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Silicon Application Induced Alleviation of Aluminum Toxicity in Xaraés Palisadegrass

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Abstract: Aluminum (Al) toxicity is a major abiotic constraint for agricultural production in acidic soils that needs a sustainable solution to deal with plant tolerance. Silicon (Si) plays important roles in alleviating the harmful effects of Al in plants. The genus *Urochloa* includes most important grasses and hybrids, and it is currently used as pastures in the tropical regions. Xaraés palisadegrass (*Urochloa brizantha* cv. Xaraés) is a forage that is relatively tolerant to Al toxicity under field-grown conditions, which might be explained by the great uptake and accumulation of Si. However, studies are needed to access the benefits of Si application to alleviate Al toxicity on Xaraés palisadegrass nutritional status, production, and chemical–bromatological composition. The study was conducted under greenhouse conditions with the effect of five Si concentrations evaluated (0, 0.3, 0.6, 1.2, and 2.4 mM) as well as with nutrient solutions containing 1 mM Al in two sampling dates (two forage cuts). The following evaluations were performed: number of tillers and leaves, shoot biomass, N, P, K, Ca, Mg, S, B, Cu, Fe, Mn, Zn, Al, and Si concentration in leaf tissue, Al and Si concentration in root tissue, neutral detergent fiber (NDF), and acid detergent fiber (ADF) content in Xaraés palisadegrass shoot. Silicon supply affected the relation between Si and Al uptake by increasing root Al concentration in detriment to Al transport to the leaves, thereby alleviating Al toxicity in Xaraés palisadegrass. The concentrations between 1.4 and 1.6 mM Si in solution decreased roots to shoots Al translocation by 259% (from 3.26 to 1.26%), which contributed to a higher number of leaves per plot and led to a greater shoot dry mass without affecting tillering. Xaraés palisadegrass could be considered one of the greatest Si accumulator plants with Si content in leaves above 4.7% of dry mass. In addition, Si supply may benefit nutrient-use efficiency with enhanced plant growth and without compromising the chemical–bromatological content of Xaraés palisadegrass.

Keywords: Al⁺³ phytotoxicity; Si accumulator plants; silicon concentrations; tropical pasture; *Urochloa brizantha* cv. Xaraés

1. Introduction

Brazil has about 180 million hectares of pastures and is one of the largest commercial cattle producers of the world, which depend on pastures as a main feed source [1], since they are less costly than other forms of feed [2]. Pasture lands represent approximately 73% of Brazil's total agricultural land; however, it is estimated that 80% of these pastures are established in degraded soils [3,4]. Generally, tropical fodder grows in low-fertility acidic soils [5].

Aluminum (Al) toxicity is represented as one of the main yield-limiting factors for crops and pastures in acidic soils [6]. This element is one of the most dominant minerals in the earth's crust, representing about 8% of its mass [7]. Acidic soils constitute $\approx 30\%$ of the world's total land area and 50% of the potentially available arable land worldwide [8]. Under acidic soil conditions ($\text{pH} < 5.5$), Al is solubilized into aluminum ion (Al^{3+}) and became biologically available [9]. Thereby, Al availability affects a wide range of physical, cellular, and molecular processes with a consequent reduction in plant growth [9–11]. Alterations in the structure and/or functions of cell wall components [12], plasma membrane properties [13], nutrient homeostasis [11,14], and signal transduction pathways [6,15] can be induced as a consequence of Al binding to numerous cell sites.

Silicon (Si) has been well documented to alleviate Al toxicity in vascular plants [6,9,10,16]. Silicon is the second most abundant element after oxygen in the earth's crust, comprising approximately 29% (28.8 wt %) of the earth's crust [17–19]. Although Si is considered a quasi-essential element rather than a plant nutrient, it is being increasingly adopted in worldwide agricultural systems [18–21]. The silicon content in the soils ranges from 1 to 45%, depending on soil type [22]. The potential of Si in improving crop yield has been demonstrated in many studies, especially under abiotic and biotic stress conditions (e.g., heavy metals toxicity, salinity, drought, high temperature and pathogens attack) [23,24]. Monocotyledons in general and *Poaceae* species such as Xaraés palisadegrass (*Urochloa brizantha* cv. Xaraés) are clearly favored due to an enhanced supply of Si [19,22,25]. It has been reported that some *Poaceae* species could accumulate Si to levels above 1% of total shoot biomass [23].

Xaraés palisadegrass was released as an option for grazing systems in Brazil in 2002 due to its greater forage accumulation and rapid regrowth compared to the standard industrial cultivar Marandu palisadegrass (*Urochloa brizantha* cv. Marandu) [26]. These above-mentioned factors are combined with good tolerance to spittlebugs (*Notozulia entre-riana* and *Deois flavopicta*), and poorly drained soils [26] increased its cultivation. However, the cultivation and harvest of Si-accumulating crops is responsible for a constant depletion of Si reservoir in soils [27,28] and therefore, it decreases Si bioavailability [29]. The enhanced Si removal by crops and pastures disrupt the recycling of Si by plants back into the soil [30]. Liang et al. [31] reported that Si content in Oxisols in tropical zone can be less than 1% due to the intense weathering process. Highly weathered tropical and subtropical soils under continuous cropping systems are generally low in available Si content due to the heavy desilication of primary silicate minerals as well as the release and leaching of basic cations with decreased base saturation [19,23,32,33]. Therefore, the decrease in Si availability in tropical soils might have significant impacts on cropping systems if not properly managed.

In general, *Urochloa* spp. show greater tolerance to Al^{3+} toxicity than most other grass crops, including maize (*Zea mays* L.), rice (*Oryza sativa* L.), or wheat (*Triticum aestivum* L.) [8,34]. These plants species have a set of desirable genetic characteristics linked to drought and waterlogging tolerance, tolerance in weathered and acidic soils, and resistance to major diseases [35]. Overall, Al^{3+} tolerance mechanisms are classified as external and internal tolerance mechanisms; the molecular genetic mechanisms underlying stress-induced exudation of organic acids are well known [8,34]. In *Urochloa* spp., Al^{3+} tolerance mechanism responses have been mostly associated with exclusion of Al^{3+} (external tolerance mechanisms) [8]. For example, studies comparing the responses of tolerant *U. decumbens* and sensitive *U. ruziziensis* under Al^{3+} stress showed that *U. decumbens* exhibited a multi-seriate root exodermis and Al accumulation in root hairs [36], and they downgraded the importance of exudation of organic acids or changes in rhizosphere pH [37]. It might be possible that the relative tolerance to Al toxicity by *Urochloa* spp. could be associated with a great uptake and accumulation of Si.

As we mentioned above, Si is known for its role in alleviating stressful effects in many plant species, especially Al^{3+} toxicity. However, the mechanisms underlying these responses in forage grasses remain poorly understood. We hypothesized that Si application might reduce Al toxicity in Xaraés palisadegrass plants by decreasing Al transport to plant

shoots without reducing Al uptake by roots. The increased Si instead of Al uptake may provide enhanced nutrient acquisition, which may lead to greater shoot development. In addition, the greater Si uptake may affect the chemical–bromatological composition, since Si could affect the structure of plant cell walls, mostly by altering linkages of non-cellulosic polymers and lignin [38,39]. This research could provide new clues on how Si application affects Xaraés palisadegrass tolerance to Al^{3+} and may be included as a strategy for improving forage growth with a better plant nutrition. Therefore, we propose a novel approach to investigate the benefits of Si application to alleviate Al toxicity on Xaraés palisadegrass nutritional status, production, and chemical–bromatological composition. Here, we assessed the effect of five Si concentrations (0, 0.3, 0.6, 1.2, and 2.4 mM) on the modulation of Si/Al uptake, leaf nutrients concentration, shoot dry mass, neutral detergent fiber (NDF), and acid detergent fiber (ADF) content in Xaraés palisadegrass plants, which were cultivated in nutrient solutions containing 1 mM Al along two forage cuts.

2. Materials and Methods

2.1. Site Description

The study was carried out in a greenhouse ($20^{\circ}38'44''$ south latitude and $51^{\circ}06'35''$ west longitude) with controlled conditions. The temperature in the greenhouse during plant growth ranged between 25°C (minimum) and 35°C (maximum), and averaged 30°C ; with average air relative humidity of 70%.

2.2. Experimental Design and Treatments

The experimental design was a randomized complete block design (RCBD) with four replicates and five treatments of Si concentrations: 0, 0.3, 0.6, 1.2 and 2.4 mM, applied as sodium silicate ($\text{Na}_2\text{O}(\text{SiO}_2) \times \text{H}_2\text{O} - \text{SiO}_2 \approx 26.5\%$ and $\text{Na}_2\text{O} \approx 10.6\%$) in nutrient solution. Silicon concentrations were established based on existing literature for *Poaceae* family [10,16,40]. Xaraés palisadegrass (*Urochloa brizantha* cv. Xaraés) plants were cultivated in plastic pots (3.6 L) containing ground quartz (size of 2 mm) as substrate and were exposed to 1 mM Al concentration (Figure 1). This Al concentration was previously reported to limit *Urochloa* sp. development [41].

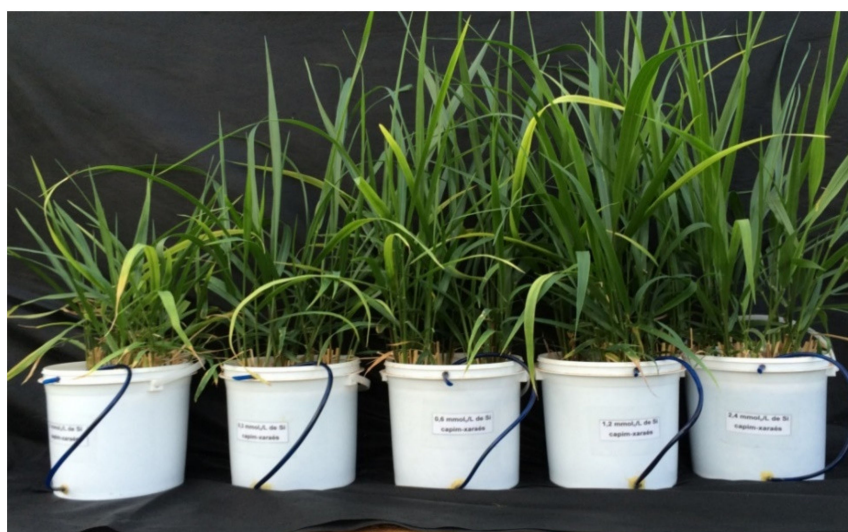


Figure 1. Xaraés palisadegrass cultivated under Al toxicity (1 mM) in ground quartz substrate and nutrients solution containing Si concentrations (0, 0.3, 0.6, 1.2, and 2.4 mM).

The ground quartz was used as growth substrate for better and erect growth of Xaraés palisadegrass, where it can develop its shoot up to one meter with a strong root system. Ground quartz is composed by silica (SiO_2), which is an acidic oxide. It will react with strong bases to form silicate salts, mainly in alkaline solutions. Under acid solutions, acid

oxides do not react under normal conditions. Therefore, the solubility of SiO_2 in acid solutions remains very low. Since the nutrient solution pH level was kept around 4.2, there was no relevant release of Si from the substrate.

The composition of the nutrient solution used in the study is shown in Table 1 and was based on Hoagland and Arnon [42] solution. The pH was daily adjusted to 4.2 ± 0.1 with HCl solution (1 M) and nutrient solutions were changed weekly. The proportion of 70% N-NO_3^- and 30% N-NH_4^+ was kept constant.

Table 1. Volumes of stock solutions used in preparation of nutrient solutions provided during the study.

Si (mM)	0	0.3	0.6	1.2	2.4
Stock solution	Volume (mL L ⁻¹)				
NaSiO ₃ (0.5 M)	-	0.6	1.2	2.4	4.8
KH ₂ PO ₄ (1 M)	1	1	1	1	1
KCl (1 M)	5	5	5	5	5
Ca(NO ₃) ₂ (1 M)	5	5	5	5	5
MgSO ₄ (1 M)	2	2	2	2	2
NH ₄ Cl (1 M)	5	5	5	5	5
Micro—Fe *	1	1	1	1	1
Fe-EDTA **	1	1	1	1	1
AlCl ₃ ·6H ₂ O (0.3 M)	3.3	3.3	3.3	3.3	3.3

* Composition of micronutrient solution, except for Fe in g L⁻¹: MnCl₂·4H₂O = 1.81; ZnCl₂ = 0.10; CuCl₂ = 0.04, H₃BO₃ = 1.49, and H₂MoO₄·H₂O = 0.02. ** 26.1 g of disodium EDTA were dissolved in 286 mL of 1 M NaOH, mixing 24.1 g of FeSO₄·7H₂O, airing overnight and completing the volume to 1 L with deionized water.

Based on Table 1, the following amounts of chemical elements were supplied for all treatments using the nutrient solutions, in mg L⁻¹: 210 of N, 31 of P, 234 of K, 200 of Ca, 48 of Mg, 66.8 of S, 4.85 of Fe, 0.5 of Mn, 0.05 of Zn, 0.02 of Cu, 0.011 of Mo, 390 of Cl, 0.26 of B and 27 of Al. For the five Si concentrations (0, 0.3, 0.6, 1.2, and 2.4 mM) were provided 0, 8.4, 16.8, 33.6, and 67.2 mg L⁻¹ of Si, respectively.

2.3. Xaraés Palisadegrass Growth and Harvest

The Xaraés palisadegrass seeds were obtained commercially and placed to germinate in a plastic tray containing sand as substrate. The plastic trays were periodically watered with deionized water until the seedlings reached around four centimeters; then, 12 seedlings were transplanted into each plastic pot.

Periodic thinning was carried out until five well-developed plants per pot remained. One day after transplanting the seedlings (DAT), 1 L of diluted solution at 20% of the corresponding initial solution was applied. Initially, the solutions remained in the pots during the day and night, being circulated by the substrate four times a day for a week to breathe the roots. They were subsequently drained at night and supplied in the morning. After 4 DAT, the solutions with definitive concentration were added to the pots and subsequently changed weekly. The water lost by evapotranspiration was replaced daily with deionized water, based on the volume of the glass where the solution was drained.

Two cuts were performed; each one was made at 5 cm from the plant's neck in relation to the substrate, when most of the mature leaves were in senescence (40 and 70 DAT in the first and second cut, respectively). Xaraés palisadegrass shoot and root were collected separately, washed in deionized water, and dried for 72 h in a forced-air oven at 60 °C. The shoots were separated into newly expanded leaves (LR = the two newly expanded leaves with visible ligula) and from the rest of the plant that was collected (leaves from the apex of the plant, mature leaves, and stems plus sheaths).

2.4. Evaluations

2.4.1. Number of Leaves and Tillers, Shoot Dry Mass, and Fibers Content

The number of leaves and tillers of each pot were obtained by manual counting before each cut. As we mentioned above, 40 and 70 DAT, Xaraés palisadegrass shoot was collected, washed in deionized water, and dried; then, the shoot dry mass (g plot^{-1}) was weighed. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) contents were measured following the methodologies of Van Soest [43].

2.4.2. Silicon and Al Concentrations in Leaf and Root Tissue and Nutrient Concentration in Diagnostic Leaves (Nutritional Status)

Silicon and Al concentrations in leaf and root tissue followed Korndörfer [44] and Malavolta et al. [45] methodologies, respectively. N, P, K, Ca, Mg, S, B, Cu, Fe, Mn, and Zn concentrations in leaf tissue were determined according to Malavolta et al. [46].

2.4.3. Silicon and Al Roots to Shoots Translocation Factor

The translocation factor of Si and Al were calculated after the second cut, following Abichequer and Bohnen [47], according to Equation (1):

$$\text{Roots to shoots translocation (\%)} = \frac{\text{Shoot Si or Al concentration}}{\text{Root Si or Al concentration}} \times 100. \quad (1)$$

Shoot and root Si concentrations are in g kg^{-1} of dry mass and shoot and root Al concentrations are in mg kg^{-1} of dry mass, respectively.

2.5. Statistical Analysis

All data were initially tested for normality using the Shapiro and Wilk test and Levene's homoscedasticity test ($p \leq 0.05$), which showed the data to be normally distributed ($W \geq 0.90$). Data were submitted to analysis of variance (F test) and adjusted to polynomial regression for the Si concentrations using R software [48].

2.6. Principal Components Analysis

Principal component analysis (PCA) was used to evaluate Xaraés palisadegrass productive components, leaf nutrient, Si and Al concentrations, root Si and Al concentrations and chemical–bromatological composition. The PCA was performed using FactoMineR and factoextra packages in R software [48]. The number of PCs was selected depending on eigenvalue. The PCs that had eigenvalues ≥ 1 were kept, and the rest were removed. The total variability of 70% or greater was expressed by the selected PCs. Then, the correlations between selected PCs and observed variables explained with factor loading, which was estimated based on Equation (2):

$$\text{Factor loading} = \text{Eigenvectors} \times \sqrt{\text{Eigenvalue}}. \quad (2)$$

A factor loading of >0.30 was considered significant according to Lawley and Maxwell [49]. The biplot graphic shows that PC1 (axis x) and PC2 (axis y) were plotted, separating the first and second cuts.

3. Results

3.1. Silicon and Aluminum Content in Leaves and Roots, Neutral, and Acid Detergent Fiber Content in Xaraés Palisadegrass

Silicon application influenced Si and Al concentration in leaves and roots and ADF content (Figure 2). Neutral detergent fiber (NDF) was not significantly affected by Si concentrations (Figure 2G).

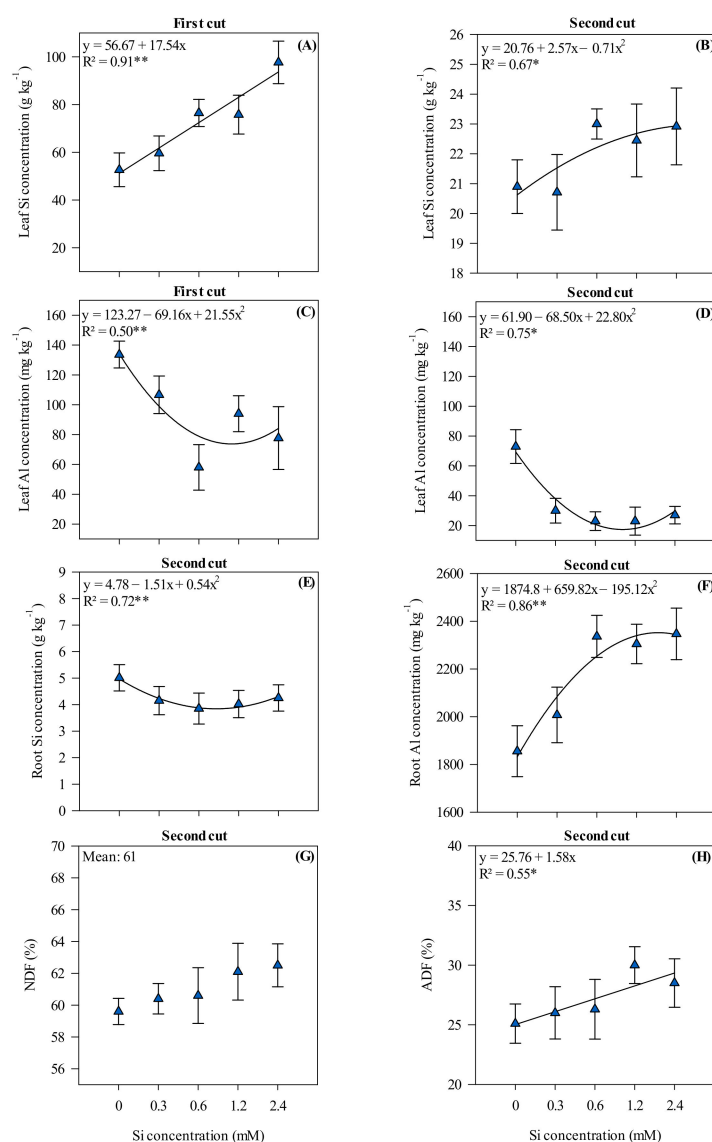


Figure 2. Leaf Si concentration in the first (A) and second cut (B), leaf Al concentration in the first (C) and second cut (D), root Si concentration (E) and root Al concentration (F) in the second cut, neutral detergent fiber (NDF) (G) and acid detergent fiber (ADF) (H) in the second cut as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

In the first cut, leaf Si concentration responded linearly to the increasing Si concentrations (Figure 2A), while leaf Al concentration showed a non-linear response to Si concentrations (P_{min} [lowest estimated value] = 1.6 mM Si) (Figure 2C). In the second cut, both leaf Si and Al concentration responded non-linearly to increasing Si concentrations (leaf Si: P_{max} [highest estimated value] = 1.8 mM Si and leaf Al: P_{min} = 1.5 mM Si) (Figure 2B,D). In the second cut, root Si and Al responded non-linearly to increasing Si concentrations (root Si: P_{min} = 1.4 mM Si and root Al: P_{max} = 1.7 mM Si) (Figure 2E,F). In contrast, ADF was found to respond linearly to Si concentrations (Figure 2H).

3.2. Number of Leaves and Tillers Per Plot and Shoot Dry Mass of Xaraés Palisadegrass

The number of leaves per plot and shoot dry mass were positively affected by increasing Si concentrations (Figure 3), whereas the number of tillers per plot was not influenced by Si concentrations (Figure 3C,D).

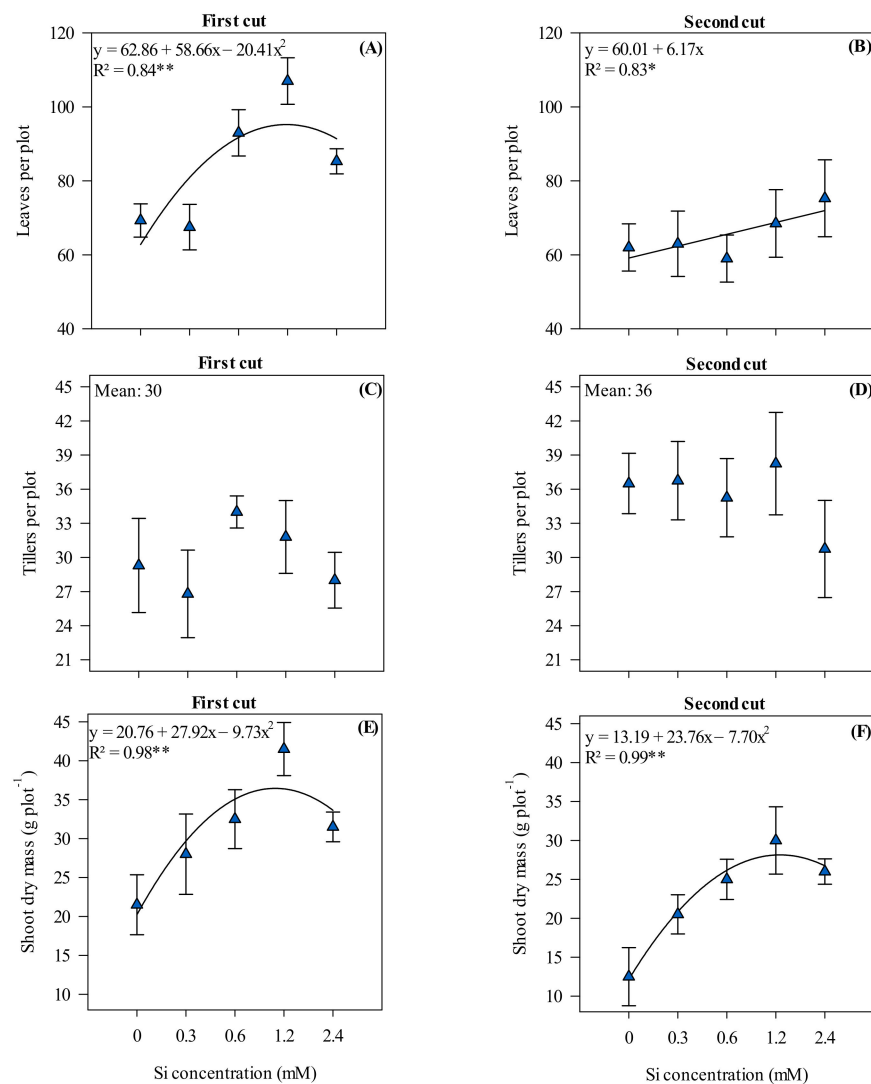


Figure 3. Number of leaves per plot in the first (A) and second cut (B), number of tillers per plot in the first (C) and second cut (D), and shoot dry mass in the first (E) and second cut (F) as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

In the first cut, leaves per plot and shoot dry mass responded non-linearly to increasing Si concentrations (Figure 3A,E). The highest estimated values were verified with 1.4 mM Si (Figure 3A,E). In the second cut, leaves per plot responded linearly to increasing Si concentrations (Figure 3B), while shoot dry mass showed a non-linear response to Si concentrations ($P_{max} = 1.5$ mM Si) (Figure 3F).

3.3. Leaf Nutrient Concentrations in Xaraés Palisadegrass

Overall, Si application influenced all tested nutrient concentrations (N, P, K, Ca, Mg, S, B, Cu, Fe, Mn and Zn) in leaf tissue (Figures 4–6). However, leaf B concentration in the first cut and leaf K and Zn concentrations in the second cut were not affected by increasing Si concentrations (Figures 4F, 5E and 6F).

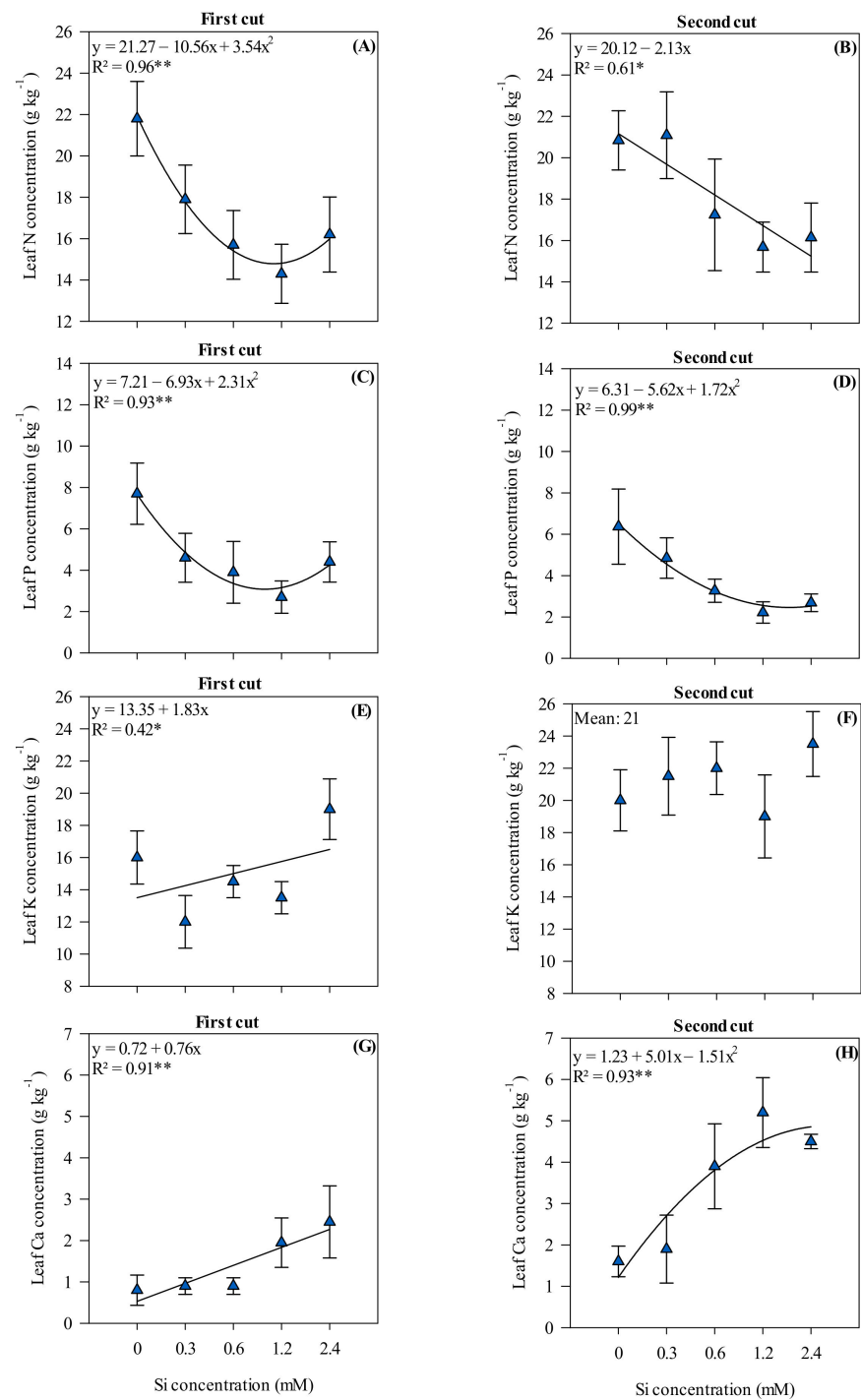


Figure 4. Leaf N concentration in the first (A) and second cut (B), leaf P concentration in the first (C) and second cut (D), leaf K concentration in the first (E) and second cut (F), leaf Ca concentration in the first (G) and second cut (H) as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

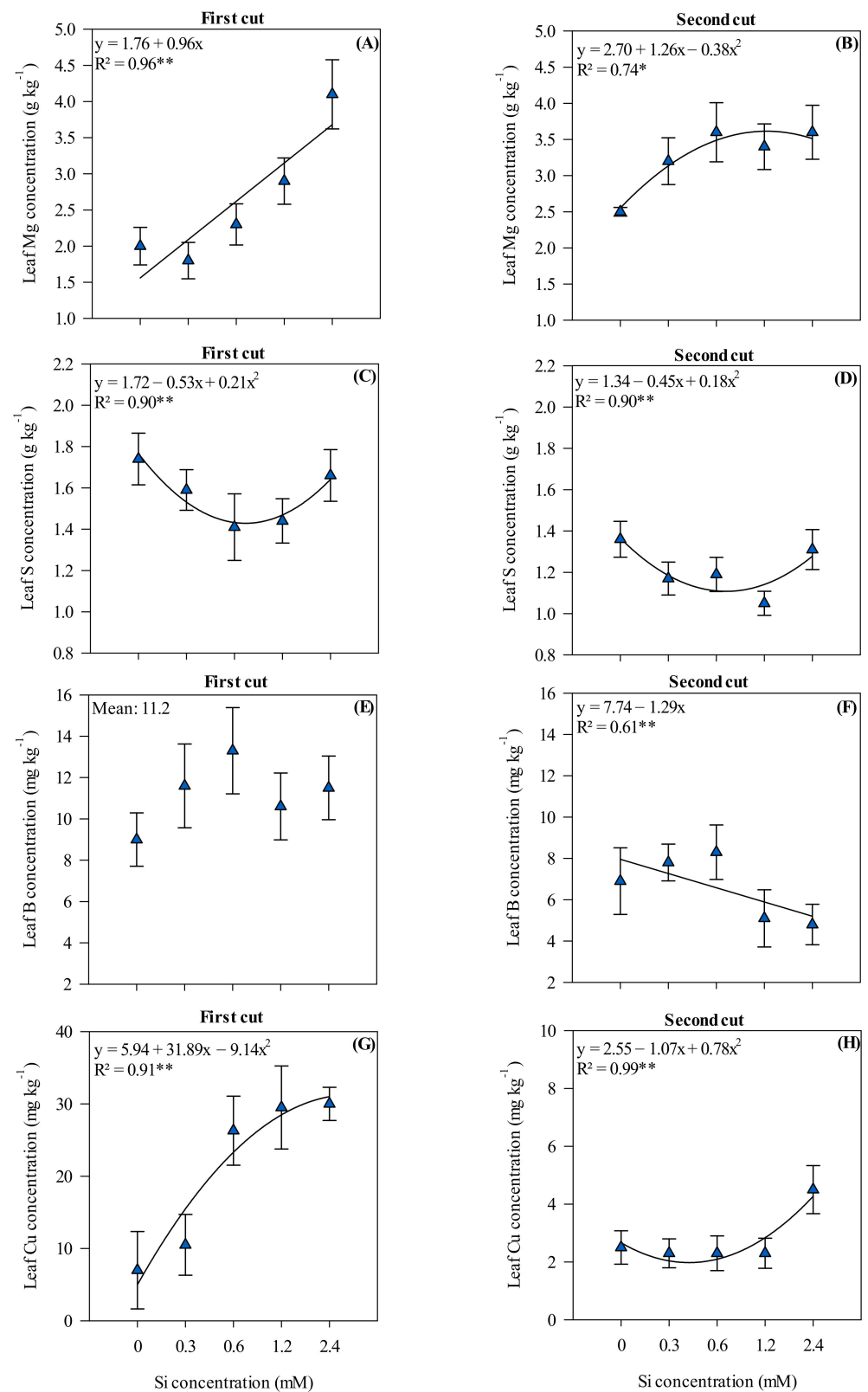


Figure 5. Leaf Mg concentration in the first (A) and second cut (B), leaf S concentration in the first (C) and second cut (D), leaf B concentration in the first (E) and second cut (F), leaf Cu concentration in the first (G) and second cut (H) as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

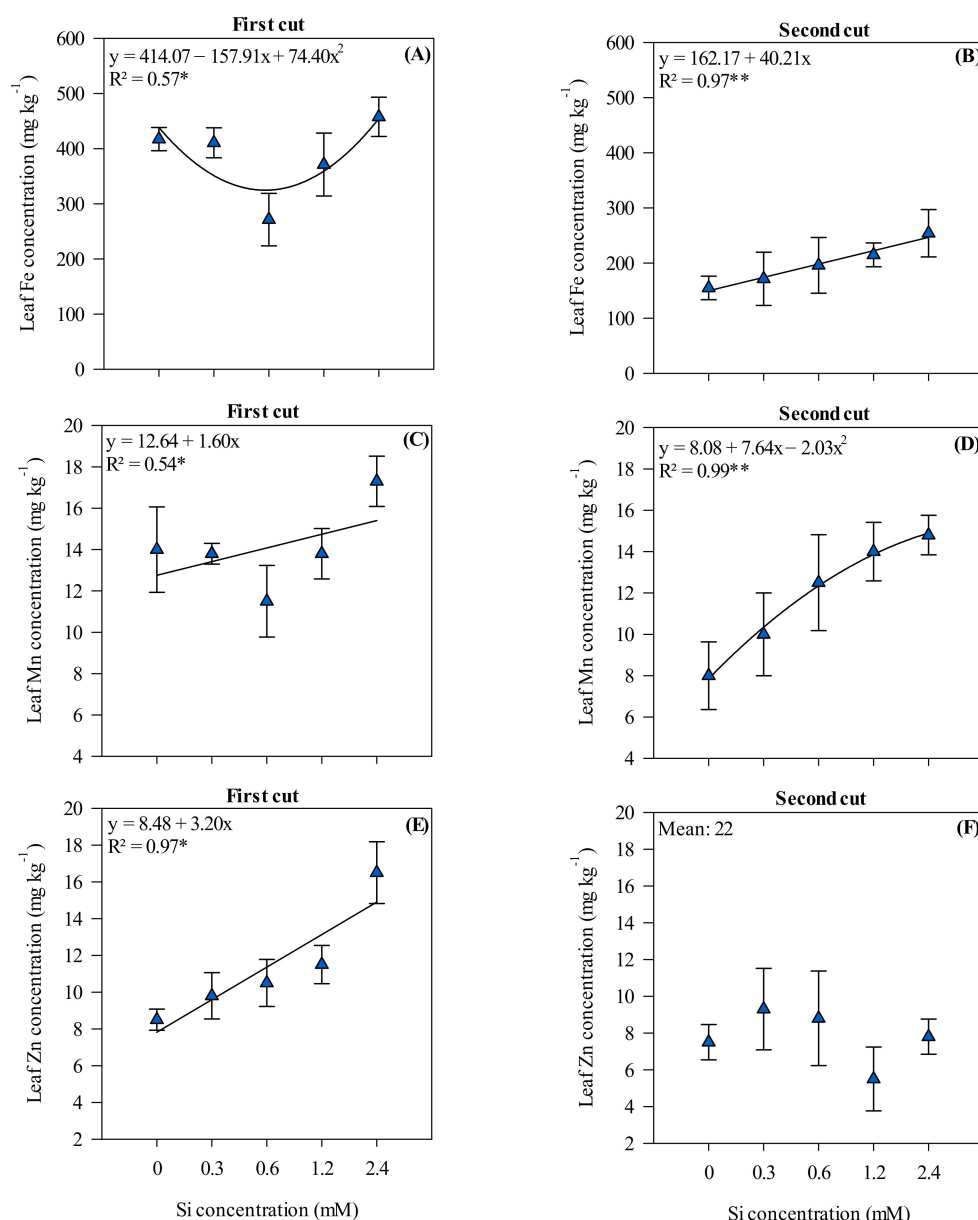


Figure 6. Leaf Fe concentration in the first (A) and second cut (B), leaf Mn concentration in the first (C) and second cut (D), leaf Zn concentration in the first (E) and second cut (F) as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

In the first cut, leaf K, Ca, Mg, Mn, and Zn concentrations increased linearly with increasing Si concentrations (Figures 4E,G, 5A and 6C,E) while leaf N, P, S, Cu, and Fe were found to respond non-linearly to Si concentrations (Figures 4A,C, 5C,G and 6A). The lowest estimated values for leaf N, P, S, and Fe concentrations ranged from 1.1 to 1.5 mM Si (Figures 4A,C, 5C and 6A). In contrast, the highest estimated value for leaf Cu concentration was obtained with 1.7 mM Si (Figure 5G). In the second cut, leaf N and B concentrations decreased linearly with increasing Si concentrations, whereas leaf Fe concentration showed positive linear response to Si concentrations (Figures 4B, 5F and 6B). Leaf P, Ca, Mg, S, Cu, and Mn concentrations responded non-linearly to increasing Si concentrations (Figures 4D,H, 5B,D,H and 6D). The lowest estimated values for leaf P, S, and Cu concentration ranged from 0.7 to 1.6 mM Si (Figures 4D and 5D,H). Differently,

the highest estimated values for leaf Ca, Mg, and Mn concentrations ranged from 1.7 to 1.9 mM Si (Figures 4H, 5B, and 6D).

3.4. Roots to Shoots Al and Si Translocation

In the second cut, both roots to shoot Al and Si translocation responded non-linearly to the increasing Si concentrations (Figure 7A,B). The lowest estimated value for Al translocation was found with 1.5 mM Si (Figure 7A). In contrast, the highest estimated value for Si translocation was verified with 1.4 mM Si (Figure 7B).

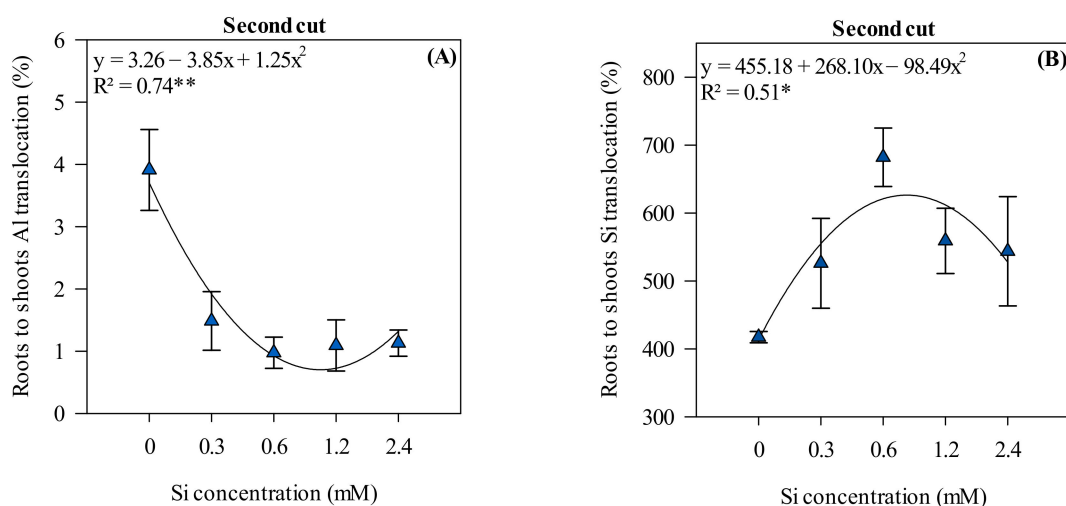


Figure 7. Roots to shoots Al translocation (A) and roots to shoots Si translocation (B) in the second cut as a function of increasing Si concentrations in Xaraés palisadegrass. Error bars indicate the standard deviation of the mean ($n = 4$). * and ** = significant at 5 and 1% probability by F test respectively.

3.5. Principal Component Analysis

The eigenvalues of the four extracted principal components were greater than 1, and therefore, these components can be grouped into a four-component model which accounts for 77% and 70% of data variation in the first and second cuts, respectively (Table 2).

In the first cut, principal component 1 (PC1) represented 31% of the variance and showed that shoot dry mass, leaves per plot, and leaf Cu concentration were positively correlated (Table 2). Conversely, leaf Al, N, and P concentrations were negatively correlated with the above-mentioned PC1 components (Table 2). Principal component 2 showed positive correlation among leaf Si, K, Ca, Mg, S, Fe, Mn, and Zn concentrations (Table 2). Principal component 1 and PC2 represented 57% of the cumulative variance (Table 2). The other two extracted factors are negligible in terms of both explained variability and eigenvalues (Table 2). The groups formed by the concentrations of 1.2 and 2.4 mM Si better comprised important production components such as shoot dry mass, leaves per plot, tillers per plot, and some nutritional components such as leaf Si, K, Ca, Mg, B, Cu, Mn, and Zn concentrations (Figure 8A,B). In contrast, without and at low Si supply, the group formed by these treatments better comprised leaf Al, N, and P concentrations (Figure 8A,B).

In the second cut, PC1 represented 37% of the variance and showed positive correlation among shoot dry mass, leaf Ca and Mn concentrations, and root Al concentration (Table 2). However, leaf Al, N, and P concentrations were negatively correlated to the above-mentioned PC1 components (Table 2). Principal component 2 showed that leaf Si concentration and leaf K, Mg, B, and Zn concentrations were positively correlated (Table 2). Principal component 1 and PC2 represented 50% of the cumulative variance (Table 2). Similarly, as observed in the first cut, the other two extracted factors were negligible in terms of both explained variability and eigenvalues (Table 2). Although the group formed by the Si supply with 0.6 mM comprised mostly of the analyzed parameters, leaf Al concentration was also included in this group (Figure 8C,D). Thus, the groups formed by the supply of

1.2 and 2.4 mM Si better comprised the most important production components (e.g., shoot dry mass and leaves per plot) and some nutritional components (e.g., leaf Si, K, Ca, Mg, Cu, Fe and Mn concentrations) (Figure 8C,D). Similarly, as verified in the first cut, without and at low Si supply, the group formed by these treatments better comprised leaf Al, N, and P concentrations (Figure 8C,D).

Table 2. Factor loadings of a principal component analysis for Xaraés palisadegrass.

First Cut				
Parameters	PC1	PC2	PC3	PC4
Shoot dry mass	0.38	−0.07	−0.26	0.16
Leaves per plot	0.34	−0.01	0.27	0.13
Tillers per plot	0.12	−0.13	0.51	0.12
Leaf Al concentration	−0.31	0.05	−0.20	0.41
Leaf Si concentration	0.21	0.31	0.10	−0.26
Leaf N concentration	−0.39	0.12	0.20	−0.01
Leaf P concentration	−0.34	0.13	0.34	−0.15
Leaf K concentration	−0.03	0.32	0.44	0.06
Leaf Ca concentration	0.21	0.31	0.14	0.17
Leaf Mg concentration	0.21	0.40	0.06	0.06
Leaf S concentration	−0.28	0.32	−0.04	−0.05
Leaf B concentration	0.11	0.08	−0.16	−0.75
Leaf Cu concentration	0.35	0.08	−0.01	0.15
Leaf Fe concentration	−0.15	0.35	−0.28	0.08
Leaf Mn concentration	−0.02	0.37	−0.25	0.22
Leaf Zn concentration	0.14	0.34	−0.09	−0.11
Variance (%)	30.9	25.8	12.95	7.53
Cumulative variance (%)	30.9	56.8	69.7	77.2
Eigenvalues	4.95	4.14	2.07	1.20
Second cut				
Parameters	PC1	PC2	PC3	PC4
Shoot dry mass	0.32	−0.08	−0.11	−0.13
Leaves per plot	0.09	−0.17	0.43	−0.30
Tillers per plot	−0.10	−0.01	−0.01	−0.46
Leaf Al concentration	−0.30	−0.19	0.08	0.26
Leaf Si concentration	0.17	0.30	−0.10	−0.12
Leaf N concentration	−0.31	0.16	0.09	−0.29
Leaf P concentration	−0.33	0.08	0.12	−0.04
Leaf K concentration	0.01	0.30	0.41	−0.33
Leaf Ca concentration	0.30	0.08	0.07	0.12
Leaf Mg concentration	0.27	0.31	0.16	0.11
Leaf S concentration	−0.16	−0.09	0.45	0.08
Leaf B concentration	−0.14	0.47	−0.17	0.14
Leaf Cu concentration	0.12	−0.15	0.29	0.01
Leaf Fe concentration	0.26	−0.01	0.33	0.21
Leaf Mn concentration	0.31	0.07	0.23	0.09
Leaf Zn concentration	−0.04	0.45	0.11	0.35
Root Si concentration	−0.20	−0.26	0.19	0.40
Root Al concentration	0.31	0.03	−0.09	−0.02
Neutral detergent fiber	0.17	−0.19	−0.13	−0.04
Acid detergent fiber	0.21	−0.27	−0.13	0.02
Variance (%)	36.9	12.82	10.81	9.16
Cumulative variance (%)	36.9	49.7	60.5	69.6
Eigenvalues	7.37	2.56	2.16	1.83

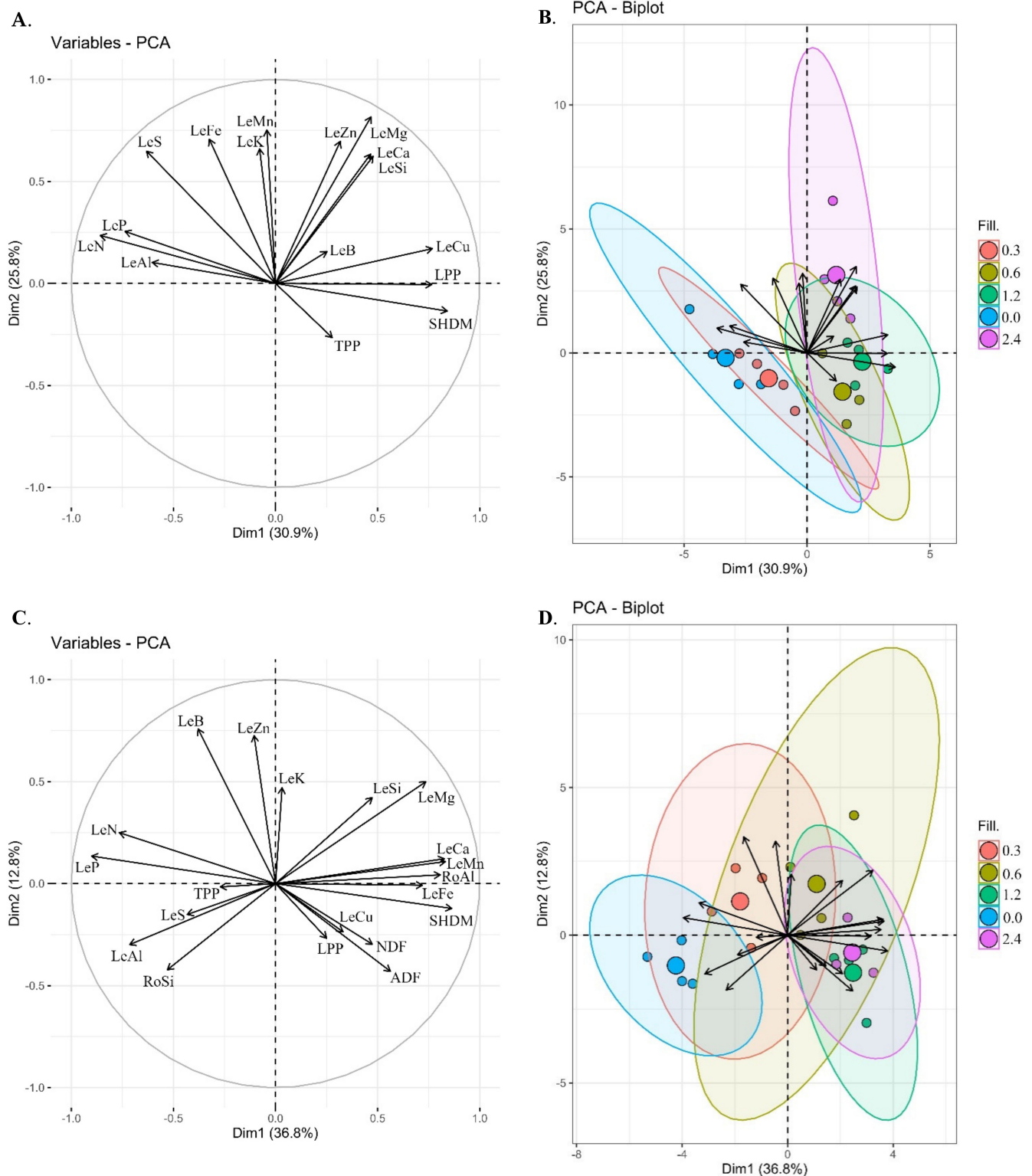


Figure 8. Loadings and biplot graphics of principal component analysis among the relationship between Xaraés palisade-grass shoot dry mass (SHDM), leaves per plot (LPP), tillers per plot (TPP), neutral detergent fiber (NDF), acid detergent fiber (ADF), leaf Al, Si, N, P, K, Ca, Mg, S, B, Cu, Fe, Mn, and Zn concentrations (LeAl, LeSi, LeN, LeP, LeK, LeCa, LeMg, LeS, LeB, LeCu, LeFe, LeMn, and LeZn), root Al and Si concentration (RoAl and RoSi) evaluated in the first (A,B) and second cuts (C,D).

4. Discussion

We verified that the increasing Si uptake in Xaraés palisadegrass leaves had directly affected the modulation of Si/Al uptake by decreasing leaf Al concentration as mediated with Si supply. The root to shoots translocation factor showed that concentrations between 1.4 and 1.5 mM Si provided greater Si translocation while reducing Al redistribution. However, the presence of Si in the nutritive solution did not reduce root Al concentration. Our results showed an opposite relation between leaf Si (Q1) and root Si (Q3) concentrations and leaf Al (Q3) and root Al (Q1) concentrations in PCA biplot graph. Moreover, the opposite direction of leaf Si and root Al concentration (Q1) loadings compared to leaf Al concentration (Q3) strengthen this hypothesis. Silicon was previously related to Al toxicity mitigation by reducing Al transport and shoot accumulation [10,50,51]. The increased concentration of Al in the roots was reported to be a strategy to inactivate or store non-toxic Al in roots and to translocate less Al to shoots, thereby alleviating Al toxicity in plants [52,53]. According to Freitas et al. [10], Si added to the solution may interact with Al, make it non-toxic to the plant by decreasing Al translocation to the shoot and hence, alleviate its toxicity in plant shoots, as verified in our study. Silicon can regulate plant resistance and/or tolerance to metal toxicity by either external (ex planta) or internal (in planta) mechanisms [6,54]. In this regard, it has been proposed that the alleviation of Al stress by Si in plants can mainly be explained by the following events: (i) Si-induced increase in solution pH [54], (ii) formation of Al-Si complexes in the growth media and/or within the plant, influencing Al speciation [55], (iii) exudation of organic acid anions and phenolic compounds [56], and (iv) increase in the contents of chlorophyll and carotenoids on leaves [50].

The increased Si uptake in Xaraés palisadegrass leaves also affected Xaraés palisadegrass content, with an increased ADF content. Silicon supply can affect the composition of plant cell walls, mostly by altering linkages of non-cellulosic polymers and lignin [38,39]. In addition, ADF contains cellulose, lignin, and insoluble minerals (mainly silica) [43]; therefore, we could expect an increase in ADF content within Si application. Acid detergent fiber content above 40% of fodder dry mass has been reported to impair animal consumption and digestibility [43]. However, the verified ADF of Xaraés palisadegrass (below 30%) indicates that Si supply would not be harmful to fodder quality, irrespective of the Si concentration in nutrient solution.

Our results showed that most of the absorbed Si was accumulated in the leaf tissue. In addition, leaf Si concentration was greater than leaf N concentration, which is the most demanded nutrient for grass production (leaf Si: 47.2 g kg⁻¹ vs. leaf N: 17.7 g kg⁻¹—average of two cuts). Plant roots take up silicic acid from soil solution and translocate it to the shoots where it is deposited and precipitated in intercellular spaces as amorphous SiO₂·nH₂O in solid structures known as phytoliths [19,57]. Si contents vary considerably between plant species, with values ranging from about 0.1% to 10% Si per dry mass [28]. Based on Si content, plants have been divided into three groups: (i) non-accumulators or excluders (Si content per dry mass < 0.5%); (ii) intermediate accumulators (Si content per dry mass 0.5–1%); and (iii) accumulators (Si content per dry mass > 1%) [28]. Field crops, especially cereal grasses of the *Poaceae* family are known as Si accumulators [58]. Seven crops (sugarcane (*Saccharum officinarum* L.), rice, wheat, barley (*Hordeum vulgare* L.), sugar beet (*Beta vulgaris* L.), soybean (*Glycine max* (L.) Merrill), and maize) are classified as accumulators among the 10 most important crops (ranked by global production) [29]. However, many pasture forage grasses also accumulate Si in their leaves at concentrations of 10–50 g kg⁻¹ [59,60]. Thus, Xaraés palisadegrass could be considered one of the greatest Si accumulator plants with a verified Si content of 4.7% in leaves dry mass.

The leaf concentrations of N, K, Mg, and Cu were observed in an adequate concentration range (13–20 (N); 12–30 (K), 1.5–4.0 (Mg), 0.8–2.5 (S) g kg⁻¹ of dry mass (DM), respectively and 4–12 (Cu) mg kg⁻¹ of DM) according to Werner et al. [61]. However, the leaf concentrations of Ca, B, Mn and Zn were below adequate concentration range (10–25 (B), 40–250 (Mn) and 20–50 (Zn) mg kg⁻¹ DM) [61]. The leaf concentra-

tions of P and Fe were above the adequate concentration (0.8–3.0 (P) g kg^{−1} of DM and 50–250 (Fe) mg kg^{−1} DM) [61].

The presence of Si in the solution decreased Al translocation to the shoots, which contributed to increasing the number of leaves per plot and leading to a greater shoot dry mass without affect tillering. Interestingly, leaf nutrient concentrations did not present a clear trend. For example, increased Si supply provided greater leaf K, Cu, and Zn in the first cut, leaf Fe in the second cut, and Ca, Mg, and Mn in both cuts. The other leaf nutrient concentrations were negative influenced or fluctuated by Si concentrations. The PCA groups formed by the supply of 1.2 and 2.4 mM of Si better comprised the most important production and nutritional components. Nonetheless, the lowest estimated values for several nutrient concentrations in leaf tissue ranged from 1.1 to 1.6 mM Si in most of the cases. The fact that Si concentrations ranging from 1.4 to 1.6 mM Si provided the greatest number of leaves per plot, shoot dry mass, and roots to shoots Si translocation together with the lowest leaf Al concentration, roots to shoots Al translocation, and other nutrients indicated that a dilution effect may occurred. This hypothesis is strengthened by the decreased leaf N concentration due to Si supply, since N is the major nutrient required by forages for being the key nutrient to achieve high dry mass yields. In another words, Si supply may benefit nutrient-use efficiency with enhanced plant growth. The positive correlations between leaf Si concentration and leaf K, Ca, Mg, S, B, Fe, Mn, and Zn concentrations together with the negative correlations between shoot dry mass and leaf Al, N, and P concentrations support this hypothesis. The increased nutrient use and uptake provided by different sources of Si (e.g., slag materials, silica powder, and silicates) was reported elsewhere for different crops [33,62–64]. In recent years, the number of studies reported the substantial increase in the effects of Si application to crops. This increased interest in Si is likely due to the beneficial effects of Si application on plant resistance to abiotic and biotic stresses such as insects and pathogens [30], salinity, drought, high temperature, freezing [65], heavy metal toxicity [66,67], and heavy rain and winds [67]. Silicon has also been reported to improve crop yield [68], plant growth, plant architecture, erectness, and photosynthesis rate [69], to decrease transpiration rate [70,71], and to improve water-use efficiency [40]. In this regard, Si fertilization might improve nutrient fertilization management while reducing the need for chemical inputs in agricultural systems and deserves more investigation.

5. Conclusions

Our study demonstrates that Si supply affected the modulation of Si/Al uptake by increasing roots to shoots Si translocation while reducing Al redistribution. The presence of Si between 1.4 and 1.6 mM in nutrient solution decreased Al translocation to the shoots, which contributed to the increase in the number of leaves per plot, leading to a greater shoot dry mass, without affect tillering. Our results revealed that Xaraés palisadegrass could be considered one of the greatest Si accumulator crops, with Si content in leaves above 4.7% of dry mass. In addition, Si supply may benefit nutrient-use efficiency with enhanced plant growth and without compromising the chemical–bromatological content of Xaraés palisadegrass. In this regard, Si fertilization might improve nutrient fertilization management while reducing the need for chemical inputs in agricultural systems, and it deserves more investigation.

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