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Silicon absorption by plants in response to the environment[1]

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ABSTRACT

Despite the importance given to Silicon in the relief of stress in cultivated plants, there are no experimental studies on abiotic stresses that address this function of Si in plants under natural environments, aiming to identify responses that would indicate acclimatisation to the conditions at their place of origin. The goal of this study was to answer the following questions: 1) Does abiotic stress increase Si absorption? 2) Does the presence of Si stimulate biomass production in natural environments? and 3) Do plants from different environments display differences in Si absorption? To do so, *Eugenia punicifolia* was selected as a study species since it has a wide distribution, occurring in three different physiognomies: Coastal Savanna, Dense Deciduous Shrubland and Seasonal Deciduous Forest. The Si absorption varied depending on the temperature and this was directly related to increases in dry matter production in *E. punicifolia* plants, suggesting that this may be a relief mechanism for temperature and water stresses. Differences in the response to stress conditions may be a result of the phenotypic plasticity which occurs in *E. punicifolia* and suggests that plasticity could be a useful asset in the use of Si fertilizer for crops.

Keywords: water stress; temperature; phenotypic plasticity; acclimatisation; relief.

INTRODUCTION

Silicon is, in plants, an element of brittle crystalline structure with enormous function in the field of plant science (Gaur *et al.*, 2020). In some plant species (e.g. grasses, Tombeur *et al.,* 2021), several dysfunctions in plant growth and development can be caused by Si deficiency.

Sustainable agricultural production is highly affected by the irregularity of favorable environmental conditions and the reduction in productivity, mainly influenced by abiotic stress factors such as drought, heat, cold and salinity (Zahra *et al.*, 2021; Raza *et al.*, 2022). Current climate change induces drought and heat stress, two of the main abiotic stress factors that result in crop and productivity loss (Zandalinas *et al.*, 2018). In the last four decades, studies have identified the role of silicon in increasing resistance and tolerance to these abiotic stress (Horiguchi & Morita, 1987; Epstein, 1999; Liang *et al.*, 2007; Mir *et al.*, 2022).

The main benefits associated with Si to alleviate stress in agroecosystems have already been documented in terms of biomass and grain yield increase (Wang *et al.*, 2021). Other benefits related to Si are stimulus to root system development (Etesami & Jeong, 2018); absorption and nutrients assimilation gains (Kim *et al.*, 2017) and maintenance of the water balance in plants (Coskun *et al.*, 2016). Among all benefits attributed to Si, Cooke & Leishman (2011)

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suggested that plants can use Si to reduce the effects of stress, allowing the permanence and occupation of areas with adverse conditions, or even to obtain an advantage in reproductive capacity over other plants. Research regarding the role of Si in the alleviation of environmental stresses in natural environments could reinforce the condition of its "essentiality" for plant science, in addition informing global patterns of species distribution and abundance (Alstad *et al.,* 2016).

The Brazilian semi-arid tropical has high environmental heterogeneity due to large variations in climate, soil and altitude, forming a mosaic of different conditions. As the altitude increases, for example, there is a reduction in temperature, an increase in precipitation, a greater availability of water in the soil and, consequently, a greater availability of some elements (Tisdale *et al.*, 1985). In addition, the position of relief slope in relation to winds direction (windward and leeward) influences environmental humidity and consequently the composition of plant species.

Despite the importance given to the alleviation of stress in cultivated plants, there are few studies that address this function of Si in plants under natural environments and that identify their adaptation to these conditions. Our study explored the following questions: 1) Does abiotic stress increase Si absorption in *E. punicifolia* plants? 2) Does the presence of Si stimulate biomass production in natural environments? and 3) Do E. *punicifolia* plants from different environments display differences in Si absorption? To answer the above questions, we evaluated Si absorption and biomass production in plants of the same species, from different physiognomies and subjected to stress caused by high and low temperatures and water deficit. In addition, we used the responses to demonstrate the possible mechanisms of acclimatisation of these plants to their places of origin.

MATERIALS AND METHODS

Focal species and study sites

The object of study was *Eugenia punicifolia* (Kunth) DC, a species of wide geographical distribution, being frequently reported in various types of vegetation in tropical South America: Seasonal Forest (Rodrigues *et al.*, 1989), Coastal Forest (Fabris & César, 1996), Cerrado (Proença, 1994), and occurs under different conditions of soil and climate (Conceição & Aragão, 2010). Besides this wide distribution, the species was selected in view of the capacity of the Myrtaceae family to alleviate the physiological stress caused by adverse climatic conditions through the accumulation of Si, according to Ramos *et al.*, 2009.

Aiming to test how abiotic stresses (temperature and water stress) influence silicon absorption in *E. punicifolia*, seeds were collected from three sites with different types of phytophysiognomy. The sites were selected considering the different soil properties and climatic conditions, which may influence the concentration of available Si in the soil and the mechanisms of Si absorption by plants in response to the environment. The first site was a fragment of savanna vegetation, classified by Moro *et al.* (2011) as Coastal Savanna (CS), located in an urban coastal zone of Fortaleza (3º43'02"S, 38º32'35"W), in the State of Ceará, Brazil, at 16 m above sea level. The climate is tropical with dry summer (Koppen's classification, Alvares *et al.*, 2014), with average annual rainfall of 1338 mm, concentrated from January to March, and mean temperature of 28 to 30 ºC, with few or absence daily and/or monthly variation (Moro *et al.*, 2011). The region includes areas of coastal plain (dunes and paleo dunes), pre-coastal tableland (*Barreiras* Formation) and fluvial plains, where different physiognomies can be found (Castro *et al.*, 2012; IPECE, 2008). According to Jacomine *et al.*, (1975), these soils originate from sandy-clay sediments (information confirmed by soil granulometry, Table 1), that related to the particular conditions of climate, such as rainfall and high temperatures, contribute to greater desilication, i.e. the removal of Si due to intense weathering (Korndörfer, 2006). The soil of the area was classified as Ultisol (Soil Taxonomy).

The remaining sites occur in the eastern margin of the Mid-North Sedimentary Basin, which forms an asymmetric cuesta, known as the *Ibiapaba* Plateau. One side with high-density small size vegetation (3 to 4 m), classified as Dense Deciduous Shrubland – DDS (locally known as *carrasco*), located on the dryer slope of the Basin (5º08'45"S, 40º55'43"W) at 700 m above sea level. The climate is semi-arid, with average annual rainfall of 636.61 mm, concentrated from January to May, and mean annual minimum and maximum temperatures of 19.14 ± 1.78 ºC and 33.6 ± 3.85 ºC respectively (Vasconcelos *et al.,* 2010), which shows a large variation in temperature for this area. The other side was a Seasonal Deciduous Forest (SDF), located on the most humid slope of the basin (5°08'29"S, 40°54'05"W), at 650 m above sea level. The climate is also tropical with dry summer, with an average annual rainfall of 1044 mm, concentrated from January to April (corresponding to more than 80% of the annual precipita-

Table 1: Physicochemical characteristics at different layers of the soil in Coastal Savanna, Dense Deciduous Shrubland and Seasonal Deciduous Forest

Property	Sites/Layers								
	Coastal Savanna			Dense Deciduous			Seasonal Deciduous Forest		
	0-10	10-20	20-40	0-10	10-20	20-40	0-10	10-20	20-40
Exchangeable Ca^{++} (cmol$_c$kg^{-1})[b]	1.02	1.00	1.23	0.60	0.58	0.67	0.62	0.50	0.50
Exchangeable Mg^{++} (cmol$_c$kg^{-1})[b]	0.80	0.50	0.54	0.51	0.52	0.60	1.02	0.51	0.50
Exchangeable Na^{+} (cmol$_c$kg^{-1})[a]	0.09	0.07	0.05	0.02	0.03	0.02	0.02	0.02	0.02
Exchangeable K^{+} (cmol$_c$kg^{-1})[a]	0.08	0.09	0.06	0.08	0.04	0.03	0.07	0.05	0.05
Available P (mg kg^{-1})[a]	6	5	8	12	13	11	16	17	12
Al^{3+} (cmol$_c$kg^{-1})b	0.00	0.00	0.00	1.29	1.00	1.10	1.30	1.28	1.74
Sum of bases (cmol$_c$kg^{-1})	1.99	1.66	1.88	1.21	1.17	1.32	1.73	1.08	1.07
Potential Acidity (cmol$_c$kg^{-1})[c]	0.90	0.83	0.83	7.12	4.70	4.38	5.50	5.16	6.62
CEC (cmol$_c$kg^{-1})	2.89	2.49	2.71	8.33	5.87	5.70	7.23	6.24	7.69
Base Saturation (%)	77	80	82	15	20	25	27	19	16
pH in water (1:2.5)	6.0	6.0	6.0	4.3	4.5	4.4	4.5	4.3	4.6
Coarse Sand (g kg^{-1})	693	661	622	353	332	300	120	80	100
Fine Sand (g kg^{-1})	230	252	261	530	534	523	730	712	641
Silt (g kg^{-1})	70	69	80	39	89	88	82	130	132
Clay (g kg^{-1})	23	44	51	74	58	59	79	160	168

Extracted using: [a]Mehlich-1, [b] KCl 1M, [c]Ammonium acetate (Embrapa, 1997).

tion) and mean annual temperature of 24.8 ºC (Lima *et al.*, 2011). The soils were classified as Typic Quartzipsamment and Lithic Udipsamment, respectively (Soil Taxonomy). The sites from the Ibiapaba Plateau differ from the site from the coastal zone in terms of soil physicochemical properties (pH, soil texture and concentration of available Si) (Table 1), and especially regarding the soil depth (being shallower, which allowed sampling only up to 40 cm depth). According to Pulz *et al.*, (2008), low pH values (as seen in DDS and SDF; mean = 4.5) contribute to higher solubility of the Si, reducing Si adsorption at these sites. The morphological description of the profiles showed that desilication was less intense in DDS and SDF compared to CS, possibly due to the lower rainfall and temperatures. Herpin *et al.* (2004) established the same relationship between desilication, temperature and precipitation under conditions similar to this study. According to Tisdale *et al.* (1985), younger soils display greater levels of Si. It can therefore be inferred that these soils are younger than the CS, with a higher content of available Si, as shown in Table 2.

Table 2: Average available Silicon (Si) content (mg kg-1) at different layers of the soil in sites of Coastal Savanna, Dense Deciduous Shrubland and Seasonal Deciduous Forest

Sites	Layer (cm)		
	0-10	10-20	20-40
	Available Si in the soil (mg kg^{-1})		
Coastal Savanna	0.133(±0.03)Ab	0.147(±0.04)Ac	0.125(±0.02)Ac
Dense Deciduous Shrubland	0.767(±0.13)Aa	0.970(±0.20)Aa	0.970(±0.20)Aa
Seasonal Deciduous Forest	0.705(±0.12)Aa	0.605(±0.10)Ab	0.506(±0.10)Ab

*Mean values followed by the same letter, lowercase in a column and uppercase in a row, do not differ by Tukey test at 5% probability.

Sampling and laboratory experiment

Ten plots of 100 m^2 (10 x 10 m) on each site were selected, and four samples of soil in each plot randomly distributed were collected, homogenized, air-dried, sieved (2 mm grid) and stored for further physicochemical analysis. Fruits from different individuals (5 plants from each plot) were collected and taken to the laboratory for pulping, disinfection, dormancy breaking by mechanical scarification, and germination, according to protocol established by Brazilian Ministry of Agriculture, Livestock and Food Supply (Brasil, 1992).

To test the influence of temperature on Si absorption, we conducted experiments simulating temperature stress at 15 ºC, 25 ºC, and 45 ºC, adopting an approximate average temperature at the three sites of study (25 ºC), and values above and below found in the field (45 ºC and 15 ºC). Three seedlings were transferred to a plastic container constantly aerated and added a nutrient solution as Johnson et al. (1957). Sodium metasilicate was added (0.9 mmol L-1, corresponding to approximately 25 mg L-1) to the nutrient solution (as source of Si, referred as +Si treatment) to five containers, each with three seedlings, for each temperature treatment (totalling 45 containers and 135 plants with treatment in the presence of Si). Treatments without Si (-Si treatment) were also kept for each replication and used treatment. The Si concentration was adopted based on reports involving stress studies (Epstein, 1999). The nutrient solution was added every seven days for treatments with and without Si. Initially, the seedlings were kept in the solution at 20% of the total concentration, then the nutrient concentration was raised to 50% (second week), and finally to 100% (third week). Considering that it is not a cultivated species (most of the studies on agricultural crops were carried out with short-cycle plants) and through tests prior to setting up the experiment, it was decided to condition the plants to a progressive stress to guarantee the observation of some effect. The pH of the nutrient solution was monitored every two days and, if necessary, corrected to 6.5 with NaOH or HCl; the initial electrical conductivity was also corrected to 2.5 mS cm^{-1}.

To test the influence of water stress on Si absorption, plastic pots containing approximately 2 kg of washed autoclaved sand was used in which three seedlings were placed per pot and kept in a greenhouse at 35 °C under sunlight. For the acclimatisation of the seedlings, the vessels were maintained at 90% soil field capacity (FC) by adding water daily for two weeks. The pots received a chemical fertiliser containing 0.25g N + 0.125g P_2O_5 and 0.125 g K_2O pot^{-1}. The treatments were then applied, consisting of two moisture levels, 60 and 40% FC, either in the presence of Si at 100 mg kg^{-1} soil or without Si, with 5 replications. The moisture levels were established considering the precipitation in each area, one level of no stress, approaching to field capacity during the rainy season (60%), and the other associated to stress (40%), as reported in the literature (Amin *et al.*, 2014). Silicon was applied in the form of $Na_2Si_3O_7$ and incorporated into the soil before seedlings introduction. The soil moisture level was checked daily by weighing the pots and adding water to reach the weight corresponding to the moisture level at 60 and 40% FC.

Determination of Si in soil and plant and relative water content

The quantification of Si in soil was done at the end of the experiment, according to Snyder (1991) and readings for Si in the extracts were taken with a spectrophotometer at a wavelength of 660 nm.

For the quantification of Si in plants (were used three plants/sample), 0.1 g of ground samples were mixed with 2.0 mL of H_2O_2 at 30% (v/v) and 3.0 mL of NaOH (0.25 mol L^{-1}) and autoclaved for 1 hour at 123 ºC and 0.15 MPa for digestion. Si concentration was determined spectrophotometrically (Carneiro, 2007; Korndörfer *et al.*, 2004). The accumulated Si was obtained considering the dry matter production of plants.

To measure Si absorption, one plant was taken at 30, 45 and 60 days, from each replication in each experiment, shoots and roots were separated, washed with deionized water, dried in an oven with force air circulation at 65 ºC until constant weight to determine the dry matter, and then ground for Si quantification. Plants with -Si treatment were sampled to evaluate the natural occurrence of Si.

The relative water content (%) was determined in the water stress experiment. For this, the youngest fully developed leaf from one seedling in each pot was collected, cut at the base of the blade, and quickly transferred to the laboratory in a sealed plastic bag, to get the leaves fresh weight (LFW) within one and a half hours of collection. The leaves were then soaked for 16-18 hours at room temperature (25 ± 2 °C), dried on paper towels and weighed again to determine the turgid weight (LTW). The dry weight (LDW) was also determined after drying the material in an oven at 65 °C for 72 hours. The relative water content (RWC) was calculated from the formula proposed by Turner (1986): RWC (%) = (LFW-LDW) / (LTW-LDW) x100.

Statistical Analysis

Normality of the data and homogeneity of the residue data were tested with the Kruskal-Wallis Test, followed by an analysis of variance (ANOVA), using Tukey's test to compare treatment means. The experiment was set up in a split-split lot design, an special analysis case with factorial structure, considering the three areas as main lots and temperature, humidity level and sampling period as the sub-lots, with five replications for each sample, using R software v. 3.1.2 (R Development Core Team, 2014).

RESULTS

Does abiotic stress increase Si absorption?

The Si absorption varied depending on the temperature (Figure 1). In general, the higher absorption of silicon occurred at the highest temperature (45 ºC). However, this pattern was more evident in DDS and in the first two-time intervals (30 and 45 days). At 60 days of experiments, there were not differences among sites or among temperatures, indicating that there must be saturation in the silicon absorption capacity over time. At the beginning, the seedlings incorporate the silicon to mitigate the effects of abiotic stress, but this effect diminishes with time and the plants began to incorporate the Si regardless the greater abiotic stress.

Evaluation of accumulated Si in plants grown with nutrient solution without the addition of Si (Figure 2) suggests that plants from DDS and SDF areas - with more available Si in the soil, (Table 2), also have higher concentrations of Si in their tissues.

Under conditions of water restriction, Si accumulation also was influenced by stress. Seedlings at 40% FC accumulated more Si than seedlings at 60% FC (Figure 3). However, unlike the temperature stress experiments, the effect of stress was more evident at 60 days, indicating that seedlings should take longer to be influenced by the negative effect of water stress than temperature stress.

Does the presence of Si stimulate biomass production in natural environments?

The addition of Si to the nutrient solution increased dry matter production of shoots and roots of *E. punicifolia* from the three areas during the evaluated periods (Figure 4). Within the areas, the DDS showed higher biomass production compared to the others, being higher at 60 days. Analysing the first sampling period, gains in roots seems higher than shoot except for SDF where the shoots were higher under the three tested temperatures. At 45 days the roots gains were higher only at CS area while in the other areas the presence of Si influences root gains and in its absence was for shoot. At the SDF area shoot was higher than root at 25 and 45 °C, while at 15 °C the presence of Si promotes shoots gains. Root gains was higher at SDF for the three tested temperatures at 60 days while at DDS at 25 and 45 °C. The shoot gain was benefited by the addition of Si at the CS area.

The presence of Si stimulated the production of biomass in the experiment for water stress, when compared to seedlings from the same area, being root gains higher than shoots with higher values found after 60 days of the experiment (Figure 5). However, there were not differences among the mean values for biomass production in the three sites. The absorption of silicon benefited the growth of seedlings independent of sites.

The presence of Si also increased the relative water content (RWC) of the leaves at the two tested moisture levels (Table 3). However, the water deficit affected this variable, reducing the RWC even in the presence of Si, compared to the condition of no water restriction.

Do plants from different environments display differences in Si absorption?

It should be noted that responses for Si absorption as a function of temperature, was more evident during the first 30 days of the experiment (Figure 1a). During that period, plants from CS and SDF areas did not absorb greater amounts of Si as a function of temperature variations. On the other hand, plants from the DDS displayed greater Si absorption at all tested temperatures, when compared to the other areas.

The same behaviour was seen at 45 days. In the first two periods, plants from the DDS absorbed more Si when subjected to the higher temperature (45 °C), whereas for plants from the SDF and CS, the variations in temperature do not appear to affect Si absorption, since no significantly differences were observed.

Finally, after 60 days of the experiment, an increase in Si absorption (30 < 45 < 60 days) was confirmed for all areas under study (Figure 1c), with no influence of temperature.

On the other hand, when evaluated the absorption of Si under water stress conditions (Figure 3), was noticed that SDF area showed greater sensitivity to stress.

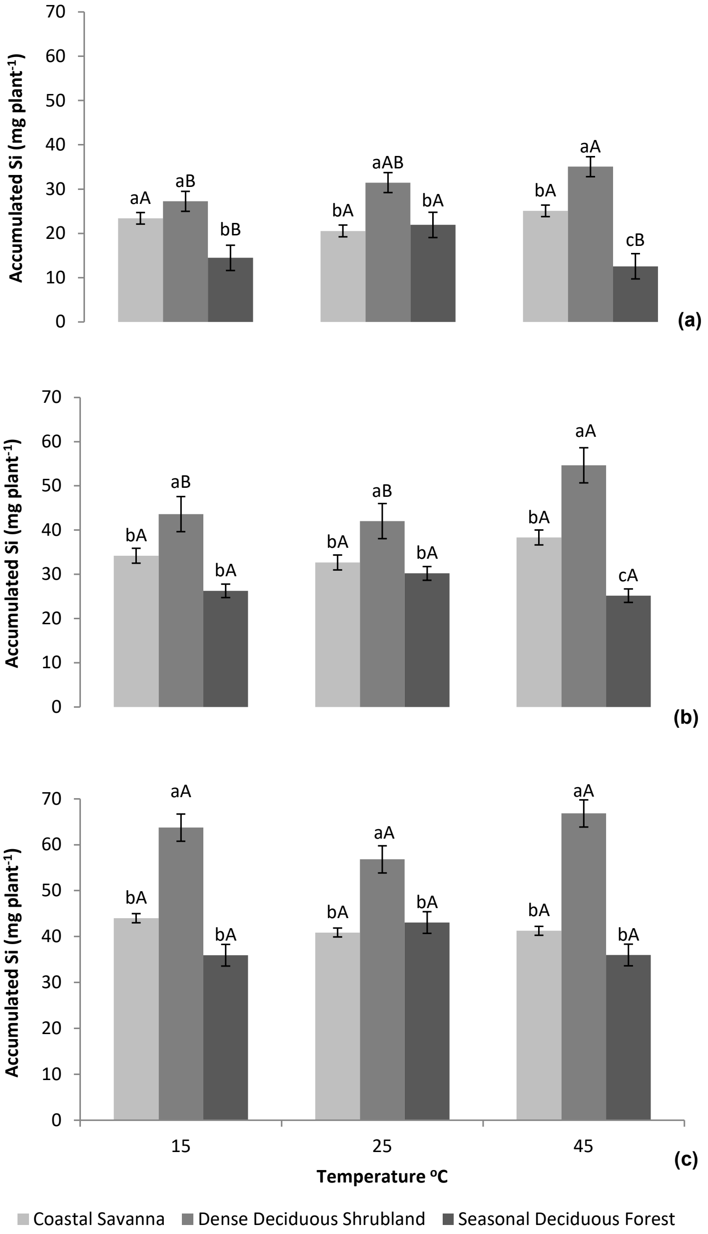

Figure 1: Accumulated silicon (Si) in plants of Eugenia punicifolia from three different areas (Coastal Savanna, Dense Deciduous Shrubland and Seasonal Deciduous Forest), grown in Si-rich nutrient solution under different temperature regimes, at 30 (a), 45 (b) and 60 (c) days of the experiment. Mean values followed by the same uppercase letter do not differ when comparing the effects of temperature for the same area, and mean values followed by the same lowercase letter do not differ when comparing areas with the same temperature, by Tukey's test at 5% probability.

DISCUSSION

Was confirmed the first prediction that abiotic stress causes changes to Si absorption, especially for plants from the DDS at 45 °C. According to Lamarca *et al.* (2011), the optimum temperature for germination and growth in *Eugenia* is 25 °C. Additionally, it is known that higher plants, when exposed to excessive heat, characterised by at least 5 °C above the optimum growth temperature, display a particular set of cellular and metabolic responses necessary for plants to survive under high temperature (Guy, 1999). Thus, was not expected for *E. punicifolia* to exhibit high growth at high temperatures (above 30 °C). However, it is possible that the presence of Si allowed the growth at high temperatures, due to mechanisms of stress relief associated with use of this element (Cooke & Leishman, 2011). For these plants, the stress

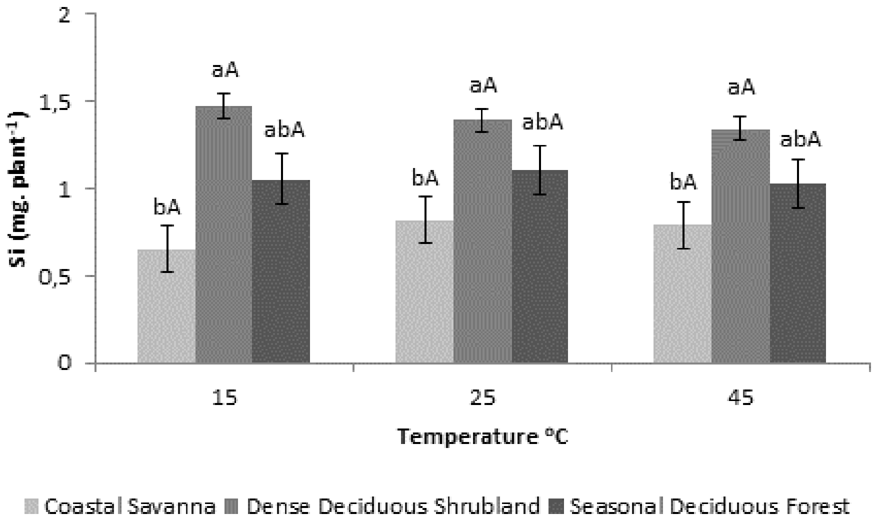

Figure 2: Accumulated silicon (Si) in plants of E. punicifolia from three different areas, grown in nutrient solution with no addition of Si, under different temperature regimes, at 60 days of the experiment (mean values followed by the same uppercase letter do not differ when comparing the effects of temperature for the same area, and mean values followed by the same lowercase letter do not differ when comparing areas with the same temperature, by Tukey's test at 5% probability).

conditions stimulated Si absorption, corresponding to a possible mechanism of stress alleviation.

It was expected that plants from the CS display similar behaviour to those from the DDS, since they are subjected to higher temperature ranges under natural conditions than those from DDS. However, low Si availability in the soil from CS induce to low Si absorption, even under extreme conditions of temperature, demonstrating that the environment to which the plants are subjected, influences the adaptation of the species to similar conditions of their place of origin.

To minimise damages due to water shortage, plants develop various strategies to resist or avoid water stress (Mir *et al.*, 2022; Yin *et al.*, 2014), such as reduction in the growth rate of leaves and stem, the synthesis of osmotic solutes that are involved in maintaining cell turgidity, and the synthesis of antioxidant proteins to prevent chlorophyll breakdown (Wilkinson & Davies, 2010). Since the plants of the study areas are normally subjected to seasonal rains, these mechanisms may have been activated before Si absorption stimulation under stress condition, thereby causing a delay in the response of the element. In that case, the relative leaf water content in plants under water stress should be considered a more efficient variable to demonstrate changes in the functions of plants under water stress over a short period of time.

The effect of Si preventing water loss from leaves, regardless the physiological mechanism involved in this benefit is not well understood, but literature suggest that may be related to the formation of a double layer of silica cuticle and silica cellulose (Chang *et al.,* 2020). This would induce a reduction in the amount of water lost by evapotranspiration throughout the vegetative cycle, requiring less water and becoming more resistant to a possible drought. However, in this study, plants from the three areas did not reflect this beneficial effect from Si when subjected to water stress. Besides the natural adaptation of plants to their original environments, it should be considered that the principal mechanism for absorbing Si is mass flow (Epstein, 1999), that varies depending on plant species (Motomura *et al.*, 2002; Gaur *et al.*, 2020). Considering that the areas of study have no anthropic intervention (e.g. irrigation), and that plants absorb more Si under regular water supply, it can be stated that water was a limiting factor that determined stress in the development of these plants under the studied conditions.

Extreme weather, including high temperatures and water stress, have a negative effect on plant growth and development, leading to a catastrophic loss of biomass production (Bita & Gerats, 2013; Wang *et al.*, 2021). In the current study, plants under high-temperature or water deficit, showed higher biomass production in the presence of Si solution than under its absence. It can therefore be assumed that Si absorption alleviated the temperature and water stress and possibly give these species a greater capacity for competition in their environments and, consequently, a wider distribution.

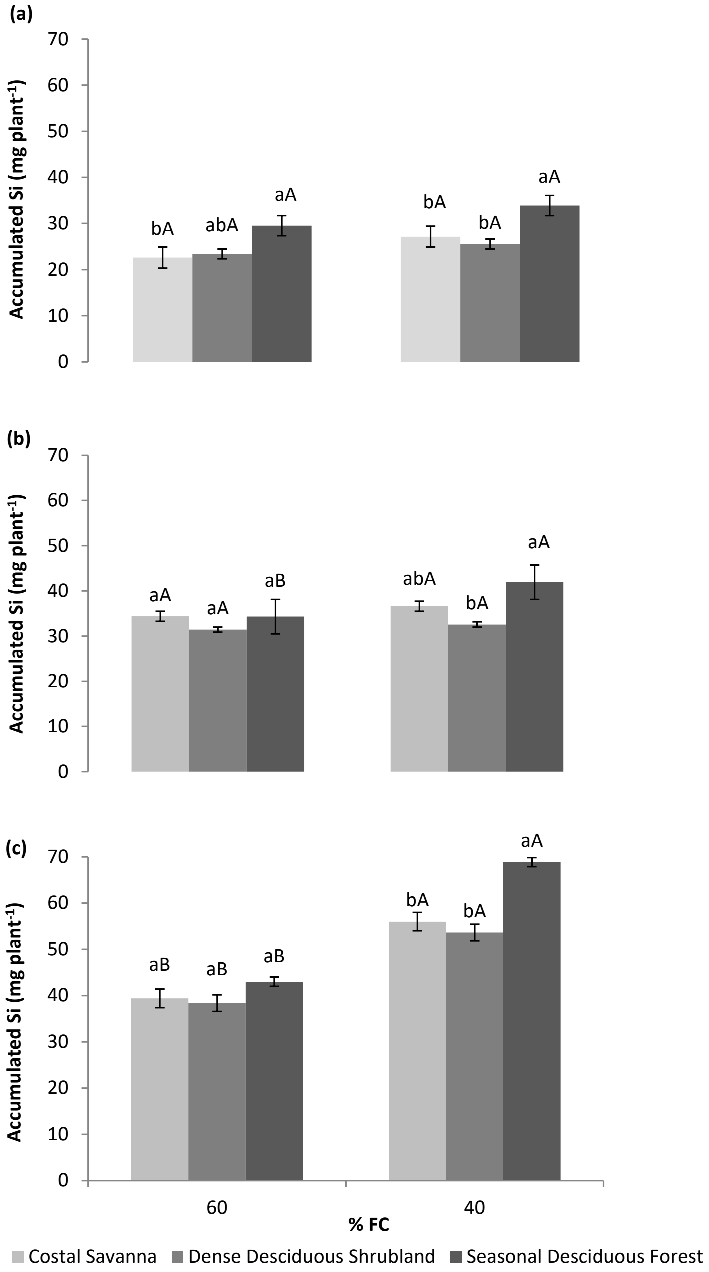

Figure 3: Accumulated silicon (Si) in plants of Eugenia punicifolia from three different areas, grown in nutrient solution with no addition of Si, under different water regimes, at 60 days of the experiment (mean values followed by the same uppercase letter do not differ when comparing the effects of water regime for the same area, and mean values followed by the same lowercase letter do not differ when comparing areas with the same water regime, by Tukey's test at 5% probability).

Moreover, it was demonstrated that Si absorption positively affects plant biomass. These results agree with other studies using both soil and nutrient solutions (Vaculík *et al.*, 2009; Shen *et al.*, 2010). However, seems that the beneficial effect of Si on the production of plant biomass may not be evident unless the plants are subjected to some type of stress (Fauteux *et al.*, 2005). In the present study, the affirmation that abiotic variations conditioned the stress in plants and stimulated Si absorption is made possible by the increase in biomass production, especially under extreme temperatures or water stress. It is believed that plants under natural and agricultural systems, subjected to stress temperature suffer by other stress such as water deficit. Considering the increases of temperature and water shortage due to climate change around the world (IPCC, 2007), it is evident the necessity to understand the impact of stress on plant functions, and especially the physiological response mechanisms of plants both during and

Table 3: Relative leaf water content (RWC) in Coastal Savanna, Dense Deciduous Shrubland and Seasonal Deciduous Forest grown under different moisture regimes (Si+: Si)

Site	Moisture (%) FC	Si	RLWC (%)
Coastal Savanna	60	+	74.43Aa
		-	49.57Ab
	40	+	26.04Ba
		-	22.07Aa
Dense Deciduous Shrubland	60	+	54.59Ba
		-	42.46Bb
	40	+	32.28Aa
		-	22.38Ab
Seasonal Deciduous Forest	60	+	72.99Aa
		-	53.69Ab
	40	+	39.67Aa
		-	28.85Ab

*Mean values followed by the same letter, lowercase in a column and uppercase in a row, do not differ by Tukey test at 5% probability.

when recovering from stress (Shen *et al.*, 2010). The plants in this study were not subjected to simultaneous stresses. However, if the pattern of absorption caused by the temperature increase occurs in the field, the plants will also benefit from Si absorption, which would take place because most of the deposited silica, in particular on the outer walls of the epidermal cells on both sides of the leaves, would form a double layer that would prevent water loss through stomatal transpiration (Hattori *et al.*, 2005). According to Balakhnina & Borkowska (2013), the combined effects of Si in plants under stress conditions remain being not understood.

Finally, it was demonstrated that the environment affected Si absorption. Plants of the same species occurring under different environmental conditions reacted differently to temperature and water variations with respect to Si absorption. The absorption of Si by plants seems to be a response of the original environment, e.g. plants from areas with higher temperatures respond to variations in temperature, increasing Si absorption. Such behaviour seems to be related to the natural Si content of these areas (see Table 2), since plants occurring in areas with higher Si availability in the soil absorbed more Si in response to temperature variations. Among the areas under study, plants from the DDS were the most influenced by variations in temperature. This may be related to the location and altitude, where temperature variations up to 10 ºC during the day are more frequent (Rocha *et al.,* 2002), leading this area to be considered as the one with most adverse conditions. In the laboratory, plants from this area had the same behaviour, absorbing more Si regardless of the temperature. In addition, the higher concentrations of Si in plants from this area, even without the addition of Si to the nutrient solution, confirms the higher availability of Si found in the soil (see Table 2), and a tendency to its absorption at temperatures which cause some stress.

Moreover, the Si absorption patterns seen in the present study suggest that *E. punicifolia* has high phenotypic plasticity. According to Scheiner (1993), phenotypic plasticity represents the ability of an organism to change its physiology and morphology in response to its interaction with the environment. Therefore, species with the potential for plasticity in characteristics related to survival or occupation, have adaptive advantages in unstable, heterogeneous, or transitional environments (Via *et al.*, 1995). In the present study, the absorption of Si in plants from the DDS under higher temperatures, and from the SDF under water stress, could be important mechanisms for the maintenance of *E. punicifolia* in hotter environments, demonstrating a greater capacity of the species to resist variations in temperature and humidity, even with a delay in the stress response of those plants that are not used to such variations naturally.

This would then explain the wide distribution of *E. punicifolia* in different environments, as found by Conceição & Aragão (2010) and Arantes & Monteiro (2002) being important information for plant scientists, since aspects related to the species adaptability, life history, origin, and

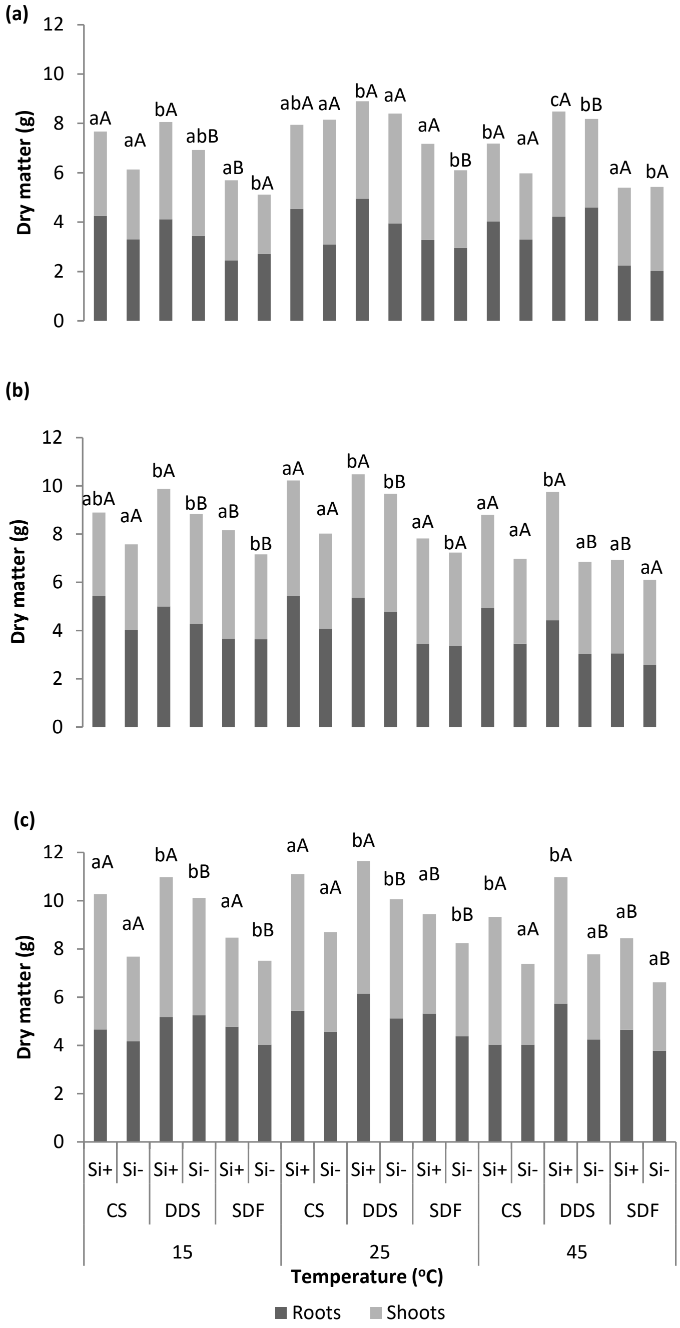

Figure 4: Dry matter production (roots and shoots) in plants of *Eugenia punicifolia* from three different areas: CS (Coastal Savanna); DDS (Dense Deciduous Shrubland); SDF (Seasonal Deciduous Forest), grown in a nutrient solution with (Si+) and without (Si-) silicon, under different temperature regimes and sampling periods: (a) 30, (b) 45 and (c) 60 days. Mean values followed by the same uppercase letter do not differ when comparing the presence or absence of Si in the nutritive solution for the same area, and mean values followed by the same lowercase letter do not differ when comparing areas with the same tested temperature, by Tukey's test at 5% probability.

spatial distribution, could direct studies in genetics and selection of attributes that enable a sustainable production, that reduce the crops susceptibility to environmental fluctuations or the increasing dependence of crop inputs.

The ability of Si to relieve stress is undeniable, but future studies should include aspects related to the adaptation of plants to their original environments and recent climate changes, in addition to the possibility of using the element in environmental recovery. In this way, silicon would become even more relevant for the scientific community, expanding knowledge about its performance in several areas, leading to important advances.

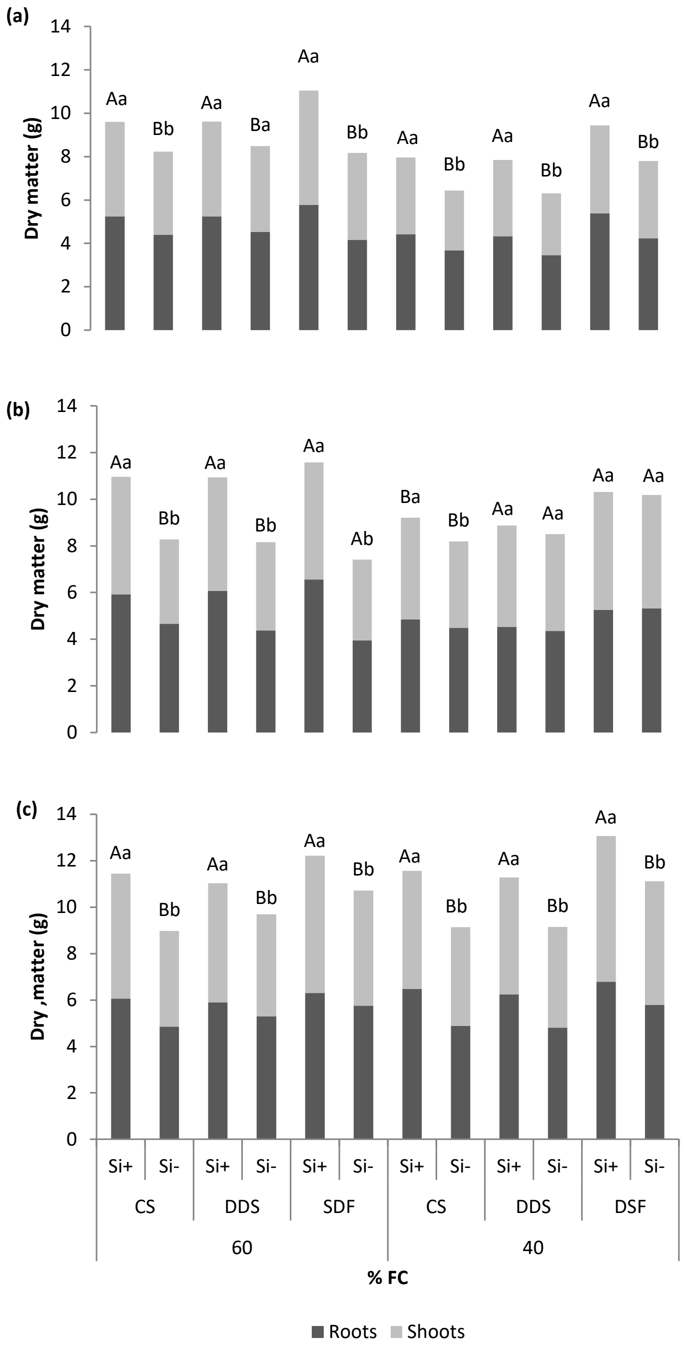

Figure 5: Dry matter production (roots and shoots) in plants of Eugenia punicifolia from three different areas: CS (Coastal Savanna); DDS (Dense Deciduous Shrubland); SDF (Seasonal Deciduous Forest), grown with (Si+) and without (Si-) silicon, under different moisture regimes and sampling periods: (a) 30, (b) 45 and (c) 60 days (mean values followed by the same uppercase letter do not differ when comparing the presence or absence of Si in the nutritive solution for the same area, and mean values followed by the same lowercase letter do not differ when comparing areas with the same tested temperature, by Tukey's test at 5% probability).

CONCLUSIONS

Si absorption by *E. punicifolia* is influenced by variations of temperature and drought, since the plants subjected to these conditions originate from locations with high soil Si availability, and temperatures close to those tested in this study under natural conditions. The plants seem to reflect adaptation to the stresses to which they are subjected, especially water stress, showing late responses to Si absorption. Increases in Si absorption, triggered by water and temperature stress, are directly related to increases in dry matter production, suggesting that this may be a relief mechanism for the stresses under test. The findings could be of relevance importance specially for cropped science, bringing new perspectives about Si behavior in agriculture.

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