006). Silicate increases soil pH and reduces toxic Al^{+3} levels in plants (Sarto et al., 2014a; Sarto et al., 2015), thus reducing transpiration (*E*) in *Brachiaria*; furthermore, the silica deposits in leaf tissues promote a reduction in the rate of *E* (Dayanandam et al., 1983). According to Dias et al. (2014), reduction in *E* demonstrated by Si-treated plants may be an important enhancement promoted by higher Si concentrations because it may lead to more plants tolerant to ex vitro environment. In addition, changes in the internal structure of leaves are determining factors for the acclimatization ability of a species (Hanba et al., 2002). These modifications promote reduced water loss and maintain plant water status; this may be related to the higher epicuticular wax deposition observed in Si-treated plants. Overall, plants under stress reduce stomatal conductance and transpiration and increase the efficiency of water use. Under these conditions, the rate of photosynthesis is also decreased (Ferraz et al., 2012), which was not observed in this experiment because net *A* and *gs* were not affected regardless of less *E* in Ox2. According to Inoue and Ribeiro (1988), this phenomenon is mainly influenced by temperature and water vapor saturation. Under the same conditions, differences in sweating may indicate a high or less efficient stomatal mechanism, resulting in saving of water by the plant.

Efficiency of water use (WUE) and instantaneous carboxylation efficiency (A/Ci)

Physiological *WUE* and A/C_i increased by $CaSiO_3$ application to the soils. *WUE* showed a peak at 2.63, 2.51, and 2.40 t ha^{-1} at 5.82, 5.63, and 5.71 µmol CO_2 $mmol^{-1}$ H_2O in Ox1, Ult, and Ox2 soils, respectively. A/C_i showed a peak at 2.77, 3.24, and 2.51 t ha^{-1} at 0.38, 0.44, and 0.40 in Ox1, Ult, and Ox2 soils, respectively. *WUE* is the amount of water transpired by a culture for the production of a certain quantity of dry matter (Silva et al., 2007). Thus, more efficient water use by crops can produce more dry matter per gram of water transpired. The most efficient use of water is directly related to stomatal opening time; as the plant absorbs CO_2 for photosynthesis, water is lost by sweating with varying intensity, depending on the potential gradient between the leaf surface and the atmosphere and a stream of water potentials (Concenço et al., 2007). For C_4 plants, even if the CO_2 concentration in the leaf mesophyll reaches very low levels, plants continue to accumulate biomass because the enzyme responsible for primary carboxylation in these plants, PEP carboxylase, has a high affinity for CO_2. This is possible because this group of plants has no detectable photorespiration (Silva et al., 2007). The C_4 plants also use water more efficiently. With $CaSiO_3$ application, Si is rapidly absorbed, which may confer beneficial effects on plants, such as reduced loss of water by transpiration (Barbosa Filho et al., 2001; Fageria et al., 2011), lodging resistance, more erect plants, improved photosynthetic efficiency (Tokura et al., 2011), and increased tolerance to pests (Goussain et al., 2002) and diseases (Prabhu et al., 2007; Buck et al., 2008; Rezende et al., 2009).

Agarie et al. (1998) studied the effect of $CaSiO_3$ slag on rice, who observed lesser perspiration from stomatal pores after $CaSiO_3$ application. They believed that reduced perspiration was linked to the density of the cuticle layer due to Si concentration.

Table 1. Brazilian soil classification, approximate equivalence to soil taxonomy and sampling site of the three soils from Paraná State.

Soil	Brazilian soil classification†	Soil taxonomy††	Sampling Municipality
Ox1	Eutroferric Red Latosol	Rhodic Acrudox	Marechal Cândido Rondon
Ox2	Distroferric Red Latosol	Rhodic Hapludox	Cascavel
Ult	Red-Yellow Argisol	Arenic Hapludult	Goioerê

† According to Embrapa (2013). †† USDA Soil Taxonomy (Soil Survey Staff, 2010).

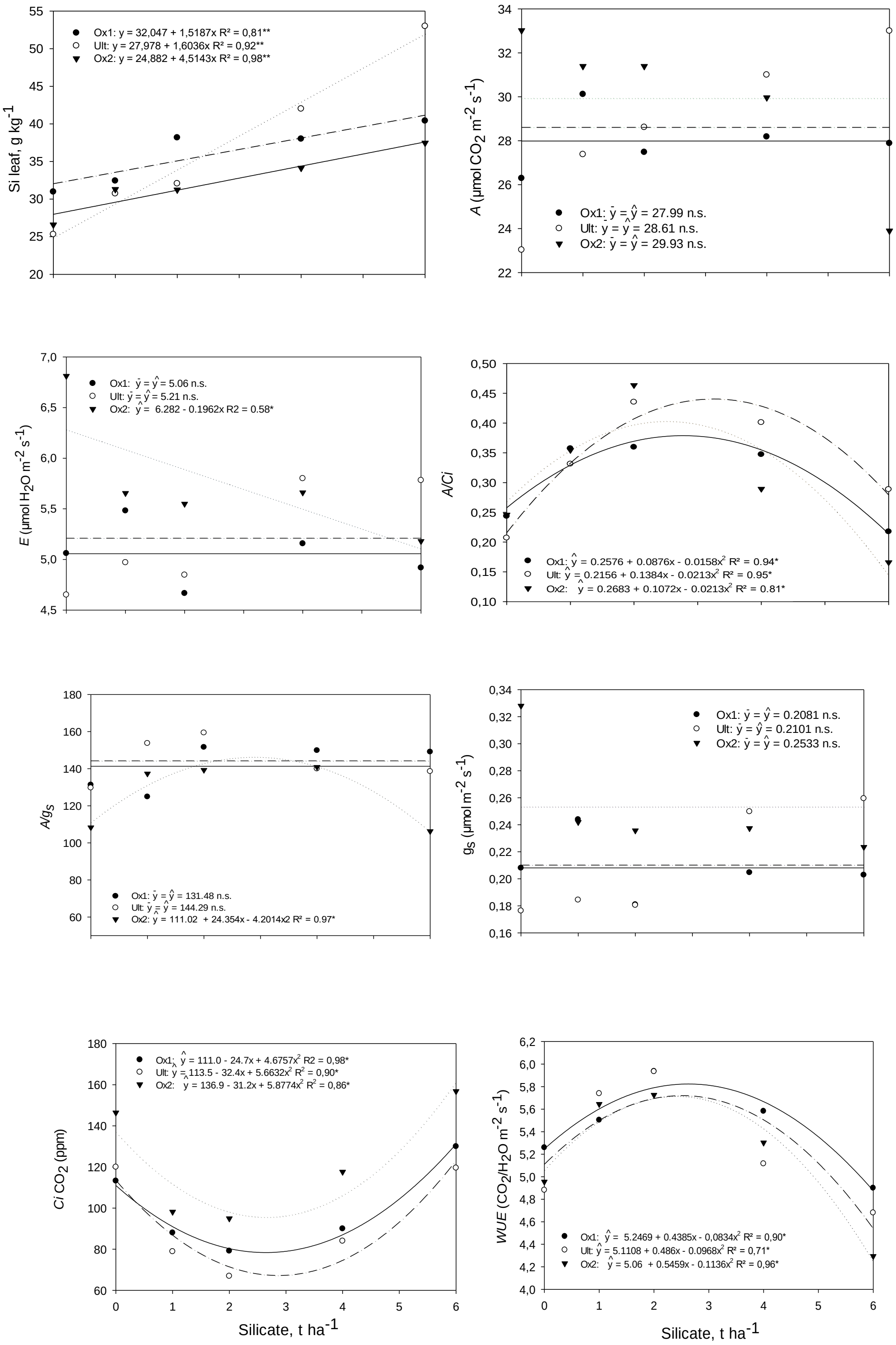

Fig 1. Mean values silicon leaf (Si), photosynthesis (*A*), stomatal conductance (g_s), intercellular CO_2 concentration (C_i CO_2), transpiration (*E*), efficient use of water (*WUE*), instantaneous efficiency carboxylation (A/C_i) and intrinsic water use efficiency (A/g_s), soils: Ox1 (—), Ult (---) and Ox2 (-·-).

Table 2. Some physical and chemical properties of the soils.

Soil characteristics	Soil		
	Acrudox	Hapludox	Hapludult
Soil pH	5.3	4.1	6.2
Clay (g kg^{-1})	550.0	535.0	100.0
Silt (g kg^{-1})	370.0	430.0	45.0
Sand (g kg^{-1})	80.0	35.0	855.0
Organic matter (g kg^{-1})	26.0	39.6	22.0
Available P (mg kg^{-1})	37.1	22.5	40.7
H + Al ($cmol_c$ kg^{-1})	4.6	10.7	2.0
Exchangeable Al ($cmol_c$ kg^{-1})	0.0	2.4	0.0
Exchangeable K ($cmol_c$ kg^{-1})	0.15	0.20	0.20
Calcium ($cmol_c$ kg^{-1})	4.8	4.0	2.5
Magnesium ($cmol_c$ kg^{-1})	1.8	0.5	0.7
CEC ($cmol_c$ kg^{-1}) †	11.4	15.4	5.4
Soil base saturation (%)	60.0	30.0	63.0
Copper (mg kg^{-1})	15.0	8.2	9.9
Zinc (mg kg^{-1})	132.0	110.0	247.0
Iron (mg kg^{-1})	41.1	35.4	28.5
Manganese (mg kg^{-1})	3.9	8.2	5.4
Silicon (mg kg^{-1})	19.3	15.8	18.0

† CEC: cation exchange capacity.

Table 3. Mean values of height, number of tillers and green leaves *Brachiaria* according to the calcium silicate.

Silicate	Plant Height			Tillers			Green leaves		
	Ox1	Ox2	Ult	Ox1	Ox2	Ult	Ox1	Ox2	Ult
t ha^{-1}		cm				nº plant			
0	35.0	40.8	32.9	8.1	7.2	7.3	4.5	4.1	4.6
1	37.5	41.3	28.8	8.1	7.2	6.1	4.9	4.2	4.4
2	31.1	38.7	33.5	6.8	6.3	5.6	4.5	4.3	4.7
4	34.4	41.9	32.8	7.2	5.0	6.6	4.8	4.3	4.0
6	32.2	39.4	35.2	7.4	7.4	6.4	4.9	3.8	5.0
Mean	34.0b	40.4a	32.6b	7.5a	6.6ab	6.4b	4.7a	4.2b	4.5a
F values									
Soil		14.4^{**}			4.28^{*}			6.9^{*}	
Rates		0.30^{ns}			2.25^{ns}			0.35^{ns}	
Soil*Rates		0.99^{ns}			0.88^{ns}			1.65^{ns}	
CV (%)		18.2			18.9			10.8	

** and * significant at 1% and 5% probability, respectively, by F test; ns not significant. Means followed by the same lowercase letter on the line do not differ statistically by 5% Tukey test.

Table 4. Mean values of stem diameter, fresh and dry biomass of *Brachiaria* according to the calcium silicate.

Silicate	Stem diameter			Fresh biomass			Dry biomass		
	Ox1	Ox2	Ult	Ox1	Ox2	Ult	Ox1	Ox2	Ult
t ha^{-1}		mm				g $plant^{-1}$			
0	4.7	4.7	5.1	65.2	96.3	50.5	19.3	22.5	18.2
1	4.7	4.2	4.5	59.8	73.3	48.4	18.0	18.8	17.2
2	5.0	4.3	4.7	67.7	78.9	39.7	19.5	20.1	16.4
4	4.8	4.7	4.6	62.4	84.4	53.0	18.5	20.0	16.9
6	5.2	4.7	4.7	63.4	71.4	46.1	18.9	19.7	17.8
Mean	4.9	4.5	4.7	63.7b	80.86a	47.5c	18.8ab	20.2a	17.3c
F values									
Soil		2.68^{ns}			43.8^{**}			9.44^{**}	
Rates		1.34^{ns}			1.90^{ns}			1.45^{ns}	
Soil*rates		0.63^{ns}			1.17^{ns}			0.50^{ns}	
CV (%)		10.11			17.6			11.3	

** and * significant at 1% and 5% probability, respectively, by F test; ns not significant. Means followed by the same lowercase letter on the line do not differ statistically by 5% Tukey test.

In plants, Si fertilization reduces the values of *E*, resulting in less loss of water vapor. Furthermore, the plants start using water more efficiently and fix a greater amount of CO_2 per molecule of water transpired. This is possible due to the accumulation of Si, which provides mechanical protection to the skin and increases drought resistance because Si accumulated in the leaf blades form a double layer of silica cellulose and confer decreased permeability to water vapor, limiting the loss of water through the cuticle and reducing cuticle transpiration (Ma et al., 2001). The results support those obtained by Chen et al. (2011), who found reductions in *E* and C_i and dry matter accumulation in rice plants supplied with Si. Gao et al. (2006) also found a positive relationship between Si in leaves and decreased transpiration rate in wheat crop different water regimes. This highlights the best use of available soil water. According Rafi et al. (1997) and Korndörfer et al. (1999), use of Si in fertilization has advantages, especially in plants subjected to stress, whether biotic or abiotic. In this situation, accumulation of Si in the epidermal cells of grasses in particular results in upright leaves, increases light intensity over the plant canopy, reduces perspiration, prevents or reduces water stress in the foliage, and increases resistance to bedding (Cruciol, 2006). According to Epstein (2001), another action of Si is its ability to increase the chlorophyll content of leaves and plant tolerance to environmental stresses such as cold, heat, drought, nutritional imbalance, and metal toxicity.

Production of components

Plant height, tillers, green leaves, stem diameter, fresh biomass, and dry biomass were not influenced significantly ($p \leq 0.05$) by $CaSiO_3$ (Tables 3 and 4). There was only a significant difference between the soils; signalgrass grown in Ox2 soil showed the highest height and fresh and dry biomass values. Korndörfer et al. (2010) investigated surface application of $CaSiO_3$ on dry matter production in *Brachiaria brizantha* 'Marandu' and *Panicum maximum* 'Mombasa'; they observed higher Si concentration in the leaves, but Si did not affect the production of dry biomass, either in the first or second cut. Sávio et al. (2011) studied the use of different sources of Si on agronomic characteristics and leaf Si content in *B. decumbens* 'Basilisk' and *P. maximum* 'Mombasa'. They observed that, although Si was accumulated in the leaves of both species in the first cut, these differences were not sufficient to affect the vegetative growth of forage on the basis of the production of fresh materials, drought, and plant height.

Materials and Methods

Study site description

Pot experiments were performed in a greenhouse in Marechal Cândido Rondon, Paraná State, Brazil (24° 31′ S, 54° 01′ W and 420 m asl), where the environmental conditions were as follows: minimum and maximum mean air temperature of 18 and 36 °C, respectively and mean air relative humidity of 65%.

Soils

Surface samples (0–0.2 m) from three representative soils of the western region of Paraná State (Brazil) were selected for Si fertilization studies (Table 1). Physical and chemical properties of the soils were determined by adopting standard procedures, and some properties are listed in Table 2. Soil pH in 0.01 mol L^{-1} $CaCl_2$ solution was determined potentiometrically in a 1:2.5 (soil:solution) suspension by using a combined calomel-reference glass electrode and pH meter. Organic matter was quantified by oxidation with potassium dichromate in the presence of sulfuric acid, followed by titration with ammonium Fe (II) sulfate (Embrapa, 2009). Available P, exchangeable potassium (K), and cationic micronutrients (Cu, Zn, Fe, and Mn) were extracted using Mehlich-1 solution in a 1:10 (w:v) soil-to-extract solution ratio (Embrapa, 2009); P was determined using colorimetry at 725-nm wavelength, and K and micronutrients were determined using atomic absorption spectrophotometry.

Ca and magnesium (Mg) were extracted by 1 mol L^{-1} KCl solution and determined using atomic absorption spectrophotometry. Cation exchange capacity (CEC) was estimated using the summation method (CEC = H + Al + Ca + Mg + K). Soluble Si was extracted by 0.5 mol L^{-1} acetic acid solution in a 1:10 (w:v) soil-to-extractant solution ratio (Korndörfer et al., 1999) and determined by beta molybdosilicic complex formation with a spectrophotometer at 660-nm wavelength. Particle size analysis was performed using the pipette method (Embrapa, 2009), according to decantation speed of different soil particles after dispersion in 0.015 mol L^{-1} $(NaPO_3)6.NaO$/1 mol L^{-1} NaOH by overnight shaking.

Experimental design and treatments

The experimental design was a 3 × 5 factorial in complete randomized blocks, with four replications. Treatments consisted of three soils—Ox1, Ox2, and Ult—and wheat plants grown using 0 (control), 1, 2, 4, and 6 t ha^{-1} of $CaSiO_3/MgSiO_3$. The silicate source used was AgroSilício® (10.5% Si, 25% Ca, 6% Mg, and 88% effective calcium carbonate equivalent (ECCE). The corrected soils were maintained for 15 days with water content at 60% field capacity. Then, the soils were placed in 8-L plastic pots and fertilized by applying 30 mg kg^{-1} of N (urea), 80 mg kg^{-1} of P (simple superphosphate), and 60 mg kg^{-1} of K (KCl).

Plant material

Twenty seeds of the *Brachiaria* hybrid 'Mulato II' (Convert HD364) were sown, and they were thinned to three plants per pot nine days after seedling emergence. The pots were irrigated daily to maintain soil moisture at near field capacity.

Gas exchange measurement

Gas exchange was performed at 45 days after sowing (DAS) by using a portable infrared gas analyzer (IRGA; open system, LICOR 6400 XT). Evaluation of gas exchange was performed using completely expanded leaves on a sunny day. The following parameters were evaluated: A (µmol CO_2 m^{-2} s^{-1}), g_s (mmol H_2O m^{-2} s^{-1}), E (mol H_2O m^{-2} s^{-1}), and C_i CO_2 (substomatic ppm within the chamber). We calculated the physiological efficiency of *WUE* by the ratio of the rate of CO_2 assimilation to A/E (µmol CO_2 $mmol^{-1}$ H_2O), A/C, and A/g_s. During the evaluation of gas exchange, air temperature varied from 29.4°C to 33.8°C, average relative humidity was 60.6%, photon density of the external environment provided by the device showed an average of 767.7 µmol m^{-2} s^{-1}, and photon flux in the IRGA chamber was 1,200 µmol m^{-2} s^{-1}. The plants were harvested at 45 DAS, and we measured fresh and dry biomass (g $plant^{-1}$), plant height (cm $plant^{-1}$), tillers (nº $plant^{-1}$), leaves (nº $plant^{-1}$), stem diameter (mm), and Si in the leaf by digestion with hydrogen peroxide and sodium hydroxide and then using colorimetry (Korndörfer et al., 2004).

Statistical analysis

Original data were analyzed using analysis of variance and regression analysis, and significant equations with the highest coefficients of determination (Tukey test, $p \leq 0.05$) were adjusted. All analyses were performed using Saeg 8.0 software for Windows (Statistical Analysis Software, UFV, Viçosa, MG, BRA).

Conclusions

Application of calcium silicate to the soil increases the concentration of Si in the leaves. Si in plants reduces internal CO_2 concentration and increases the efficiency of water use and instantaneous carboxylation efficiency. In soils with low pH and a high Al^{+3} level, which is toxic, reduction in plant sweating increases the intrinsic efficiency of water use in *Brachiaria*. Si helped to alleviate the toxic effects of Al^{+3}.

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