

Full Length Research Paper

Is silicon capable to affect the photosynthetic performance of green maize plants?

Raquel Caroline dos Santos¹, Marta Donato de Souza¹, Giovana Michele da Cruz¹ and Daniel Baron^{1*}

Laboratory of Plant Physiology and Biochemistry, Centre of Natural Sciences (CCN), Federal University of São Carlos (CCN-UFSCar), Buri Municipality, São Paulo State, Brazil.

Received 6 May, 2019; Accepted 21 June, 2019

Green maize (*Zea mays* L.) is a cultivated species of significant importance in the agricultural scene. The literature reports that Si has been used as an alternative option for sustainable agricultural systems. We examined the hypothesis that this beneficial element will improve the photosynthetic performance and biological productivity of crop plants, under field conditions, without nutritional stress. In this context, leaf gas exchanges, physiological indexes, and growth parameters were investigated in green maize, AG4051 and CATIVERDE 02, under Si availabilities at the initial stage of vegetative development. The treatments were: Via shoot; 0, 130, 260, 390 and 520 g ha⁻¹; and via roots; 0, 100, 500, 1000 and 2000 kg ha⁻¹. The experimental design was randomized blocks (RB) with 5 blocks (experimental plots). The beneficial mineral element Si did not have an improvement on gas exchanges of green maize plants and, consequently, plant development. In conclusion, we reject our initial hypothesis and we accepted the alternative hypothesis, that the beneficial element Si did not optimize the photosynthetic performance and biological productivity of green maize plants, without nutritional stress.

Key words: Leaf gas exchange, silicon, sustainability, *zea mays* l.

INTRODUCTION

Green maize (*Zea mays* L.) is a crop plant of immense importance on the agricultural scenery, primordial as a raw material for the formulation of several industrialized products (Shen et al., 2017). It is one of the most produced plants worldwide in a conventional system and

has influence in the economic development of countries, like USA, China and Brazil (Fao, 2017). However, the conventional production system, most commonly used by agriculture, has become limited in terms of sustainability, making this type of production unfeasible in natural

*Corresponding author. E-mail: danielbaron@ufscar.br; Tel.: +55 (15) 32569049.

ecosystems.

The major starting point to overcome this problem is the implantation of sustainable agricultural systems. It is necessary to the local rational use of non-renewable natural resources, as well as the use of appropriate technologies to the local reality (Rótolo et al., 2015). The literature shows some studies that use the mineral element silicon (Si) as an alternative source of plant nutrition on sustainable agricultural systems. Although Si is the second most abundant element after oxygen in soil, this element is little investigated by crop plants physiologists and its relevance for plant growth has been recognized, because it is beneficial for triggering physiological effects.

In the contemporary agriculture, Si currently has a very promising use perspective, by recent advances in the understanding of the ionic accumulation of this mineral element in the crop plants physiology (Hobara et al., 2016). It confers resistance to insect pests, microorganisms and environmental abiotic factors, and, consequently, reduction of the use of pesticides and environmental risks (Dallagnol et al., 2009; Filha et al., 2011; Datnoff and Rodrigues, 2015; He et al., 2015; Dudley et al., 2017). In addition, it improves the photosynthetic performance, which favors their growth and plant reproductive development (Song et al., 2014).

The agricultural success is linked to many physiological factors, for example, leaf gas exchanges and biomass productivity, which are regulated by biochemical processes. Gas exchanges and the loss of water in the plants occur through stomatal movement, opening and closing, respectively, according to environmental stimulation that promotes the difference on the water potentials in the guard cells. Light is a major environmental factor that stimulates an opening of the stomata, controlling the rate of CO₂ assimilation, fundamental to the photosynthetic process. In this physiological aspect, some reasearches studied the effect of Si in the gas exchanges under biotic and abiotic stress (Paula et al., 2015).

The penetration of Si into the roots is in the form of monosilicic acid (H₄SiO₄), through the process of diffusion or mass flow. This element is transported to the interior of the plant by carrier proteins (uptake) of the channel type, which are expressed by the *ZmLsi1* gene, previously described in maize plants (Imtiaz et al., 2016). The uptake of Si, via leaf, was also reported through the expression of the *ZmSi6* gene (Mitani et al., 2009) and this absorption pathway has been an alternative with development and characteristics benefits in several crops (Ma and Yamaji, 2015).

Thus, our objective in this study was to evaluate the influence of Si availabilities via soil and foliar biomass production of the green maize plants under field conditions without abiotic stress. We examined the hypothesis that this beneficial element will improve the

photosynthetic performance and biological productivity of crop plants under field conditions without nutritional stress.

MATERIALS AND METHODS

Experimental conditions and soil fertilization

The study was conducted in an experimental area belonging to the Federal University of São Carlos (UFSCar), Lagoa do Sino campus, located in the Buri municipality, State of São Paulo, Brazil (average altitude of 596 m, geographical coordinates 23° 47' 57" S latitude and 48° 35' 15" W longitude). The water application was made by using center-pivot (CP) irrigation, low-pressure spray sprinklers systems, with necessary and sufficient water volume according to Pereira-Filho (2002), the soil is labeled as Red Latosol Eutroferic as indicated in Table 1, and fertilization was performed according to Rajj et al. (1997). We used 446.28 kg ha⁻¹ of the macronutrients chemical formulation 8-28-16 of N, P and K, respectively, and plus 1% micronutrient Zn. The authors of this study emphasized that the conditions of field cultivation were rigorous, especially giving great attention to the protection of plants (phytosanitary management) and irrigation performance.

Plant materials and treatments

The treatments used were different availabilities of the silicon (Si) mineral element, applied via leaf (shoot) and soil (root), under different levels on green maize plants, *AG4051* and *CATIVERDE 02*, transgenic and non-transgenic maize plants, respectively, at 17 days after sowing (DAS), when the plants had a V2 phenological stage (2 pairs of fully expanded and photosynthetically active leaves).

The application of Si, via leaf (shoot), was performed using a backpack sprayer equipped with a manometer and a flat-fan nozzle (*Teejet® 110 02 XR*). The Si resource used was K silicate (K₂SiO₃, 12% K₂O and 10% Si) were; 0, 130, 260, 390 and 520 g ha⁻¹, according to Freitas et al. (2011). The Si resource used via soil was calcium-magnesium silicate granulated (9% Si, 9% Ca and 2% Mg) were; 0, 100, 500, 1000 and 2000 kg ha⁻¹, according to Sandim et al. (2010).

Leaf gas exchange measurements

Foliar gas exchange was measured with the aid of the portable complete system equipment with microclimate control for measurement of photosynthesis and transpiration, ADC BioScientific Ltd (model LCpro-SD). The variables measured by the equipment were net carbon assimilation rate (*A*, μmol m⁻² s⁻¹), internal carbon concentration in the substomatal chamber (*C_i*, μmol CO₂ mol air⁻¹), stomatal conductance (mol m⁻² s⁻¹), transpiration (*E*, mmol water vapor m⁻² s⁻¹), instantaneous carboxylation efficiency (*A/C_i*, μmol m⁻² s⁻¹ Pa⁻¹) and water use efficiency (*WUE*, μmol CO₂ (mmol H₂O) s⁻¹) at 124 days after sowing. The reference CO₂ concentration that was used during the evaluation was 380 μmol mol⁻¹ of air.

To ensure that the experimental conditions were consisted, the photosynthetically photons flux density (PPFD) was standardized through the use of a light-emitting diode coupled to a photosynthesis chamber, and the light-emitting diode emitted 1700 μmol m⁻² s⁻¹, as this saturating luminosity, according to light curves previously performed (Yarami and Sepaskhah, 2015).

Table 1. Chemical attributes of the Eutrophic Red Latosol of the experimental area in the 0-20 cm depth layer.

Layer (cm)	pH CaCl ₂	P mg dm ⁻³	M.O. g m ⁻³	H+Al	Al ³⁺	K ⁺	Ca ²⁺ mmol _c dm ⁻³	Mg ²⁺	CTC	SB	V %
0-20	5.2	48	31	36	2	4.1	50	15	104.7	68.7	66

Laboratory of Chemical Analysis of Soil and Plant belong to Federal University of São Carlos (Araras campus), Araras, State of São Paulo, Brazil.

Plant growth measurements

The evaluations were performed at phenological growth stages V4 and R5 (22 and 124 days after sowing DAS, respectively) with five replicates of five plants collected for each treatment for the maize cultivars. The variables measured were stem diameter (collar diameter) (mm), plant height (cm), number of leaves per plant (leaves units) and leaf area (dm²), and was performed according to Lopes et al. (2009).

Physiological indexes measurements

Through the determination of leaf area, shoot dry matter mass and total dry matter mass, physiological indexes were calculated among 22 and 124 DAS, such as leaf area ratio (LAR, dm⁻² dia⁻¹), specific leaf area (SLA, dm⁻² dia⁻¹), net assimilation rate (NAR, g dm⁻² dia⁻¹), leaf weight ratio (LWR, g/g) and relative growth rate (RGR, g g⁻¹ dia⁻¹) (Baron et al., 2018).

Experimental design and statistical analysis

The experimental design was randomized blocks (RB) with five blocks (experimental plots). Each experimental plot was composed of four sowing rows of 5.0 m in length, spacing 0.5 m between rows, totaling a population of 50,000 plants per hectare, the data were subjected to the homogeneity test (Levene test), the statistical assumptions (homoscedasticity among the variances) were analyzed statistically by analysis of variance (ANOVA), and averages compared by the Tukey test at 5% of probability using SAS 9.0 statistical analysis software.

RESULTS

The Levene's test showed homogeneity of variances between treatments. This study aimed to check if Si is capable to improve the photosynthetic performance of green maize plants cultivated in field conditions without nutritional stress. The results obtained ensure only effects of Si treatments supplied to the green maize plants.

From the measurements of leaf gas exchange, we report that there were no statistical differences in the evaluated parameters of gas exchange of green maize plants between the different levels of the mineral element Si as indicated in Table 2, and the data of vegetative growth of green maize plants with different Si availabilities, applied shoot and root, did not present

differences, except for the number of leaves at 22 DAS, for cultivar *AG4051*, and stem diameter for cultivar *CATIVERDE 02* (both applied via root) as presented in Table 2.

However, we report that for the cultivar *CATIVERDE 02*, there were no differences between the treatments except for the number of leaves (22 DAS) with Si applied via shoot as described in Table 3. In the physiological indexes in both cultivars, no differences were observed between the different availabilities of Si (shoot and root) as indicated in Table 4.

DISCUSSION

Our strategy of Si application occurred in the vegetative phenological growth stage (V2) of green maize plants (*Zea mays* L.). The Si physiological effects under photosynthetic performance using maize plants in early phenological growth stages are not elucidated in the literature, but it can be stated that the Si uptake is sufficient to trigger biochemical effects in photosynthetic processes. In addition, we can speculate that the shoot application of Si from potassium silicate (K₂SiO₃), has allowed the biopolymers formations, which would impair Si uptake by the leaves (Xie et al., 2014).

In general, the monocots species, such as rice (*Oryza sativa* L.) and sugarcane (*Saccharum officinarum* L.), uptake large quantities of Si; however, eudicots species, such as tomato and potato, appear to be impervious to the Si (Deshmukh et al., 2015). The improvements of leaf gas exchange, from the use of the Si element, were not noticed in the present study. According to the literature, the silicic acid transport in the plants by xylem vessels is generally favored by leaf transpiration (Etesami and Jeong, 2018). The Si transported from the roots uptake sites to the sprout formation allow the leaves to remain semi-upright, which reduces the transpiratory area of the leaves (Tamai and Ma, 2008; Adrees et al., 2015).

The element Si plays a key role in the maintenance and cellular integrity. It is possible that the Si was not only deposited in the shoot cell wall of vegetative development (Ali et al., 2013), although, the maize plants have Si accumulation (Ma and Yamaji, 2015). Crop plants, for example, rice, show panicles increase to plants treated

Table 2. Leaf gas exchange in green maize at phenological growth stage 'R5' (124 DAS) (*AG 4051* and *CATIVERDE02*) cultivated in different Si availabilities.

Green maize plant	Availability	Treatment (kg ha ¹)	A (μmol m ⁻² s ⁻¹)	C _i (μmol CO ₂ mol air ⁻¹)	g _s (mol m ⁻² s ⁻¹)	E (mmol m ⁻² s ⁻¹)	A/C _i (μmol m ⁻² s ⁻¹ Pa ⁻¹)	WUE (μmol mmol ⁻¹)
AG4051	Shoot	0	21.53 ± 2.94 ^a	174.00 ± 38.50 ^a	0.31 ± 0.02 ^a	4.20 ± 1.16 ^a	0.13 ± 0.04 ^a	5.30 ± 0.87 ^a
		0.13	19.06 ± 3.23 ^a	169.80 ± 35.31 ^a	0.27 ± 0.08 ^a	3.74 ± 0.50 ^a	0.11 ± 0.04 ^a	5.15 ± 1.06 ^a
		0.26	19.20 ± 3.10 ^a	176.80 ± 29.98 ^a	0.28 ± 0.09 ^a	3.84 ± 0.60 ^a	0.11 ± 0.03 ^a	5.10 ± 1.13 ^a
		0.39	20.12 ± 2.01 ^a	185.20 ± 25.95 ^a	0.33 ± 0.08 ^a	4.21 ± 0.73 ^a	0.11 ± 0.01 ^a	4.89 ± 0.98 ^a
		0.52	21.09 ± 2.43 ^a	174.20 ± 30.00 ^a	0.31 ± 0.02 ^a	4.23 ± 0.74 ^a	0.12 ± 0.03 ^a	5.05 ± 0.65 ^a
		F	0.78 ^{ns}	0.16 ^{ns}	0.69 ^{ns}	0.45 ^{ns}	0.33 ^{ns}	0.12 ^{ns}
	CV (%)	13.78	18.32	22.42	19.44	28.75	18.8	
	Root	0	26.27 ± 0.91 ^a	133.6 ± 13.41 ^a	0.344 ± 0.02 ^a	5.38 ± 0.46 ^a	0.230 ± 0.02 ^a	5.34 ± 0.47 ^a
		100	27.94 ± 0.63 ^a	146.8 ± 10.07 ^a	0.426 ± 0.02 ^a	5.45 ± 0.42 ^a	0.200 ± 0.01 ^a	5.58 ± 0.48 ^a
		500	25.42 ± 1.94 ^a	150.2 ± 13.98 ^a	0.394 ± 0.04 ^a	5.23 ± 0.29 ^a	0.192 ± 0.02 ^a	4.99 ± 0.47 ^a
		1000	25.38 ± 1.17 ^a	147.4 ± 6.82 ^a	0.350 ± 0.02 ^a	4.93 ± 0.43 ^a	0.181 ± 0.01 ^a	5.71 ± 0.56 ^a
		2000	25.25 ± 1.12 ^a	156.8 ± 14.19 ^a	0.380 ± 0.01 ^a	5.60 ± 0.43 ^a	0.187 ± 0.02 ^a	4.71 ± 0.23 ^a
		F	0.26 ^{ns}	0.15 ^{ns}	0.40 ^{ns}	0.12 ^{ns}	0.25 ^{ns}	0.25 ^{ns}
	CV (%)	19.01	32.78	31.41	31.18	42.99	35.10	
CATIVERDE 02	Shoot	0	16.11 ± 3.17 ^a	174.00 ± 38.50 ^a	0.31 ± 0.02 ^a	4.20 ± 1.16 ^a	0.13 ± 0.04 ^a	5.30 ± 0.87 ^a
		0.13	16.73 ± 3.89 ^a	169.80 ± 35.31 ^a	0.27 ± 0.08 ^a	3.74 ± 0.50 ^a	0.11 ± 0.04 ^a	5.15 ± 1.06 ^a
		0.26	18.68 ± 3.97 ^a	176.80 ± 29.98 ^a	0.28 ± 0.09 ^a	3.84 ± 0.60 ^a	0.11 ± 0.03 ^a	5.10 ± 1.13 ^a
		0.39	17.89 ± 3.49 ^a	185.20 ± 25.95 ^a	0.33 ± 0.08 ^a	4.21 ± 0.73 ^a	0.11 ± 0.01 ^a	4.89 ± 0.98 ^a
		0.52	17.33 ± 2.33 ^a	174.20 ± 30.00 ^a	0.31 ± 0.02 ^a	4.23 ± 0.74 ^a	0.12 ± 0.03 ^a	5.05 ± 0.65 ^a
		F	0.42 ^{ns}	0.58 ^{ns}	0.58 ^{ns}	0.73 ^{ns}	0.49 ^{ns}	0.42 ^{ns}
	CV (%)	19.77	18.44	31.91	22.92	34.37	24.38	
	Root	0	20.69 ± 1.22 ^a	164.0 ± 10.52 ^a	0.312 ± 0.03 ^a	4.972 ± 0.36 ^a	0.130 ± 0.01 ^a	4.486 ± 0.47 ^a
		100	20.17 ± 0.67 ^a	162.0 ± 10.81 ^a	0.270 ± 0.007 ^a	4.752 ± 0.34 ^a	0.134 ± 0.01 ^a	4.467 ± 0.26 ^a
		500	22.02 ± 0.85 ^a	150.6 ± 15.01 ^a	0.310 ± 0.02 ^a	4.986 ± 0.17 ^a	0.167 ± 0.01 ^a	4.432 ± 0.14 ^a
		1000	22.20 ± 0.58 ^a	163.4 ± 11.66 ^a	0.318 ± 0.01 ^a	4.708 ± 0.29 ^a	0.147 ± 0.01 ^a	4.967 ± 0.32 ^a
		2000	19.40 ± 1.34 ^a	176.6 ± 11.44 ^a	0.292 ± 0.02 ^a	4.934 ± 0.51 ^a	0.120 ± 0.01 ^a	4.266 ± 0.38 ^a
		F	0.47 ^{ns}	0.18 ^{ns}	0.24 ^{ns}	0.04 ^{ns}	0.56 ^{ns}	0.19 ^{ns}
	CV (%)	18.81	29.39	29.88	29.33	38.28	29.69	

Means followed by the same letter in the column do not differ by Tukey's test at 5% probability. ($n = 5$, ± standard error).

with Si and the supply of Si was beneficial to the commercial grain production (Lavinsky et al.,

2016). These authors affirm that the Si plays a physiological function on photosynthesis, which is

justified by the increase in stomatal conductance and ability to atmospheric CO₂ assimilation.

Table 3. Plant growth data of green maize (CATIVERDE 02 and AG 4051) under different Si availabilities among 22 DAS ('V4') and 124 DAS ('R5').

Green plant	maize	Availability	22 days after sowing				124 days after sowing		
			Treatment (kg ha ⁻¹)	Plant height (cm)	Number of leaves (leaves units)	Stem diameter (mm)	Plant height (cm)	Number of leaves (leaves units)	Stem diameter (mm)
AG4051	shoot	0	45.2 ± 5.27 ^a	5.00 ± 0.70 ^a	9.40 ± 1.94 ^a	289.10 ± 7.10 ^a	9.4 ± 1.51 ^a	24.6 ± 2.19 ^a	
		0.13	48.90 ± 5.76 ^a	4.80 ± 0.44 ^a	9.40 ± 3.64 ^a	280.06 ± 10.46 ^a	8.8 ± 1.09 ^a	25.8 ± 3.19 ^a	
		0.26	40.62 ± 4.62 ^a	5.00 ± 0.00 ^a	8.60 ± 3.04 ^a	275.88 ± 19.59 ^a	9.4 ± 1.34 ^a	26.8 ± 0.44 ^a	
		0.39	45.44 ± 4.62 ^a	4.2 ± 0.83 ^a	7.00 ± 1.22 ^a	296.20 ± 11.98 ^a	8.6 ± 2.70 ^a	24.40 ± 3.50 ^a	
		0.52	44.90 ± 7.29 ^a	5.40 ± 1.14 ^a	9.00 ± 3.24 ^a	278.12 ± 16.43 ^a	9.8 ± 1.09 ^a	23.20 ± 2.38 ^a	
		F	1.38 ^{ns}	1.78 ^{ns}	0.65 ^{ns}	1.90 ^{ns}	0.43 ^{ns}	1.44 ^{ns}	
		CV (%)	12.44	15.05	31.92	4.87	18.05	10.32	
	root	0	42.52 ± 5.74 ^a	5.6 ± 0.54 ^a	8.6 ± 2.30 ^a	266.5 ± 24.1 ^a	10.8 ± 1.92 ^a	24.6 ± 3.57 ^a	
		100	43.22 ± 12.24 ^a	5.0 ± 0.00 ^{ab}	8.8 ± 2.48 ^a	273.2 ± 6.05 ^a	11.4 ± 1.14 ^a	26.4 ± 9.86 ^a	
		500	40.40 ± 6.36 ^a	5.2 ± 0.44 ^{ab}	7.8 ± 2.58 ^a	267.5 ± 21.69 ^a	11.4 ± 1.34 ^a	24.6 ± 4.72 ^a	
		1000	34.36 ± 4.01 ^a	4.4 ± 0.54 ^{ab}	7.8 ± 2.04 ^a	276.0 ± 7.77 ^a	11.0 ± 1.41 ^a	23.2 ± 1.91 ^a	
		2000	41.08 ± 9.28 ^a	4.6 ± 0.54 ^b	7.6 ± 3.64 ^a	271.5 ± 19.12 ^a	11.0 ± 1.41 ^a	26.6 ± 2.79 ^a	
		F	0.95 ^{ns}	5.18 ^{ns}	0.20 ^{ns}	0.27 ^{ns}	0.18 ^{ns}	0.35 ^{ns}	
		CV (%)	20.02	9.45	32.90	6.42	12.58	21.39	
CATIVERDE 02	shoot	0	41.64 ± 4.94 ^a	5.4 ± 0.54 ^{ab}	9.4 ± 2.50 ^a	286.40 ± 10.59 ^a	9.00 ± 2.44 ^a	24.6 ± 2.88 ^a	
		0.13	40.08 ± 2.43 ^a	5.40 ± 0.54 ^{ab}	8.00 ± 1.87 ^a	284.98 ± 17.25 ^a	8.60 ± 2.07 ^a	21.40 ± 4.03 ^a	
		0.26	40.52 ± 4.69 ^a	5.60 ± 0.54 ^a	8.8 ± 1.92 ^a	271.90 ± 20.08 ^a	8.60 ± 1.34 ^a	23.00 ± 5.09 ^a	
		0.39	43.44 ± 5.30 ^a	5.20 ± 0.83 ^{ab}	8.60 ± 2.60 ^a	277.94 ± 7.44 ^a	8.20 ± 1.78 ^a	24.40 ± 4.97 ^a	
		0.52	39.82 ± 7.05 ^a	4.40 ± 0.54 ^b	6.20 ± 1.30 ^a	297.50 ± 24.00 ^a	10.20 ± 1.64 ^a	23.80 ± 2.28 ^a	
		F	0.45 ^{ns}	2.89 [*]	1.70 ^{ns}	1.61 ^{ns}	0.82 ^{ns}	0.52 ^{ns}	
	CV (%)	12.04	11.85	25.58	5.99	21.27	17.12		
	root	0	47.22 ± 7.85 ^a	5.6 ± 0.54 ^a	7.8 ± 2.94 ^{ab}	297.44 ± 44.41 ^a	11 ± 1.41 ^a	24.2 ± 2.94 ^a	
		100	48.58 ± 8.73 ^a	5.4 ± 0.54 ^a	10.8 ± 1.30 ^a	277.80 ± 13.08 ^a	10 ± 0.70 ^a	20.4 ± 2.40 ^a	
		500	42.08 ± 5.71 ^a	4.8 ± 0.44 ^a	8.5 ± 1.11 ^{ab}	281.20 ± 9.23 ^a	9.8 ± 1.09 ^a	22.4 ± 4.66 ^a	
1000		43.24 ± 7.30 ^a	5.2 ± 0.44 ^a	7.4 ± 2.07 ^{ab}	275.30 ± 25.5 ^a	10.4 ± 0.54 ^a	23.4 ± 6.10 ^a		
	2000	49.01 ± 7.53 ^a	5.5 ± 0.50 ^a	7.1 ± 2.07 ^b	286.40 ± 36.33 ^a	8.4 ± 2.70 ^a	26.4 ± 2.40 ^a		
	F	0.89 ^{ns}	2.00 ^{ns}	2.93 [*]	0.46 ^{ns}	2.06 ^{ns}	1.55 ^{ns}		
	CV (%)	16.28	9.43	23.27	10.18	15.15	17.05		

Means followed by the same letter in the column do not differ by Tukey's test at 5% probability. ($n = 5$, \pm standard error).

In our present study, the availabilities of Si do not increase photosynthetic rates in maize plants,

because this mineral element is more relevant in plants under biotic and abiotic stress. This finding

is corroborated by other studies in higher plants which affirm that Si effect on plants may not be

Table 4. Physiological Indexes (SLA, LWR, RGR, NAR and LAR) of green maize (*AG4051* and *CATIVERDE 02*) cultivated in different Si availabilities among 22 DAS ('V4') and 124 DAS ('R5').

Green maize plant	Availability	Treatment (kg ha ⁻¹)	SLA (dm ⁻² dia ⁻¹)	LWR (g/g)	RGR (g g ⁻¹ dia ⁻¹)	NAR (g dm ⁻² dia ⁻¹)	LAR (dm ⁻² dia ⁻¹)
AG4051	Shoot	0	0.35 ± 0.06 ^a	0.95 ± 0.01 ^a	0.019 ± 0.001 ^a	0.87 ± 0.40 ^a	0.24 ± 0.15 ^a
		0.13	0.31 ± 0.02 ^a	0.95 ± 0.008 ^a	0.019 ± 0.0008 ^a	0.74 ± 0.13 ^a	0.27 ± 0.04 ^a
		0.26	0.31 ± 0.06 ^a	0.94 ± 0.01 ^a	0.021 ± 0.001 ^a	0.80 ± 0.13 ^a	0.33 ± 0.05 ^a
		0.39	0.34 ± 0.10 ^a	0.95 ± 0.01 ^a	0.019 ± 0.008 ^a	0.67 ± 0.11 ^a	0.28 ± 0.06 ^a
		0.52	0.38 ± 0.07 ^a	0.96 ± 0.005 ^a	0.019 ± 0.002 ^a	0.66 ± 0.18 ^a	0.25 ± 0.05 ^a
		F	0.84 ^{ns}	0.84 ^{ns}	2.27 ^{ns}	0.78 ^{ns}	0.95 ^{ns}
		CV (%)	20.47	1.26	6.73	29.67	30.70
	Root	0	0.4576 ± 0.05 ^a	0.9598 ± 0.02 ^a	0.021 ± 0.001 ^a	1.201 ± 0.15 ^a	0.030 ± 0.01 ^a
		100	0.5220 ± 0.07 ^a	0.9518 ± 0.12 ^a	0.019 ± 0.002 ^a	1.090 ± 0.19 ^a	0.026 ± 0.004 ^a
		500	0.4782 ± 0.11 ^a	0.9454 ± 0.03 ^a	0.020 ± 0.002 ^a	1.226 ± 0.33 ^a	0.025 ± 0.006 ^a
		1000	0.4598 ± 0.05 ^a	0.9446 ± 0.02 ^a	0.022 ± 0.001 ^a	1.415 ± 0.13 ^a	0.023 ± 0.002 ^a
		2000	0.4898 ± 0.06 ^a	0.9502 ± 0.02 ^a	0.0204 ± 0.003 ^a	1.228 ± 0.27 ^a	0.023 ± 0.004 ^a
		F	0.56 ^{ns}	0.29 ^{ns}	1.09 ^{ns}	1.28 ^{ns}	0.85 ^{ns}
		CV (%)	16.02	2.68	10.91	18.75	26.45
Shoot	0	0.40 ± 0.14 ^a	0.96 ± 0.007 ^a	0.019 ± 0.001 ^a	0.56 ± 0.06 ^a	0.30 ± 0.07 ^a	
	0.13	0.28 ± 0.08 ^a	0.95 ± 0.009 ^a	0.020 ± 0.0006 ^a	0.73 ± 0.18 ^a	0.34 ± 0.06 ^a	
	0.26	0.38 ± 0.06 ^a	0.94 ± 0.01 ^a	0.019 ± 0.002 ^a	0.57 ± 0.20 ^a	0.36 ± 0.09 ^a	
	0.39	0.26 ± 0.12 ^a	0.97 ± 0.01 ^a	0.022 ± 0.003 ^a	0.81 ± 0.06 ^a	0.56 ± 0.52 ^a	
	0.52	0.29 ± 0.08 ^a	0.95 ± 0.01 ^a	0.021 ± 0.002 ^a	0.82 ± 0.22 ^a	0.43 ± 0.19 ^a	
	F	1.78 ^{ns}	2.25 ^{ns}	1.90 ^{ns}	2.88 ^{ns}	0.79 ^{ns}	
	CV (%)	31.79	1.35	11.28	23.17	64.19	
CATIVERDE 02	Root	0	0.4705 ± 0.06 ^a	0.9650 ± 0.008 ^a	0.0194 ± 0.002 ^a	1.182 ± 0.30 ^a	0.025 ± 0.005 ^{ab}
		100	0.6663 ± 0.44 ^a	0.9520 ± 0.019 ^a	0.0181 ± 0.001 ^a	0.912 ± 0.33 ^a	0.032 ± 0.006 ^a
		500	0.4538 ± 0.06 ^a	0.9499 ± 0.22 ^a	0.0194 ± 0.001 ^a	1.195 ± 0.16 ^a	0.025 ± 0.002 ^{ab}
		1000	0.4338 ± 0.10 ^a	0.9445 ± 0.019 ^a	0.0209 ± 0.002 ^a	1.405 ± 0.45 ^a	0.025 ± 0.004 ^{ab}
		2000	0.3869 ± 0.11 ^a	0.9499 ± 0.03 ^a	0.0194 ± 0.001 ^a	1.405 ± 0.32 ^a	0.023 ± 0.004 ^b
		F	1.24 ^{ns}	0.64 ^{ns}	1.56 ^{ns}	1.89 ^{ns}	2.61 ^{ns}
		CV (%)	44.83	2.25	9.15	27.10	19.01

Means followed by the same letter in the column do not differ by Tukey's test at 5% probability. ($n = 5$, \pm standard error).

noticed in environmental conditions without stress (Tamai and Ma, 2008). Similarly, maize plants

evaluated in a stress-free field conditions obtained an increase in the photosynthetic rate and

stomatal conductance, nevertheless, a decrease in transpiration rate and internal carbon

concentration in the leaf substomatal chamber (Xie et al., 2014).

We found studies that report Si positive effects occurred in stressful field conditions to the plants, for example, salt stress, drought stress, nutrient imbalance, presence of heavy metal (Ali et al., 2013) and inoculation of the pathogenic fungus (Polanco et al., 2014; Etesami, 2018). Phytoremediation plants treated with Si also presented positive results in the leaf gas exchanges and the photosynthetic performance of higher plants results directly in biological productivity during plant development; for example, rice plants under arsenic (As) cultivation (Sanglard et al., 2016) and green maize under cadmium (Cd) cultivation (Vaculík et al., 2015). On the other hand, in non-stressing field conditions, for potato plants (*Solanum tuberosum* L.), it was verified that the transpiration rate increased in response to Si applied through soil and foliar, due to its favorable effect in the stomatal conductance with improvements in the photosynthetic processes of plants cultivated with Si availability (Pilon et al., 2013).

Considering our results, we did not report differences on plant growth, however, the effects of Si on reducing cadmium (Cd) toxicity evaluated in tobacco (*Nicotiana tabacum* L.) show that the application of Si favored the plant growth once, and that the Cd element non-essential is a limiting factor (phytotoxicity) especially about the growth of plants (Lu et al., 2017). In the angiosperms clades, most species, particularly eudicots, are unable to accumulate elevated levels of Si and the difference in Si accumulation between species has been attributed to Si uptake ability of the roots.

Currently, different Si uptake mechanisms between monocotyledons and eudicotyledons plant species are reported in the literature. The rice plants, a monocot species, *Cucumis sativus* L. (cucumber) and *Solanum lycopersicum* L. (tomato), both eudicots species, show a similar ionic carrier transporting Si from the external solution to the cortical cells, with the same K_m value; however, the different V_{max} suggests that the density of ionic carrier differs from all three species (Mitani and Ma, 2005).

In this way, it seems like the transport of Si from cortical cells to the xylem vessels shows that the Si concentration in the xylem sap is much higher in monocots species than in eudicots species; however, Si xylem loading is mediated by passive transport (without energy expenditure) or absence of carrier, to transport Si from cortical cells to the xylem vessels in eudicots species unlike in monocots species, where xylem loading of Si is mediated by membrane-specific ionic carriers (active transport or with energy expenditure) (Mitani et al., 2009). These results provide a powerful predictive tool to classify plants on the basis of their natural capability to take up Si from the soil so that a spacing of a specific length between the two NPA domains is a

necessary and selective feature for Si among all Si-transporting plants.

On the other hand, Deshmukh et al. (2015) provide an accurate and clarified molecular basis to classify eudicots plants into accumulators of Si. Plant species that possess nodulin intrinsic proteins (NIPs), a subclass of aquaporins (AQPs) with a precise distance of 108 amino acids (AA) among the asparagine–proline–alanine (NPA) domains is fundamental to absorb Si because tomato NIP gene mutated from 109 to 108 AA exhibited a rare gain of function. Scientific evidence suggests AQPs with specific characteristics will filter Si in (Si accumulator) or out (Si excluder) of plants.

Indeed, the Si fertilization used in the eudicotyledons plant species under field conditions have lower or no accumulate in plant tissues, for example, tomato (*Solanum lycopersicum* L.) and mango (*Mangifera indica* L.), respectively. However, monocotyledons plant species, such as rice and sugarcane present a significant tissue leaf Si transported from the external solution to the cortical cells (Ma and Yamaji, 2015; Helaly et al., 2017) increasing plant growth parameters such as relative growth rate and CO_2 net assimilation rate.

Plant physiologists use the analysis of growth data in the different development stages to monitor the increased organic matter by photosynthetic activity, and the growth analysis provides a plausible study of the physiological activities of the plant influenced by the edaphoclimatic conditions to which the plant is cultivated. The relative growth rate (RGR) is established by the accumulation of plant biomass in a given period due to the greater photosynthetic performance (NAR), biomass leaf (SLA) or both.

In addition, the literature conceptualizes as part of the importance for the RGR, the leaf weight ratio (LWR), emphasizing in all cases the need for nutrients and light to plants, however do not describe if this conditioning rule is equated with beneficial mineral elements, for example, Si. The NAR is dependent of individual changes or the whole on photosynthesis and cellular respiration (Li et al., 2016) which directly impacts the leaf area useful for photosynthesis (SLA) (Skidmore et al., 2015). Moreover, Si shoot and root supplied increased the photosynthetic rate per leaf unit, even in conditions without stress (Pilon et al., 2013), which is the most rational way to explain the action of the environment on the capture of light and CO_2 assimilation for the plant; however, the response mechanisms in crop plants are not elucidated.

Although in the present study we did not report differences in the plant growth and physiological indexes, differences in plant biomass were observed, mainly related to the decline in the acquisition and use of nutrients under environmental conditions (Baret et al., 2017). In addition, greater leaf area per plant unit (LAR) was obtained in all treatments with Si applied via soil to the potato crop, but the authors did not present the

biochemical mechanisms that elucidate the role of Si in the studied plant physiology (Pilon et al., 2013).

Our study offers some advances in understanding the photosynthetic performance of maize plants (*Z. mays* L.) cultivated with Si availabilities applied via shoot and root. We reject our initial hypothesis and accepted alternative hypothesis that the beneficial element Si did not optimize the photosynthetic performance and biological productivity of green maize plants without nutritional stress.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interest.

ACKNOWLEDGMENTS

The authors wish to thank Marconi Equipamentos Para Laboratórios Ltda – Brazil for equipment loan, ADC BioScientific Ltd (LCpro-SD model), to measure leaf gas exchange and CNPq (National Council for Scientific and Technological Development) – Brazil for CNPq-PIBIC Grant n° 139870/2015-6 to Raquel Caroline dos Santos.

REFERENCES

- Adrees M, Ali S, Rizwan M, Zia-ur-Rehman M, Ibrahim M, Abbas F, Farid M, Qayyum MF, Irshad MK (2015). Mechanisms of silicon-mediated alleviation of heavy metal toxicity in plants: A review. *Ecotoxicology and Environmental Safety* 119:186-197.
- Ali S, Farooq MA, Yasmeen T, Hussain S, Arif MS, Abbas F, Bharwana SA, Zhang G (2013). The influence of silicon on barley growth, photosynthesis and ultra-structure under chromium stress. *Ecotoxicology and Environmental Safety* 89:66-72.
- Baret M, Pepin S, Ward S, Pothier D (2017). Long-term changes in stand growth dominance as related to resource acquisition and utilization in the boreal forest. *Forest Ecology and Management* 400:408-416.
- Baron D, Amaro ACE, Campos FG, Boaro CSF, Ferreira G (2018). Plant Physiological Responses to Nutrient Solution: An Overview. In: Ahmad P, Ahanger MA, Singh VP, Tripathi DK, Alam P, Alyemini MN. (eds.) *Plant Metabolites and Regulation Under Environmental Stress*, Academic Press, London. <https://doi.org/10.1016/B978-0-12-812689-9.00024-8>
- Dallagnol LJ, Rodrigues FA, Mielli MV, Ma JF, Datnoff LE (2009). Defective active silicon uptake affects some components of rice resistance to brown spot. *Phytopathology* 99(1):116-121.
- Datnoff LE, Rodrigues AF (2015). Highlights and Prospects for Using Silicon in the Future. In: Rodrigues AF, Datnoff L.E (eds). *Silicon and Plant Diseases*. Springer, Netherlands. [Http://doi.org/10.1007/978-3-319-22930-0](http://doi.org/10.1007/978-3-319-22930-0)
- Deshmukh RK, Vivancos J, Ramakrishnan G, Guérin V, Carpentier G, Sonah H, Labbé C, Isenrig P, Belzile FJ, Bélanger RR (2015). A precise spacing between the NPA domains of aquaporins is essential for silicon permeability in plants. *The Plant Journal* 83:489-500.
- Dudley N, Atwood SJ, Goulson D, Jarvis D, Bharucha ZP, Pretty J (2017). How should conservationists respond to pesticides as a driver of biodiversity loss in agroecosystems? *Biological Conservation* 209:449-453.
- Etesami H, Jeong BR (2018). Silicon (Si): Review and future prospects on the action mechanisms in alleviating biotic and abiotic stresses in plants. *Ecotoxicology and Environmental Safety* 147:881-896.
- Etesami H (2018). Can interaction between silicon and plant growth promoting rhizobacteria benefit in alleviating abiotic and biotic stresses in crop plants? *Agricultural, Ecosystems and Environment* 253:98-112.
- FAO - Food and Agriculture Organization of the United Nations (2017). Production quantities of maize. <http://www.fao.org/faostat/en/#data/QC>.
- Filha MSX, Rodrigues FA, Domiciano GP, Oliveira HV, Silveira PR, Moreira WR (2011). Wheat resistance to leaf blast mediated by silicon. *Australasian Plant Pathology* 40(1):28-28.
- Freitas LBD, Coelho EMX, Maia EM, Silva TRB (2011). Adubação foliar com silício na cultura do milho. *Revista Ceres* 58(2):262-267.
- He W, Yang M, Li Z, Qiu J, Liu F, Qu X, Qiu Y, Li R (2015). High levels of silicon provided as a nutrient in hydroponic culture enhances rice plant resistance to brown planthopper. *Crop Protection* 67:20-25.
- Helaly MN, El-Hoseiny H, El-Sheery NI, Rastogy A, Kalaji HM (2017). Regulation and physiological role of silicon in alleviating drought stress of mango. *Plant Physiology and Biochemistry* 118:31-44.
- Hobara S, Fukunaga-Yoshida S, Suzuki T, Matsumoto S, Matoh T, Ae N (2016). Plant silicon uptake increases active aluminum minerals in root-zone soil: Implications for plant influence on soil carbon. *Geoderma* 279:45-52.
- Imtiaz M, Rizwan MS, Mushtaq MAAshraf M, Shahzad SM, Yousaf B, Saeed DA, Rizwan M, Nawaz MA, Mehmood S, Tu S (2016). Silicon occurrence, uptake, transport and mechanisms of heavy metals, minerals and salinity enhanced tolerance in plants with future prospects: A review. *Journal of Environmental Management* 183(3):521-529.
- Lavinsky AO, Detmann KC, Reis JV, Ávila RT, Sanglard ML, Pereira LF, Sanglard LMVP, Rodrigues FA, Araújo WL, DaMatta FM (2016). Silicon improves rice grain yield and photosynthesis specifically when supplied during the reproductive growth stage. *Journal of Plant Physiology* 206:125-132.
- Li X, Schmid B, Wang F, Paine CET (2016). Net Assimilation Rate Determines the Growth Rates of 14 Species of Subtropical Forest Trees. *Plos One* 11:1-13.
- Lopes JP, Machado EC, Deuber R, Machado RS (2009). Análise de crescimento e trocas gasosas na cultura de milho em plantio direto e convencional. *Bragantia* 68(4):839-848.
- Lu Y, Ma J, Teng y, He J, Christie O, Zhy L, Ren W, Zhang M, Deng S (2017). Effects of silicon on the growth, physiology and cadmium translocation of tobacco (*Nicotiana tabacum* L.) in cadmium contaminated soil. *Pedosphere*, pp. 1-18.
- Ma JF, Yamaji NA (2015). Cooperative system of silicon transport in plants. *Trends in Plant Science* 20(7):435-442.
- Mitani N, Ma JF (2005). Uptake system of silicon in different plant species. *Journal of Experimental Botany* 56(414):1255-1261.
- Mitani N, Yamaji N, Ma JF (2009). Identification of maize silicon influx transporters. *Plant and Cell Physiology* 50(1):5-12.
- Paula LS, Silva BC, Pinho WCS, Barbosa MAM, Guedes-Lobato EMS, Segura FR, Batista BL, Barbosa Júnior F, Lobato AKS (2015). Silicon (Si) ameliorates the gas exchange and reduces negative impacts on photosynthetic pigments in maize plants under Zinc (Zn) toxicity. *Australian Journal of Crop Science* 9(10):901-908.
- Pereira-Filho IA (2002). O cultivo do milho verde. *Embrapa Milho e Sorgo, Sete Lagoas, DF*. 31.
- Pilon C, Soratto RP, Moreno LA (2013). Effects of soil and foliar application of soluble silicon on mineral nutrition, gas exchange, and growth of potato plants. *Crop Science* 53:1605-1614.
- Polanco LR, Rodrigues FA, Nascimento KJT, Cruz MFA, Curvelo CRS, DaMatta FM, Vale FXR (2014). Photosynthetic gas exchange and antioxidative system in common bean plants infected by *Colletotrichum lindemuthianum* and supplied with silicon. *Tropical Plant Pathology* 39(1):35-42.
- Rajiv BV, Cantarella H, Quaggio JA, Furlani AMC (1997). *Recomendações de adubação e calagem para o Estado de São Paulo*. 2nd edn. Instituto Agrônomo – Fundação, Campinas, São Paulo P. 285.

- Rótolo GC, Francis C, Craviotto RM, Ulgiati S (2015). Environmental assessment of maize production alternatives: Traditional, intensive and GMO-based cropping patterns. *Ecological Indicators* 57:48-60.
- Sandim AS, Ribon AA, Diogo LO, Savi MA. (2010). Doses de silício na produtividade do milho (*Zea mays* L.) híbrido simples na região de Campo Grande – MS. *Cultivando o Saber* 3:171-178.
- Sanglard LMVP, Detmann KC, Martins SCV, Teixeira RA, Pereira LF, Sanglard ML, Fernie AR, Araújo WL, DaMatta Fábio M (2016). The role of silicon in metabolic acclimation of rice plants challenged with arsenic. *Environmental and Experimental Botany* 123:22-36.
- Shen L, Huang Y, Li T (2017). Top-grain filling characteristics at an early stage of maize (*Zea mays* L.) with different nitrogen use efficiencies. *Journal of Integrative Agriculture* 16(3):626-639.
- Skidmore AK, Pettoelli N, Coops NC, Geller GN, Hansen M, Lucas R, Múcher CA, O'Connor B, Paganini M, Pereira HM, Schaepman ME, Turner W, Wang T, Wegmann M (2015). Environmental science: agree on biodiversity metrics to track from space. *Nature* 523:403-405.
- Song Z, Müller K, Wang H (2014). Biogeochemical silicon cycle and carbon sequestration in agriculture ecosystems. *Earth-Science Reviews* 139:268-278.
- Tamai K, Ma JF (2008) Reexamination of silicon effects on rice growth and production under field conditions using a low silicon mutant. *Plant and Soil* 307(1-2):21-27.
- Vaculík M, Pavlovič A, Lux A (2015). Silicon alleviates cadmium toxicity by enhanced photosynthetic rate and modified bundle sheath's cell chloroplasts ultrastructure in maize. *Ecotoxicology and Environmental Safety* 120:66-73.
- Xie Z, Song F, Xu H, Shao H, Song R (2014). Effects of Silicon on Photosynthetic Characteristics of Maize (*Zea mays* L.) on Alluvial Soil. *The Scientific World Journal* 2014 (718716):1-6.
- Yarami N, Sepaskhah AR (2015). Physiological growth and gas exchange response of saffron (*Crocus sativus* L.) to irrigation water salinity, manure application and planting method. *Agricultural Water Management* 154:43-51.