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TEMPORAL CHANGE IN SILICA ACCUMULATION, COVARIATIONS WITH FOLIAR MINERALS AND FODDER VALUE OF *LOXODERA LEDERMANNII* (PILGER) EX LAUNERT FROM THE SUDANIAN BENIN (WESTERN AFRICA)

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ABSTRACT

Silica in forage grasses has been found to be an important factor in reducing cell-wall constituents' digestibility. As the more the silica concentration, the less the grasses digestibility, techniques for silica reduction in grasses are needed. The silica rate reduction might induce other important nutrients 'reduction. This study examines temporal change in *Loxodera ledermannii* (Pilger) chemical composition and silica concentration in leaves from individuals collected at 15-days intervals from April to October in W National Park. Some 100 g of fresh leaves from 90 clumps were oven dried and analyzed for silica, Ashes, N, Na, Ca, P, K, Mg. Digestible Nitrogen Matter and Fodder Energetic value were calculated using Demarquilly formula. SiO₂ negatively related to K, P, N and UF, but positively to MAD, Ashes and Ca. This suggests that SiO₂ concentration could be reduced without affecting significantly the concentration of the important nutrients such as Ashes and MAD.

Key index: *Loxodera ledermannii*, silicification, chemical traits, fodder value, sudanian Benin

1. INTRODUCTION

Plant silica accumulation has recently received increasing attention, especially where agriculture and animal breeding were basic for economy. Benefits include resistance to pests and diseases [1] and a more erect disposition of leaves, which increases the photosynthetic rate [2], as well as increased availability of P and micronutrients in the soil [3], and tolerance to salinity [4]. However, the excess uptake of Si by grasses provides a higher mechanical resistance to degradation [5].

Other studies had already showed that fodder species differ in silica content and this may affect their palatability and digestibility [6] [7] [8]. Silica may reduce livestock preference or palatability for certain plants [9]. The annual grass Medusahead (*Taeniatherum caput-medusae*) showed a very low forage value, because of its extremely high silica content (72-89% silica) which making it unpalatable to livestock [10]. Silicon may also reduce digestibility of fodder grass species [11] by: (i) acting as a varnish on the plant cell wall and reducing access to rumen microflora; (ii) forming insoluble compounds with trace elements like Zn, reducing their availability to rumen microflora; or (iii) forming compounds with enzymes involved in rumen metabolism [12][6]. Other reports indicated that a water soluble form of Si inhibits activities of some digestive enzymes, but the insoluble form is chemically inert [9].

Since tropical grass species were found to be highly silicified [13][14], the current preoccupation is how to reduce leaf silica concentration to improve their palatability, digestibility and nutrient value for animal high productivity.

Investigations had focused *Loxodera ledermannii* (Pilger), an earlier sudanian grass species. This species is a perennial, highly dominant in sudanian and sudano-sahelian savanna and early flowered [15] [16]. It is strongly grazed [17]. It good fodder quality production and developmental potentialities on dry lands increase its exploitation in breeding [13]. The species contributes essentially to the biomass of West Africa tropical grasslands [13] [18]. Apart from the morphological and germinative traits of the caryopses [19], data are still needed on nutritional aspects.

In the present study, we mainly analyzed: (i) the temporal variability in silica concentration, mineral composition and fodder values of leaves of *Loxodera ledermannii* throughout its growth season; and (ii) leaf silica concentration relationship with its other minerals and fodder value (MAD, UF).

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted in the W National Park in W Biosphere Reserve in Benin (WBR), 11°26'-12°26'N and 2°17'-3°05'E (Fig. 1). It covers 6,102 km² representing 56.32 % of the trans-boundary Biosphere reserve shared by Benin, Niger and Burkina-Faso. There is trade wind from April to November in south-west direction and

Harmattan from November to March in north-east direction. This generates very low air humidity and environmental dry conditions. Minimum temperature decreases by 17°C during the period of Harmattan in which the air dryness is the highest and the relative humidity is lower than 30 %. Climate is sudanian and characterized by a rainy season and a dry season. Rainy season occurs from May to October with average annual rainfall from 900 to 1100 mm [21]. Monthly mean temperature ranges from 25°C to 35°C and the relative moisture is the highest in August (81%) while the lowest in February (26%). Relative irradiance averages 2950 hours [20] and determines the environmental water balance. Annual earlier rains provide soil humidification followed by the humid period and the period of establishment of the active herbaceous vegetation. At the end of the rainy season, soil still remains relatively humid and some herbaceous species may still use available water for a maximum growth.

Agriculture, cattle breeding and hunting are the most important socio-economic activities which highly threat the landscapes conservation of the WBR [21]. The human density is about 18.2 inhabitants/km² and the most dominant ethnic groups are Batonou (32.6%), Peul (22.1%) and Dendi (18.2%) [22].

The geological substratum rock is composed of quartzite, basilar rock, micaschist, schist, granite, gneiss and sandstone. Mineral, ferruginous and gley soils occur [24]. The main vegetation type encountered was shrubby and grass savannah and dry forest.

2.2. Materials and samplings

A *Loxodera ledermannii* pasture was sampled in the protected area at the establishment of the native pasture in 25th march 2004. Clumps that are showed good growth were sampled among the species population in the W national Park (2°19'16"E; 11°40'38"N). Leaves were collected on various 90 clumps sampled among the grassland. Standardized leaves were marked on the same internodes on each clump plant stem. Blades were collected from the 3rd most recently expanded leaves from April to October at 15 days intervals except April and June. The leaves were washed to remove dust and stored in envelopes, sun dried for three days, oven dried for 2 days and used for mineral analyses. Ninety samples were harvested (i.e. 3 plants x 5 months x 2 treatments x 3 replicates). All fresh samples were weighed and oven dried at 65°C for 48 h.

2.3. Measurement of leaf traits

Fresh samples were weighted just after harvest (FM) and oven-dried for 48 h at 65°C. Dry mass was noted. Silica (SiO₂), nitrogen (N) and soluble ashes (SA) concentrations were analyzed in samples. Nitrogen was analyzed by the Kjeldahl method. Silica was analyzed gravimetrically by dry ashing. Samples were oven-dried for 48 h at 105°C and ground with a mill (Retsch ZM 100). The samples were ashed in crucibles at 550°C in a muffle furnace (Lenton LCO4-1.06 Eurotherm 2416CG temperature/programmer; multi-program version 2416P8, Brussels, Belgium) for about 12 hours. Ashes were weighted (total ashes) and dissolved in hydrochloric acid (36-38%) on a sand bath at 100°C for 2 h, and filtered with ash-free filters (Schleicher and Schüll ashless, 589², 90 mm diameter). Filters were ignited in the muffle furnace for 12 hours. The residue (i.e. silica) was weighted and soluble ashes were calculated as (total ashes – silica). Soluble ashes and silica concentrations were expressed on an organic matter basis as follows:

$$\text{ODM} = \text{DM} - \text{SiO}_2 \quad (1); \quad \% \text{SA} = 100 \times (\text{TA} - \text{SiO}_2) / \text{ODM} \quad (2); \quad \% \text{SiO}_2 = 100 \times \text{SiO}_2 / \text{ODM} \quad (3)$$

DM= dry mass, ODM= Organic Dry Mass; TA = Total Ashes.

Ninety samples of blades were analyzed for silica and soluble ashes, Na, K, Ca and Mg were analyzed in filtered solutions by Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES). Percentage based on dry mass was calculated for each parameter. Fodder value traits i.e. Digestible Nitrogen Matter (MAD) and Fodder Energetic value (UF) were calculated using Demarquilly formula.

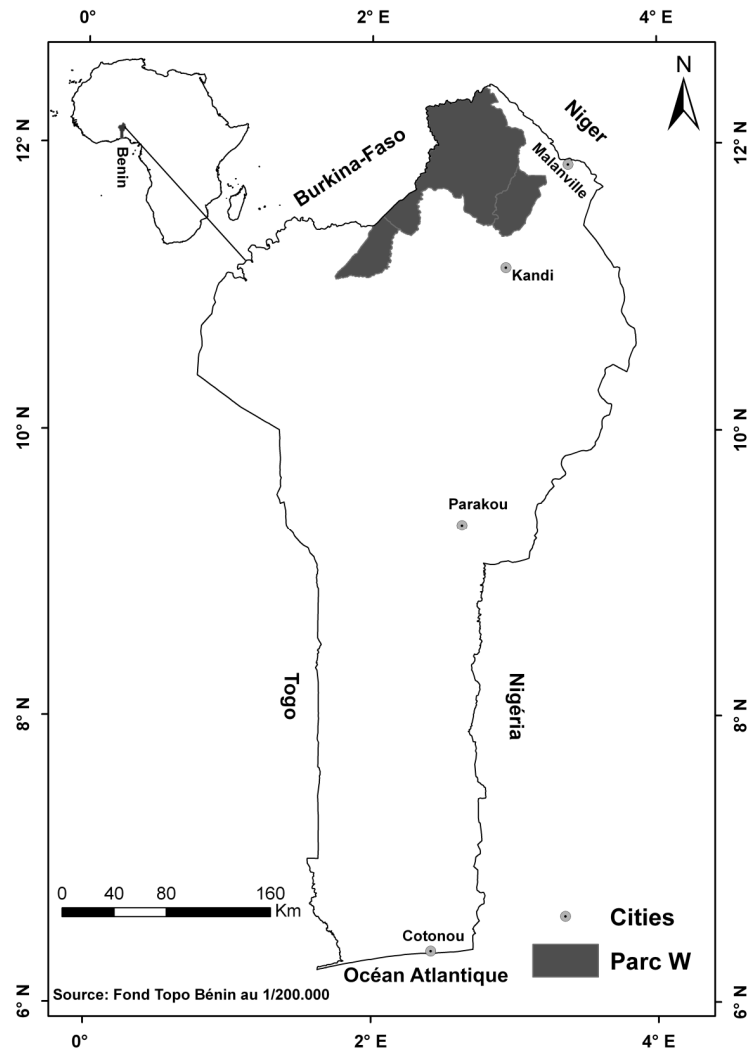


Fig. 1. The study area in northern Benin

2.4. Data analysis

Data were examined with Dixon test to detect outliers [23]. Chemical concentrations were compared to standards of Epstein & Bloom [24]. Statistical analyses were performed with STATISTICA 7.1 software (StatSoft Inc 2005). Most data (except SiO₂ and SA), were log-transformed before analysis to restore homoscedasticity, i.e. N, P, K, Na, Ca, and Mg. ANOVAs were performed on the whole chemical and nutritional traits (N, P, K, Mg, Na, Ca, UF, MAD, Ash, and SiO₂). One-way ANOVAs with the date of cutting mimicking the growth period as main factor were performed to test differences between treatments (dates). No transformation was performed for nutritional traits, i.e. UF, MAD. Relationships between SiO₂ and the other traits (Ca, Mg, K, Na, MAD and UF) were also assessed by means of Pearson correlation coefficients at 5%.

3. RESULTS

3.1. Silica concentration

The value of the leaves SiO₂ concentration of *Loxodera ledermannii* ranging other the growing period are given in the table 1. SiO₂ concentration in these leaves ranged from 2.54% to 6.90%, depending on harvest days of growth periods. There was a highly significant harvest date effect (Table 2). Middle and end of May, end-July and mid-August generally showed lower values (<3%), whereas April and end-October showed much higher values (>5%) and ranked respectively first and second in all treatments compared to all other growth periods (Table 1). Silica concentration varied 2.4 fold between the earliest and the latest growth periods, i.e. Mid-May and end-October respectively, and there was a strong correlation among harvest dates of the growth period (Table 2; F_{9,29}=202.73; p<0.00001; CV=36.56%).

Table 1. Temporal change in chemicals concentrations and nutritional value of *Loxodera ledermannii* leaves in sudanian Benin during the period 2002-2003

Months	SiO ₂ (%DM)	N (%DM)	K (%DM)	Mg (%DM)	Ca (%DM)	P (%DM)	Na (ppm)	UF (/100 kgDM)	MAD (g kg ⁻¹ DM)
April	5.50	0.88	1.45	0.32	0.28	0.10	440.00	89.17	15.70
	±	±	±	±	±	±	±	±	±
Mid. May	0.40e	0.04cd	0.20bc	0.03c	0.03b	0.05ab	18.08f	2.90b	0.92b
	±	±	±	±	±	±	±	±	±
End May	2.54	1.32	1.86	0.15	0.20	0.22	235.00	93.13	41.90
	±	±	±	±	±	±	±	±	±
June	0.41a	0.08f	0.10d	0.03a	0.05ab	0.06c	21.00e	3.05bc	3.52d
	±	±	±	±	±	±	±	±	±
Mid. July	2.79	1.22	1.39	0.24	0.20	0.13	123.67	92.03	34.43
	±	±	±	± 0.04abc	±	±	±	±	±
End July	0.21ab	0.04f	0.12bc		0.04ab	0.06abc	23.54cd	3.46bc	4.95cd
	±	±	±	±	±	±	±	±	±
Mid. August	3.47	1.12	1.77	0.16	0.26	0.16	107.00	78.67	29.00
	±	±	±	±	±	±	±	±	±
End August	0.32bcd	0.06e	0.21d	0.03a	0.04ab	0.03abc	28.65bcd	6.25a	4.00c
	±	±	±	±	±	±	±	±	±
Mid. October	3.68	1.30	1.02	0.28	0.26	0.11	94.67	92.80	40.00
	±	±	±	±	±	±	±	±	±
End October	0.32cd	0.05f	0.04a	0.07bc	0.02ab	0.04ab	25.01ab	2.66bc	5.00d
	±	±	±	±	±	±	±	±	±
Mid. May	2.74	0.92	1.22	0.20	0.19	0.12	48.50	86.83	18.30
	±	±	±	±	±	±	±	±	±
End May	0.23ab	0.06d	0.10ab	0.05ab	0.04ab	0.02ab	20.00a	3.61b	3.15b
	±	±	±	±	±	±	±	±	±
Mid. July	2.80	0.81	1.66	0.13	0.20	0.20	93.50	71.83	11.83
	±	±	±	±	±	±	±	±	±
End July	0.17ab	0.07bcd	0.10cd	0.06a	0.03ab	0.03bc	20.00ab	4.05a	3.95ab
	±	±	±	±	±	±	±	±	±
Mid. August	3.04	0.78	1.41	0.14	0.18	0.09	153.00	76.97	10.57
	±	±	±	±	±	±	±	±	±
End August	0.21abc	0.09bc	0.13bc	0.06a	0.04a	0.03a	30.00d	1.68a	4.42ab
	±	±	±	±	±	±	±	±	±
Mid. October	3.83	0.72	1.04	0.13	0.26	0.08	64.00	79.60	6.77
	±	±	±	±	±	±	±	±	±
End October	0.24d	0.03b	0.08a	0.05a	0.03ab	0.04a	29.21ab	4.50a	2.95a
	±	±	±	±	±	±	±	±	±
Mid. May	6.90	0.62	1.08	0.16	0.39	0.05	75.00	99.70	5.50
	±	±	±	±	±	±	±	±	±
End May	0.60f	0.02a	0.07a	0.05a	0.03c	0.03a	23.00ab	2.85c	0.40a
	±	±	±	±	±	±	±	±	±

M±SD (means plus and minus standard deviations); letters corresponded to post hoc groups at 5%.

3.2. Other leaf traits

As for silica, there was a highly significant harvest date effect in all other *L. ledermannii* leaf traits (Table 2). This was most large for K, N and Na concentrations and for nutritional traits.

Table 1 of the chemical concentrations of *L. ledermannii* during the growth period indicate that these leaves are: (a) rich in Na (>10 ppm DM), K (>1%DM), and in SiO₂ (>0.1%DM); (b) poor in Ca (<0.5%DM) and N (<1.5%DM); (c) poor in Mg (<0.2%DM) except the leaves that are harvested in April, at the end-May and July; (d) poor in P (<0.2%DM) except the leaves that are harvested at mid-May and mid-August.

Compared to other periods, mid-May generally showed higher values of N (>1.30%), K (>1.80 %), P (>0.2%), of Na (>200 ppm), UF (>90/100kg DM) and MAD (>40 g.kg⁻¹DM). End-October showed lower values of N (<0.65%), K (<1.2%), P (<0.1%), MAD (<10 g.kg⁻¹DM) and higher values of UF (>99/100kgDM) and Ca (>0.35%) (Table 1).

Table 2. One way ANOVA of the Effect of the growth period on chemical and fodder value traits with *Loxodera ledermannii* (Pilger): $F_{(9,29)}$ values and significance at 5% threshold; *****: $9.98 \times 10^{-10} < p < 7.88 \times 10^{-22}$; ****: $3.19 \times 10^{-06} < p < 4.31 \times 10^{-08}$; ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$.

Source of variation	DF	SiO ₂	Na	K	Mg	Ca	P	N	Ash	MAD	UF
Growth period	(9, 29)	202.73	535.25	19.78	2.85	2.51	3.62	30.20	3.11	11.79	73.14
Prob. Sign.		*****	*****	****	*	*	**	****	*	*****	****
CV (%)	-	36.56	78.90	21.57	34.06	31.14	46.69	25.08	29.11	10.84	63.40

Prob. Sign.: probability significance; CV: coefficient of variation

3.3. Correlations between Silica and the other major nutrients

Table 3 shows coefficients of correlation between silica and the other parameters. Across the whole data set, silica concentrations are correlated positively with Ash, Ca and MAD, but negatively with N, P, K and UF (Table 3).

Table 3. Pearson correlations among the *Loxodera ledermannii* (Pilger) leaves chemical and fodder value traits. *****: $p < 0.0001$; ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$.

	Na	K	Mg	Ca	P	N	SiO ₂	Ash	MAD	UF
Na	1									
K	0.512**	1								
Mg	-0.029ns	-0.109ns	1							
Ca	-0.289ns	-0.165ns	0.093ns	1						
P	0.190ns	0.659****	0.125ns	-0.149ns	1					
N	0.272ns	0.329*	0.443*	-0.163ns	0.485**	1				
SiO ₂	0.112ns	-0.44*	-0.006ns	0.472**	-0.597****	-0.491**	1			
Ash	0.073ns	-0.08ns	0.062ns	0.708****	-0.298ns	-0.061ns	0.676****	1		
MAD	0.116ns	-0.308*	0.457*	0.247ns	-0.171ns	0.315*	0.379*	0.447*	1	
UF	0.241ns	0.415*	0.520**	-0.109ns	0.587***	0.936****	-0.500**	-0.085ns	0.252ns	1

SiO₂ negatively correlated respectively with N concentrations (Fig.2), K (Fig. 3), P (Fig.4) and UF (Fig.5). The general negative trend is due to leaves which were harvested at the Mid-May and showed the lowest SiO₂ concentration (<2.5%) with the highest N (>1.30%), K (>1.80%), P (>0.2%) and UF (>90/100kg DM), and the opposite trend with leaves from End October which showed higher values of SiO₂ (>6.5%) and lower values of N (<0.65%), K (<1.2%), P (<0.1%).

Fig. 6, 7 and 8 respectively show the positive correlation between SiO₂ concentration and Ash, Ca and MAD. Generally, the positive trend is mostly due to leaves which are harvested at the middle-end-August and show lower values for SiO₂, ash (<6%DM), Ca (<0.20%DM) and MAD (<11 g.kg⁻¹DM), and those which are harvested at the end-October with highest values (respectively >11%DM and >0.35%DM). The pattern was not consistent for MAD. In fact, MAD and UF values in the leaves of *L. ledermannii* varied significantly within the growth period (tables 1, 2). While, both traits highlighted the highest values at the mid-July, UF showed the lowest values at the end October and MAD in the mid-August. SiO₂ showed strong negative correlation with UF while positive with MAD (fig. 6-7).

It clearly appeared that the leaves that are harvested at the mid-May generally showed higher values of N (>1.30%), K (>1.80 %), P (>0.2%), Na (>200 ppm), UF (>90/100kg DM) and MAD (>40 g.kg⁻¹DM). At the end-October, they showed lower values of N (<0.65%), K (<1.2%), P (<0.1%), MAD (<10 g.kg⁻¹DM) and higher values of UF (>99/100kgDM) and Ca (>0.35%). Otherwise, earliest leaves from April showed higher values of SiO₂ (>5%), K (>1.40%), Mg (>0.30%) and Na (>400 ppm).

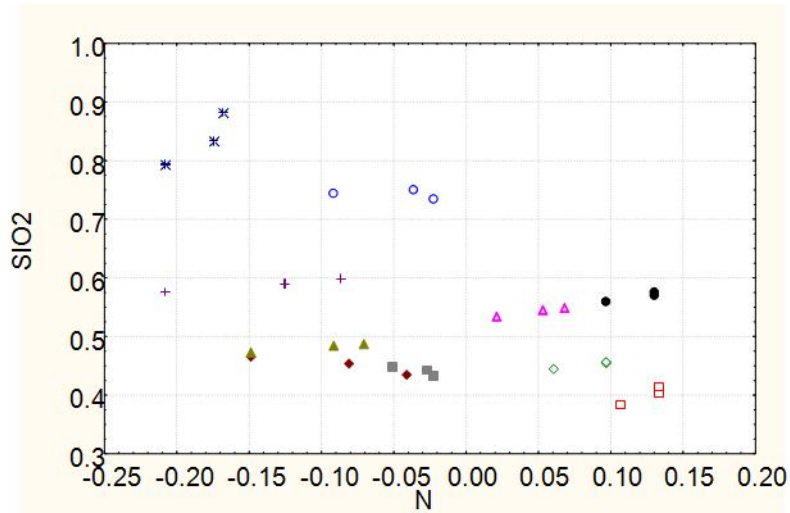


Fig. 2. Relationships between SiO_2 and nitrogen concentrations (%DM) in leaf blades;

Where $R = -0.49$; $p < 0.01$; $N = 30$ (5 months. \times 2 treatments \times 3 replicates); Symbols: *: end October; +: mid October; ▲: end August; ◆: mi August; ■: end July; ●: mid July; △: end June; ◇: end May; Y: mid May; O: end April.

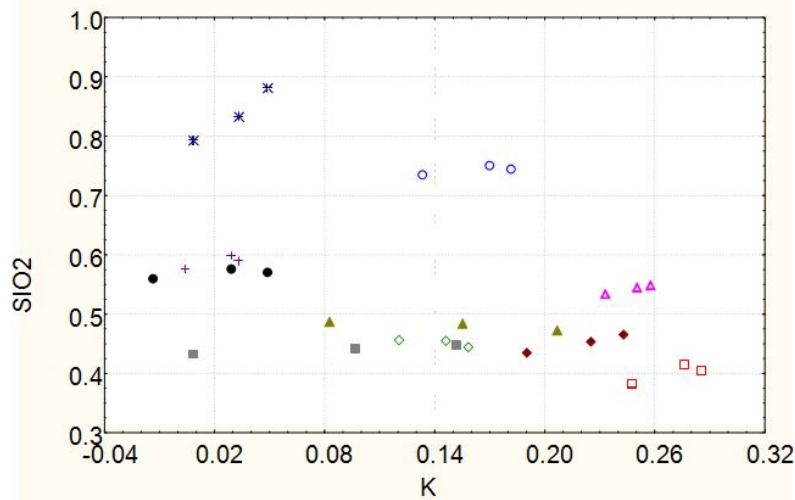


Fig. 3. Relationships between SiO_2 and potassium concentrations (%DM) in leaf blades
Where $R = -0.44$; $p < 0.05$; $N = 30$.

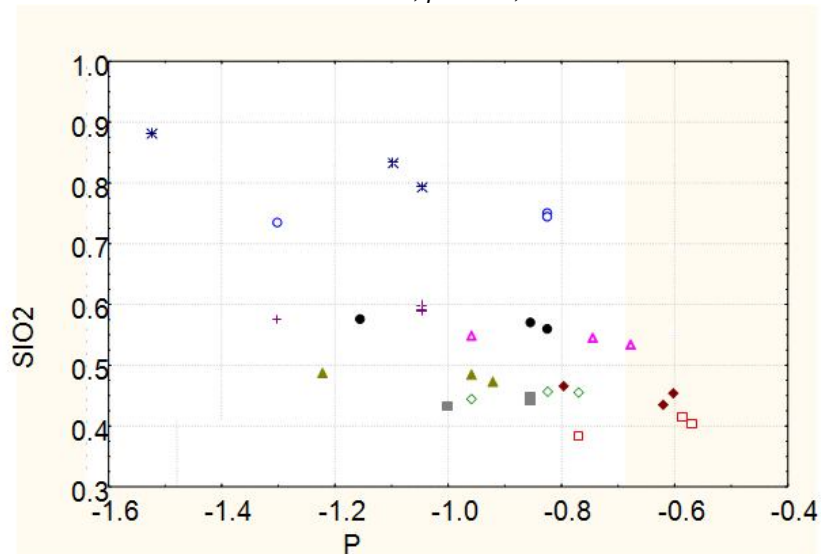


Fig. 4. Relationships between SiO_2 and phosphorus concentrations (%DM) in leaf blades
Where $R = -0.60$; $p < 0.0001$, $N = 30$.

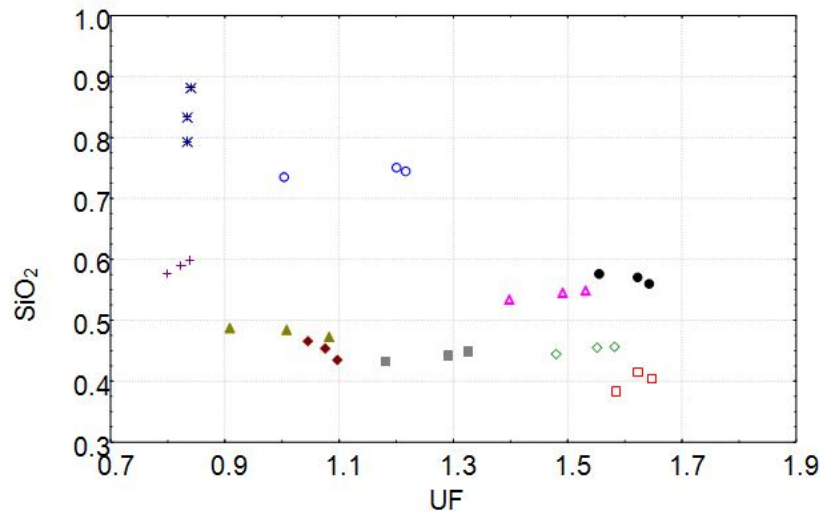


Fig. 5. Relationships between SiO_2 concentrations (%DM) and energy (/100 kgDM) in leaf blades
Where $R = -0.50$; $p < 0.01$; $N = 30$.

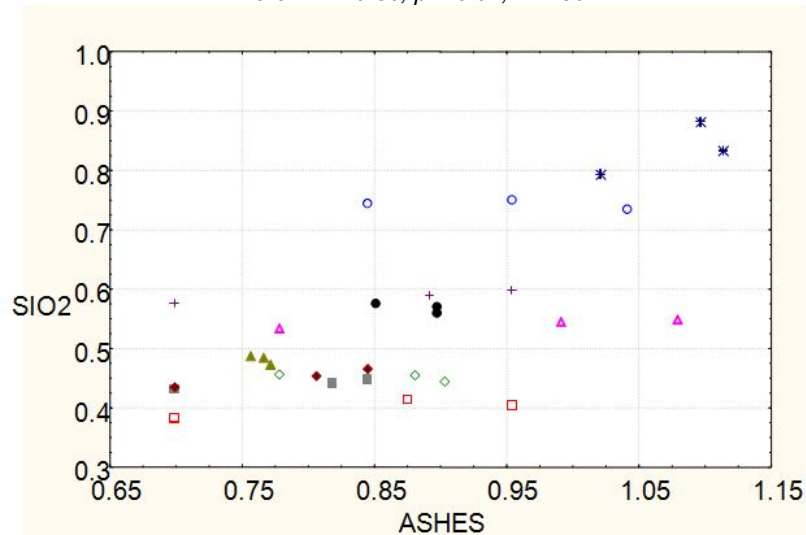


Fig. 6. Relationships between SiO_2 and ashes concentrations (%DM) in leaf blades
Where $R = 0.68$; $p < 0.00001$; $N = 30$.

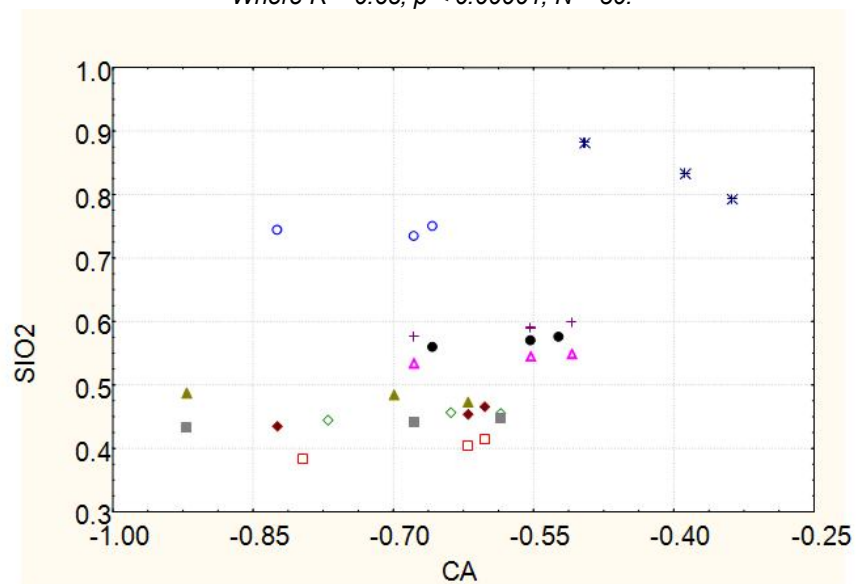


Fig. 7. Relationships between SiO_2 and Ca concentrations (%DM) in leaf blades
Where $R = 0.47$; $p < 0.01$; $N = 30$.

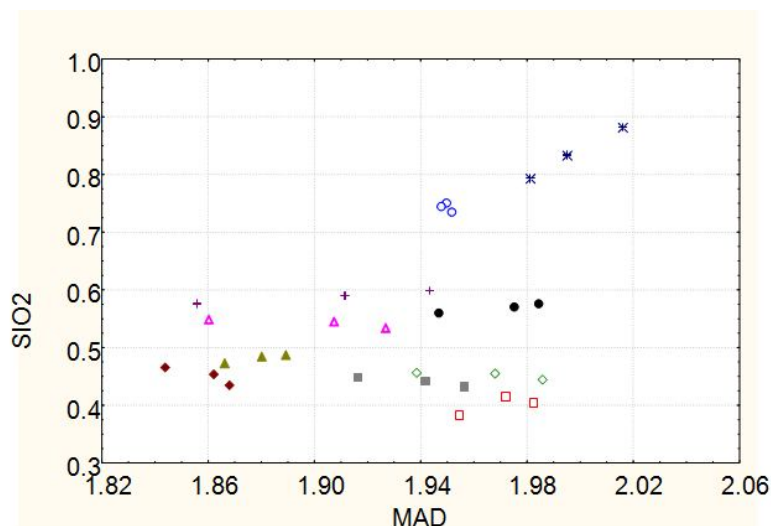


Fig. 8. Relationships between SiO_2 concentrations (%DM) and proteins contents ($\text{g.kg}^{-1}\text{DM}$) in leaf blades
Where $R = 0.38$; $p < 0.05$; $N = 30$.

4. DISCUSSION

4.1. Effect of season on foliar silica accumulation

Our results confirm that silica concentration often increases with growth season. But the pattern is not completely consistent as the earliest leaves that have been harvested in April showed higher SiO_2 . There have been relatively few tests of the response of silica content to phenology. Takahashi & Miyake [25] and Sinsin [13] are often found as field demonstrating the character of silica increase with the growing season. However, among the species they examined only *Eustachys paspaloides* and *Andropogon schirensis* showed enhanced silica accumulation with the growth period. Most other authors found lower concentrations of silica in plant leaves grown in the season ([26]-[29]). Furthermore, Georgiadis & McNaughton [30] observed opposite responses to growing season in *Agrostis tenuis* depending on phenological stage, with increases at 14 day intervals and decreases at 7 day intervals. Moreover, they found large variation among genotypes in the response to phenology, with both increases and decreases in silica concentration. Our data suggest that conflicting results in the literature may arise from species-specific responses, interactive effects of environmental factors and different experimental protocols.

We found contrasting responses depending on phenological stage. Phenological stage is well known to influence silica accumulation [27], but contrasted patterns have been reported (higher SiO_2 concentration in young leaves: [8], lower SiO_2 concentration in young leaves: [30] [31]). The higher SiO_2 content of *L. ledermannii* earlier leaves is consistent with the hypothesis that silica accumulation might defend plants against herbivorous ([8] [35]). However, herbivorous herds preferred seasonally earlier leaves [13]. Consequently, it would appear that silica accumulation is complex and hardly predictable.

Our study indicates that *L. ledermannii* increased its SiO_2 concentrations during the first three months (April to mid-July) and the four latest months (end-July to end October) of the growth season. Increasing SiO_2 concentration with age has already been reported ([31] [32] [33]). The mechanisms by which phenological stage may affect silica accumulation need more investigation.

Our study examines other leaf parameters. Interestingly, growing season affected other leaf traits. A recurring pattern was the production of leaves with higher nitrogen concentration. Why silica concentration could increase in those leaves?

Higher nutritional quality and lower silica content were found as a pattern in grass from heavily grazed sites ([30][34]). Increased silica accumulation might actually have been selected as a protective mechanism in leaves that would otherwise be highly palatable (high water and nitrogen content, low fiber content). Alternatively, enhanced silica accumulation might be an inevitable response. It is well known that silica accumulation is correlated to transpiration ([35][36]). Juvenile leaves with a high photosynthetic capacity may have higher transpiration rates, thus increasing silica deposition rate.

4.2. Silica correlations with other leaf traits

In some cases, the response of other traits is similar to that of silica. However, the results are complex. Globally, there is a highly significant effect of growth period on leaf chemical accumulation (table 2). Generally, pattern of foliar SiO_2 concentration is not clear throughout the growth period. Decreased SiO_2 accumulation during the growth period might also result from interaction with uptake of other mineral elements. The positive correlation between SiO_2 and ash and Ca suggests that the pattern of *L. ledermannii* foliar SiO_2 accumulation is identical to that of Ash and Ca. This is consistent with previous results on tropical grass species [37]. SiO_2 and Ca might be synergistic in these leaves. The more silicified leaves (harvested at end-October) show extreme values for ash and Ca in the season and the lowest N, P and K. The low silicified leaves (i.e. harvested at the mid-May) hold the highest values of N, K, P and MAD early in the season. These elements show strong decreasing concentrations throughout the growth period, which might result from mineral dilution.

Furthermore, SiO₂ was positively correlated with Ca (table 3; $r = 0.472$; $p < 0.01$). Both Ca and SiO₂ passively accumulated in plant organs having a high transpiration, and little mobile in the phloem. SiO₂ was in synergy with Ca in rice iron-stressed conditions [38]. In contrast to the SiO₂ synergism with Ca and antagonism with N, P, K, Van der Vorm [39] observed that high SiO₂ content in nutrients solutions exerted suppressive effects on the contents of Ca and Mg in the leaves of rice and sugarcane. Further investigations are needed to well clarify the mechanisms of tropical grass silicification.

Otherwise, K is necessary for the sap moving [3]. If SiO₂ is accumulated through transpiration stream [40], the plants that are poor in K might show lower SiO₂ concentration. K might be a functional regulator that reduces plant water loss. We found high K values in leaves harvested in April and August. This may imply that SiO₂ is either excluded for preferential uptake of K. Indeed, SiO₂ and K antagonistic and synergistic relationships have been documented [38]. Moreover, more silicified leaves i.e. harvested at end-October, show extreme values for ash and Ca and the lowest values in N, P and K. The low silicified leaves i.e. harvested at the mid-May, showed the highest values of N, K, P and MAD early in the season. Positive correlation of SiO₂ with MAD and negative with N make inconclusive the hypothesis that silica reduces the nutritional value of forage. Further studies are needed to analyze covariations between SiO₂ and structural and organic compounds to well characterize tropical grass silicification and modeling their nutritional performances.

Plant silica generally increased during the growth period, Responses of other leaf traits are generally badly correlated to that of silica, with exception of soluble ashes and Ca. The mechanism of the apparent response is not clear. The correlation between silica and soluble ashes attest that the intensity of transpiratory stream can be an important determinant of the silica concentration, but this does not explain in itself the decrease of the leaf silica concentration during the growth season.

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