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Sclerophylly in *Qualea parviflora* (Vochysiaceae): influence of herbivory, mineral nutrients, and water status

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Abstract

Qualea parviflora Mart. (Vochysiaceae) is a deciduous tree, commonly observed in campo sujo, cerrado *sensu stricto* and cerradão vegetation types in Brazilian cerrado (savannas). In this study we investigated herbivory, nutritional, and water status effects on leaf sclerophylly of *Q. parviflora*. Twenty fully expanded leaves were taken from 10 plants in each vegetation type four times a year. Mean leaf concentration of N, P, K, Ca, C, Al, Si, and percentage of total phenols, herbivory and tannins were measured on a plant basis. Leaf specific mass (LSM) (g m^{-2}), a sclerophylly index, and pre-dawn leaf water potential (MPa) were also recorded. Soil samples below each tree were collected to quantify $N{-}NO_3$, $N{-}NH_4$, P, K, Mn, soil moisture, organic matter, Si, and Al. *Qualea parviflora* showed a LSM from 69 to 202 g m^{-2} and leaves were younger and less sclerophyllous in November (beginning of rainy season). *Q. parviflora* inhabiting the cerradão had leaves with higher concentration of nutrients and lower sclerophylly while trees in campo sujo and cerrado *sensu stricto* did not show significant differences in leaf sclerophylly. The concentrations of N, P, K and tannins had an inverse relationship with leaf age. Concentration of phenols, Al, C, Ca, Si, C/N and Ca/K increased with leaf age. The concentrations of P and Ca/K ratio in leaves explained 60% of variation observed in leaf sclerophylly. We did not find any significant relationship between the level of sclerophylly and water potential or herbivory. Our results corroborate the hypothesis that predicts lower concentrations of essential macronutrients would be the main factors influencing higher sclerophylly in leaves of *Q. parviflora* plants in Cerrado.

Introduction

The first to introduce the term 'sclerophyll' was Schimper (1903) who defined sclerophylly in terms of textural properties, as synonymous of hard and leathery leaves. Different leaves show varying degrees of hardness, and the description of a particular leaf as sclerophyllous merely means that it is a typical leaf at one extreme in a continuous range of leaf texture types (Loveless 1962). Sclerophyllous leaves are common in areas with a Mediterranean climate (e.g., fynbos vegetation in South Africa), as well in low-nutrient soils in the bana vegetation of Amazonas, and Neotropical savannas (e.g., Llanos in Venezuela, Brazilian cerrado) (Sarmiento and Monasterio 1975; Sobrado and Medina 1980; Specht and Rundel 1990; Edwards et al. 2000).

The typical sclerophyllous leaf posses greater proportion of mechanical tissues, thicker and more rigid living cells walls, thicker cuticle and multi-layer leaf tissues, high resistance to desiccation, and long life-spans (Sarmiento and Monasterio 1975; Sobrado and Medina 1980; Turner 1994; Read et al. 2000; Salleo and Nardini 2000). The toughness and rigidity of the leaf blade are mainly due to abundance of cell fibre and sclereids (Bussotti et al. 1997; Salleo and Nardini 2000), and several substances, such as cellulose, hemicellulose and silica (Howe and Westley 1988).

Some previous studies (e.g., Lucas and Pereira 1990; Choong et al. 1992) have shown that the fracture toughness (ability to resist crack propagation) is a good measurement of mechanical properties of sclerophyllous leaves. However, sclerophylly has been measured indirectly; using indexes such as the ratio of crude fibre to crude protein (Loveless 1961, 1962) or as leaf specific mass (LSM) (Witkowisk and Lamont 1991; Groom and Lamont 1999). The LSM, the ratio of leaf mass to area, is by far the most widely used because it incorporates two recognized components of sclerophylly, leaf thickness and dry density (Lamont et al. 2002). Also, it is considered to reflect relative carbon accumulation, and is easy to measure (Witkowisk and Lamont 1991).

In contrast with many studies on sclerophylly in Mediterranean species (e.g., Salleo and Gullo 1990; Specht and Rundel 1990; Witkowski et al. 1992; Bussotti et al. 1998; Read et al. 2000; Lamont et al. 2002), there are still few studies on the adaptive function of sclerophylly in species from the Brazilian cerrado (e.g., Goodland 1971; Goodland and Ferri 1979; Salatino 1993; Marques et al. 1999) in spite the fact that it is the most common feature of their plant species. Arens (1958a,b) proposed the hypothesis of 'oligotrophic scleromorfism' in which low nutrient levels in Brazilian cerrado soils, especially nitrogen would influence on sclerophyllous traits in vegetation. Goodland (1971) suggested the term 'aluminotoxic scleromorfism' for the sclerophylly gradient observed in cerrado vegetation types, which could also be related to the soils.

Nowadays, there are three main hypotheses that consider sclerophylly as: (i) an adaptation to seasonal water deficits (e.g., Schimper 1903; Oearteli et al. 1990); (ii) an adaptation to or consequence of a low-nutrient poor soils (Loveless 1961, 1962; Goodland and Ferri 1979; Chapin 1980, Medina and Francisco 1994); and (iii) as adaptation to anti-herbivore defense (Coley 1983a, b; Choong et al. 1992; Salatino 1993; Turner 1994).

Qualea parviflora Mart. (Vochysiaceae) inhabits water and nutrient poor soils and accumulates aluminum (above 10,000 mg kg^{-1} in leaves). It is a typical and widespread sclerophyllous tree of Brazilian cerrado, representing a suitable system to test hypotheses about functional role of sclerophylly. Thus, the aim of this study was to verify what factors – mineral nutrients, herbivory or water status – could better explain the intraspecific changes of leaf sclerophylly on *Q. parviflora* in three cerrado types that are different in relation to their soil nutrients and vegetation cover.

Material and methods

Study site

The study was carried in the Ecological Station of Pirapitinga (ESP). ESP is located in southeastern Brazil (18°20′ S to 18°23′ S and 45°17′ W to 45°20′ W) at an altitude from 590 to 630 m. above sea level. The vegetation is formed by cerrado biome (savanna) with three floristic formation types: campo sujo, a widely scattered tree and shrub savanna with a canopy cover of less 2%; cerrado *sensu stricto*, a savanna woodland with total woody cover about 20%; and cerradão, a xeromorphic forest with a fairly continuous tree and a canopy cover which ranges from 15 to 85% (Eiten 1972). The structure and physiognomies of cerrado reflect climatic and other environmental variables, but in general, the more fertile mesotrophic soils tend to support cerradão vegetation and show higher pH and relatively higher phosphorous and nitrogen concentration than dystrophic soils which support frequently campo sujo vegetation (Goodland and Ferri 1979; Felippe and Dale 1990). The climate is wet and hot tropical with a long dry season (up to four months), the mean annual temperature ranges from 20 to 26 °C, and the mean annual precipitation is above 1600 mm.

Vochysiaceae is among the most important plant families in the cerrado with 36 species. *Qualea parviflora* Mart. (Vochysiaceae) can attain 2–10 m of height and stay leafless throughout 1 month in the end of dry season. Its stomata are restricted to abaxial leaf surface and tannins are often present in the palisade or spongy tissue and in the midrib ground tissues (Sajo and Rudall 2002). In ESP, *Q. parviflora* is commonly observed in the vegetation types of campo sujo, cerrado *sensu strictu*, and cerradão and are attacked by folivorous insects belonging to Blattodea, Coleoptera, Hemiptera, and Lepidoptera species (Gonçalves-Alvim and Fernandes 2004).

Samplings and chemical analyses of leaves

To verify temporal and intraspecific variations in nutrient concentration, defenses, herbivory and sclerophylly of leaves, 10 plants of *Q. parviflora* were randomly selected and sampled in each one of the cerrado types in ESP four times a year: January (middle of rainy season), April (end of rainy season-beginning dry season), July (middle of dry season) and November (beginning rainy season) in 2000. Fully expanded and non-damaged leaves were taken for analyses of nutrients (20 per tree), total polyphenols (10 leaves per tree), and tannins (3 leaves per tree). The mean concentration of macro and micronutrients, total phenols (%) and tannins (%) were obtained for each plant along the year.

The macro and micronutrients analyses were performed after humid digestion using HNO_3, $HClO_4$ and 400 mg of dry plant tissue. Nitrogen was analyzed by Flow Injection Analysis-FIA (Carlson et al. 1990). Phosphorous was determined colorimetrically using a spectrophotometer (Silva 1999). Carbon was determined indirectly by Walkley and Black method (1934). An air-acetylene flame was used for sodium and potassium (Johnson and Ulrich 1959). Silica was analyzed colorimetrically (Elliott and Snyder 1991). Calcium and aluminum were analyzed with an atomic absorption spectrophotometer (Meyer and Keliher 1992).

Condensed and hydrolysable tannins were obtained by the method of radial diffusion (Hagerman 1987), in which fresh leaves were used with three replicates for each plant, and tannic acid was used as standard. For total phenols, the leaves were dried previously under air temperature, triturated, and analyzed using the method of Swain (1979).

For each tree, 10 shoots were randomly collected around the circumference of each plant. Free-living insect damage to the foliage was quantified in two mature leaves per shoot (20 leaves per plant). Leaves were drawn and digitized by a plat bed-scanner. The total leaf area and percentage of leaf area damaged were calculated using the computer program Scion-Image. Herbivorous attack was estimated by the mean percentage of leaf area damaged.

Leaf specific mass (g m^{-2}) was calculated in 20 fully expanded and non-damaged leaves for each plant. Leaves were drawn and scanned to measure the leaf area, and then were oven-dried at 45 °C for at least 72 h, after which the mass of the dry matter component was determined.

Pre-dawn leaf water potential (Φ_{pd}) was measured from 03:00 to 06:00 h with a Scholander pressure chamber (PMS-600) using one shoot per plant, in order to certify the leaf water status (MPa) for each plant (Scholander et al. 1964, 1965).

Samplings and soil analyses

Samplings to 20 cm of soil depth, under each plant, were obtained and verified the concentrations of N-ammonium (g dm^{-3} – gram per cubic decimeter of soil), N-nitrate (g dm^{-3}), P (g dm^{-3}), K ($cmol_c$ dm^{-3} – centimole of charges per cubic decimeter of soil), organic matter (g kg^{-1} – gram per kilogram of soil), Mn (g dm^{-3}), Si (g kg^{-1}), and Al ($cmol_c$ dm^{-3}). Percentage of soil water (%) was obtained by difference between fresh and dry mass of soil (by a time of 72 h or until reaching constant weight at 45 °C). Phosphorous was determined colorimetricallly using a spectrophotometer (Silva 1999). Organic matter was determined indirectly by Walkley and Black method (1934). Inorganic nitrogen was analyzed by the adapted methods of Mullin and Riley (1955) and Kempers and Zweers (1986). An air-acetylene flame was used for potassium (Johnson and Ulrich 1959). Silica was analyzed colorimetrically (Hallmark et al. 1982). Aluminum and manganese concentrations were obtained with an atomic absorption spectrophotometer (Meyer and Keliher 1992).

Statistical analyses

All variables used in statistical analyses were initially submitted to the Ryan–Joiner test for normality and to the Bartlett test for homogeneity of variances ($\alpha = 0.05$). When appropriate, decimal logarithm (x), decimal logarithm (x) $+1$ or arc-sin transformations were used for normalization of data.

Differences in sclerophylly between months and vegetation types were tested using analysis of variance (ANOVA) or Friedman test, followed by Tukey test for multiple comparisons with the significance level of 0.05 (Zar 1996). The soil and leaf variables of *Q. parviflora* were analyzed by Principal Component Analysis (PCA), using correlation and two factors. Correlation and multiple regression analyses were also used to obtain the relationships among the observed variables on plants and soil with sclerophylly of *Q. parviflora*.

Results

Sclerophylly and mineral nutrients in Qualea parviflora

Qualea parviflora showed sclerophylly index from 69 g m^{-2} (in younger leaves) to 202 g m^{-2} (in mature leaves). Leaves were younger and less sclerophyllous in November, while mature and more sclerophyllous leaves were found in April and July (Friedman = 38,710; Figure 1). Concentrations of C, Ca, Al, Si, C/N and Ca/K ratios, and herbivory also increased with leaf age, while concentration of N, P, K, and tannins were higher in young leaves (Table 1).

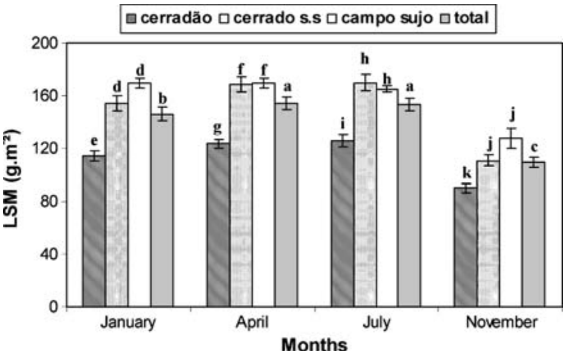

Figure 1. Means (±SE) of sclerophylly of *Q. parviflora* leaves for each vegetation type and for selected months in 2000 in ESP. Inside one sequence, different letters have significant statistical differences ($n = 120$, $\alpha = 0.05$, Tukey test for differences among vegetation types and Wilcoxon test for differences among months).

Among vegetation types, *Q. parviflora* had the least sclerophyllous leaves in cerradão, while plants in campo sujo and cerrado *sensu stricto* did not show significant differences, independently of

Table 1. Variation in plant traits ($\bar{x} \pm$ SE) of *Qualea parviflora* (Vochysiaceae) and soil water ($\bar{x} \pm$ SE) for selected months in 2000 in ESP, southeastern Brazil.

Plant traits	Months				Friedman	p
	Jan	Apr	Jul	Nov		
Leaf area (cm^2)	22.1 ± 0.91	21.76 ± 0.88	22.48 ± 1.01	24.63 ± 1.00	10.92	>0.05
Water potential (MPa)	-0.257 ± 0.032^b	-0.232 ± 0.109^b	-0.698 ± 0.178^a	-0.56 ± 0.164^a	57.58	<0.001
Herbivory (%)	4.96 ± 0.45^c	6.26 ± 0.48^b	8.06 ± 0.55^a	4.93 ± 0.60^c	29.16	<0.001
Soil water (%)	13.72 ± 0.35^b	11.17 ± 0.31^c	9.49 ± 0.49^d	15.51 ± 0.39^a	67.72	<0.001
Tannins (%)	0.93 ± 0.10^b	0.42 ± 0.09^c	0.38 ± 0.05^c	2.56 ± 0.19^a	63.37	<0.001
Total phenols (%)	2.21 ± 0.18^a	2.59 ± 0.22^a	1.06 ± 0.12^b	0.94 ± 0.11^b	53.32	<0.001
N (%)	1.14 ± 0.03^b	1.12 ± 0.03^b	1.03 ± 0.03^c	1.71 ± 0.05^a	60.34	<0.001
P (%)	0.059 ± 0.001^b	0.056 ± 0.001^b	0.0547 ± 0.003^b	0.107 ± 0.005^a	67.47	<0.001
K (%)	0.51 ± 0.02^b	0.45 ± 0.01^{bc}	0.39 ± 0.02^c	0.86 ± 0.03^a	68.03	<0.001
C (%)	62.14 ± 0.86	60.00 ± 0.13	60.36 ± 1.06	39.53 ± 1.47	75.72	<0.001
Ca (%)	0.394 ± 0.019^b	0.469 ± 0.025^a	0.453 ± 0.023^a	0.342 ± 0.017^c	35.05	<0.001
C/N	55.49 ± 1.61^b	54.35 ± 1.19^b	59.95 ± 1.48^a	23.92 ± 0.97^c	62.76	<0.001
Ca/K	0.82 ± 0.06^b	1.07 ± 0.07^a	1.22 ± 0.08^a	0.41 ± 0.02^c	70.00	<0.001
Al (%)	1.40 ± 0.02^a	1.25 ± 0.03^b	1.29 ± 0.02^b	0.87 ± 0.030^c	51.64	<0.001
Si (%)	0.36 ± 0.03^a	0.33 ± 0.03^a	0.35 ± 0.04^a	0.18 ± 0.02^b	58.00	<0.001

Different letters are statistically significant ($n = 120$, $\alpha = 0.05$, Friedman test followed by Wilcoxon test).

Table 2. Plant traits ($\bar{x} \pm \mathrm{SE}$) of *Qualea parviflora* (Vochysiaceae), and soil nutrients from three vegetation types, independent of month, in ESP, southeastern Brazil.

Plant traits	Vegetation types					
	Cerradão	Cerrado	Campo sujo	*F**	*H***	*p*
LSM (g m^{-2})	114.0 ± 18.0^{b}	151.0 ± 30.0^{a}	158.0 ± 23.0^{a}		44.52	<0.001
Leaf area (cm^{2})	24.21 ± 6.01^{a}	24.83 ± 4.52^{a}	19.20 ± 2.86^{b}	19.97		<0.001
Water potential (MPa)	−0.439 ± 0.293	−0.383 ± 0.272	−0.491 ± 0.176		5.88	>0.05
Total Phenols (%)	2.11 ± 0.15	2.01 ± 0.21	0.98 ± 0.09		3.46	>0.05
Tannins (%)	2.21 ± 0.18	2.59 ± 0.22	1.06 ± 0.12		3.16	>0.05
Herbivory (%)	5.92 ± 3.40^{ab}	7.61 ± 2.91^{a}	4.61 ± 2.23^{b}	10.71		<0.001
N (%)	1.33 ± 0.33	1.22 ± 0.36	1.19 ± 0.28		5.87	>0.05
P (%)	0.078 ± 0.032^{a}	0.067 ± 0.027^{b}	0.062 ± 0.021^{b}		14.13	<0.001
K (%)	0.60 ± 0.23	0.55 ± 0.21	0.51 ± 0.18		4.74	>0.05
C (%)	55.61 ± 1.54	55.35 ± 1.50	55.57 ± 1.43		0.87	>0.05
Ca%	0.365 ± 0.093	0.433 ± 0.108	0.445 ± 0.153		0.90	>0.05
C/N	45.29 ± 14.67	50.25 ± 17.80	49.74 ± 15.55		4.47	>0.05
Ca/K	0.71 ± 0.34	0.92 ± 0.44	1.01 ± 0.53		7.45	>0.05
Al (%)	1.14 ± 0.17	1.16 ± 0.19	1.11 ± 0.26		0.41	>0.05
Si (%)	0.35 ± 0.21	0.33 ± 0.21	0.34 ± 0.18		0.52	>0.05
Soil characteristics						
N-nitrate (g dm^{-3})	7.6 ± 3.1^{a}	5.5 ± 1.6^{b}	4.6 ± 1.2^{c}		35.39	<0.001
N-amonium (g dm^{-3})	218.9 ± 94.4^{a}	181.4 ± 107.7^{b}	223.1 ± 126.2^{a}		6.83	<0.001
K (cmol$_{c}$ dm^{-3})	0.18 ± 0.05^{a}	0.14 ± 0.04^{b}	0.20 ± 0.04^{a}		34.42	<0.001
P (mg dm^{-3})	1.90 ± 0.78^{ab}	1.60 ± 0.54^{b}	2.05 ± 0.75^{a}	4.00		<0.001
MO (g kg^{-1})	27.1 ± 4.4^{a}	22.5 ± 3.7^{b}	24.5 ± 4.2^{b}		20.17	<0.001
Si (mg kg^{-1})	12.04 ± 4.85^{a}	10.71 ± 4.95^{a}	6.05 ± 2.95^{b}	35.50		<0.001
Al (cmol$_{c}$ dm^{-3})	1.07 ± 0.37^{ab}	0.95 ± 0.20^{b}	1.10 ± 0.26^{a}		6.39	<0.001
Mn (mg dm^{-3})	9.86 ± 7.61	12.25 ± 7.38	11.10 ± 7.14		2.57	>0.05
Soil water (%)	11.86 ± 2.52	12.15 ± 2.52	13.42 ± 3.99	2.88		>0.05

Precentages of elements and compounds refer to their concentration in dry matter of leaves. Soil moisture is expressed relative to moist soil. Different letters are statistically significant ($n = 120$, $\alpha = 0.05$, One-way ANOVA followed by Tuckey test* or Kruskal-Wallis test followed by Mann–Whitney test**).

month (Figure 1 and Table 2). However, leaves of *Q. parviflora* in campo sujo had smaller area when compared to leaves of plants in the other two physiognomies (Table 2), and a negative relationship between leaf area and sclerophylly were found ($r = -0.32$).

There was a tendency of higher concentrations of nutrients in *Q. parviflora* leaves in cerradão but lower in the campo sujo (Table 2). The highest concentration of phosphorous was found in cerradão, while the lowest was in trees in campo sujo (Table 2). However, all values for P were very low and are inside the limit (below 0.3%) regarded by Loveless (1961, 1962) as an indication of sclerophyllous condition. In addition, concentration of silicium, N–NO$_3$ and organic matter – a nutrient reservoir of the soil that can reduce negative effects of heavy metals on plants – is higher in cerradão and lower in campo sujo (Table 2).

Tests of hypothesis on sclerophylly in Qualea parviflora

The projection of the soil and plant variables on the two axes of PCA shows two negatively correlated groups in relation to axis 1 (Figure 2). Concentrations of K, N and P in leaves are negatively correlated with axis 1, while sclerophylly, Ca/K ratio, Mn, in soil and Ca in plant showed a direct relationship with this axis. More than 50% of the variance of all variables is explained by the first two axes, with the first axis accounts for 40.59% of the variance, and the second 12.02%. The variables that load highly on axis 1 were sclerophylly, water, Mn and Al in soil, tannins; Al, N, C, P, K, Ca, Ca/K in leaves; while the N-NH4, N-NO3, K, OM, Si, and P in soil load highly on axis 2. Other variables do not load highly on any specific axis (Figure 2).

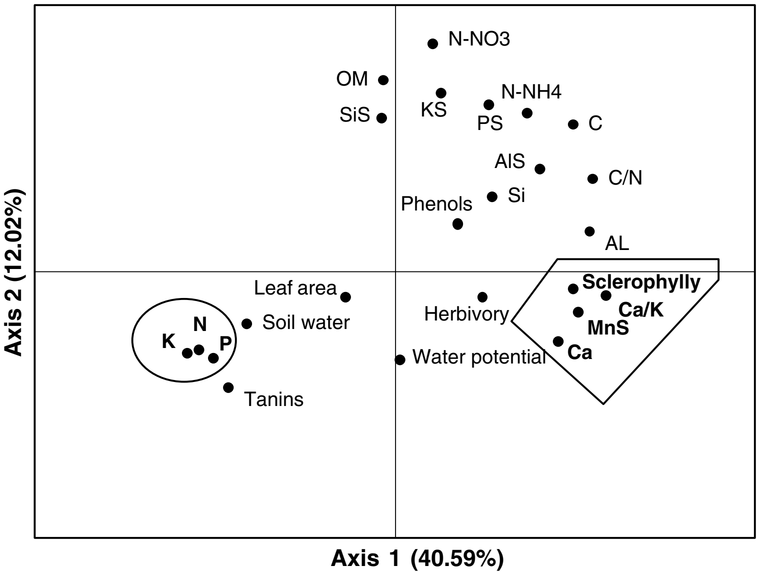

Figure 2. Ordination of the variables in *Q. parviflora* and soil (S) by Principal Component Analysis (PCA). Two negatively correlated groups in relation to axis 1 were identified (inside line drawings): (I) concentration of potassium, nitrogen and phosphorus in leaves; and (II) sclerophylly, concentration of calcium and ratio Ca/K in leaves and concentration of manganese in soil of ESP. Other nutrients in soil tended to group and are positively correlated in relation to axis 2.

Despite the higher soil moisture in the beginning of rainy season (15.51 ± 0.39%), *Q. parviflora* had lower values of Φ_{pd}. in January and April. The highest values occurred in July (Table 1) when significant differences were not observed among the plants of the three types of vegetation (ANOVA, $F_{27,2}$ = 0.06; $p > 0.05$), and with values of water potential below −0.6 Mpa. Also, we did not find any significant variation in leaf sclerophylly with increasing water potential (Table 3).

Trees of *Q. parviflora* in campo sujo showed lower herbivory rates, however there were no significant differences in concentration of tannins and phenols between plants of the three vegetation types (Table 2). We did not find any significant correlation between sclerophylly and total phenols or between sclerophylly and tannins in *Q. parviflora* (Table 3 and Figure 2). In addition, non-significant correlation was found between herbivory and sclerophylly (Table 3).

We found a strong negative correlation among leaf area, N, P, K, and sclerophylly (Table 3). Besides, C/N and Ca/K ratios, C, and Al concentration were positively correlated with leaf sclerophylly, indicating that more sclerophyllous leaves

Table 3. Spearman correlation index (r_s) between leaf sclerophylly in *Q. parviflora* and plant traits, herbivory (% leaf area damaged), and soil nutrients (n = 120, α = 0.01).

Plant traits	r_s	p
Leaf area (cm)	−0.30	> 0.01
Water potential (MPa)	−0.08	> 0.01
Herbivory (%)	0.19	> 0.01
Tannins (%)	−0.35	> 0.01
Total phenols (%)	0.42	> 0.01
N (%)	−0.65	< 0.01
P (%)	−0.73	< 0.01
K (%)	−0.63	< 0.01
C (%)	0.33	> 0.01
Ca (%)	0.44	< 0.01
C/N	0.61	< 0.01
Ca/K	0.65	< 0.01
Al (%)	0.45	< 0.01
Si (%)	0.17	> 0.01
Soil characteristics		
N-Nitrate (g dm^{-3})	−0.14	> 0.01
N-Amonium (g dm^{-3})	−0.32	> 0.01
P (mg dm^{-3})	−0.30	> 0.01
K ($cmol_c$ dm^{-3})	0.17	> 0.01
MO (g kg^{-1})	−0.07	> 0.01
Mn (mg dm^{-3})	0.46	< 0.01
Al ($cmol_c$ dm^{-3})	0.40	> 0.01
Si (mg kg^{-1})	−0.10	> 0.01
Soil water (%)	−0.26	> 0.01

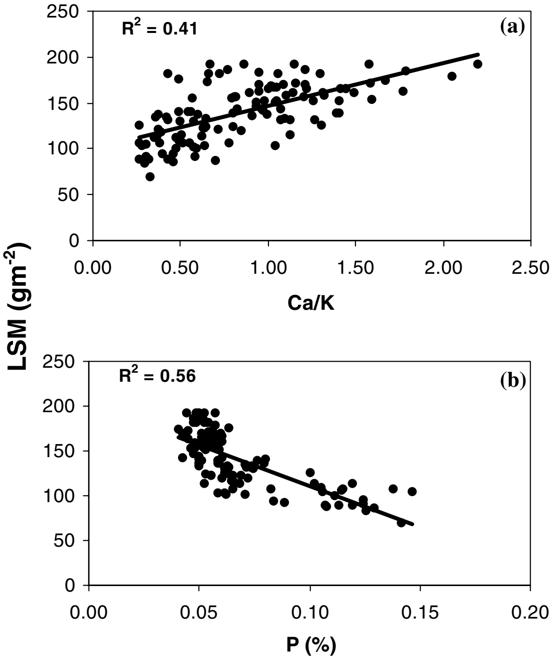

Figure 3. Relationship between sclerophylly and (a) Ca/K ratio, and (b) concentrations of P, in *Q. parviflora* (Vochysiaceae) leaves in ESP, southeastern Brazil. Multiple regression model: $y = 170.03 + 20.95*Ca/K-701.5*P$, $r^2 = 0.60$, $F_{113,2} = 88.93$, $p < 0.001$.

have high Ca/K ratio and the lowest concentration of essential nutrients (Table 3 and Figure 3). Among all variables observed in plant and soil, the concentrations of P and Ca/K ratio in leaves better explained the variation observed in the sclerophylly (Figure 3).

Discussion

The values of sclerophylly in *Q. parviflora* leaves are close to those found in other savanna species (from 90 to 400 g m^{-2}; Montes and Medina 1977), and agree with those observed in *Q. grandiflora* Mart. (76 to 313 g m^{-2}; Paulilo and Felipe 1992), and *Q. dichotoma* Warm. (a mean of 142 g m^{-2}; to mature leaves; Prado and Moraes 1997). Also, according to Cowling and Campbell (1983) leaves with leaf mass per area greater than 75 g m^{-2} should be considered as sclerophyllous.

In addition, *Qualea parviflora* leaves were younger, less sclerophyllous, and with higher K and P and lower Al concentrations in November. These results corroborate other studies. For example, Sobrado and Medina (1980) found lower concentrations of K and P in mature leaves, while Medeiros (1983) observed lower concentration of Al in leaves of *Q. parviflora* in November in a cerrado near Brasília, in central Brazil.

Leaves in plants in campo sujo (sunnier habitat) were more sclerophyllous and had smaller leaf area than plants in cerradão. A negative relationship between leaf area and sclerophylly was also found in other studies (e.g., Bussotti et al. 1997, Madeira et al. 1998). Marques et al. (1999) observed that shade leaves of sclerophyllous species had lower leaf dry mass than leaves of same species in sunny habitats. In addition, costs of the larger and ticker petioles can make sun plants less effective than shade plants of the same size, for intercepting PAR (photosynthetic active radiation), provide negative effects of size and thickness on the efficiency of resource use (Gutshick 1999).

According to Sarmiento (1996), in seasonal savannas after the rainy season, the water potential of the soil stays with very negative values (below −4.0 MPa) along the dry season with the less seasonality in deeper stocks of water which are just available for species of plants with longer and deeper roots. Although *Q. parviflora* has roots with intermediary length (A. Franco, personal communication), our results suggest that this species spend a long time to improve the level of water in its tissues, as we can observe in the high values of water potential even at the beginning of rainy season (November).

However, we did not find any significant relationship between sclerophylly and water status, hence not corroborating the hypothesis that predicts sclerophylly is an adaptation to seasonal water deficits for savannas. Salleo and Gullo (1990) also showed that sclerophylly was not related with a species ‘water saving strategy’. They observed equal peak values of leaf conductance to water vapor for *Quercus ilex* (hard-leaved) and *Q. suber* (less sclerophyllous leaves) trees studied, while *Q. ilex* was also underwent a larger water loss.

Some authors (e.g., Choong et al. 1992; Turner 1994) argue that leaf sclerophylly can influence generalist folivorous predation rates because low digestibility and time spent to eat tough leaves energetically expensive. Coley (1983a, b) observed that the toughness of leaves represents a more efficient means of antiherbivore defense than a high concentration of tannins in Central America plants. However, there is no significant correlation between herbivory and sclerophylly of *Q. parviflora* leaves, therefore not corroborating the hypothesis that predicts sclerophylly is an adaptation to anti herbivore defense in *Q. parviflora*. Similarly, Madeira et al. (1998) did not found any correlation between herbivory with either sclerophylly or tannin concentration in *Chamaecrista linearifolia* Barneby (Fabaceae) in southeastern Brazil. Thus, the relationship between sclerophylly, tannins and herbivory is quite variable and dependent of the species investigated. Hence, it is necessary more studies to test adequately the hypothesis on sclerophylly as an anti herbivore defense in plants.

Silica is one of the most widespread abrasive compound and can limits herbivory on grasses and other plants (Gutshick 1999), but contradicting some studies (e.g., Sarmiento and Monasterio 1975; Howe and Westley 1988) we found no relationship between deposition of silica and sclerophylly. Perhaps these findings are due to the fact that *Q. parviflora* is not a species that accumulates silica; differently of *Curatella americana* L. (Dilleniaceae) and *Davilla elliptica* St. Hil. (Dilleniaceae) whose sclerophyllous leaves are rich in silica (Korndörfer 1999).

There was a linear relationship between sclerophylly and the leaf P and Ca/K ratio. Felippe and Dale (1990) also observed increased sclerophylly index with decreasing phosphate supply on two species of the Brazilian cerrado. Arens (1958a, b) attributed the scleromorphic traits of cerrado plant species to the mineral deficiency, particularly N, P, Ca and S, which would limit plant growth, provide accumulation of carbohydrates, and deposit in the wall of plant cell, as cellulose, sclerenchyma and other mechanical structures. Also, some authors (Eklund and Eliasson 1990; Dunisch et al. 1998) found that the reduction of the thickness of the cellular wall in some plants is influenced by potassium, which in high concentration decrease calcium absorption. These authors observed an increased of synthesis of cellular wall, and higher lignification with increasing concentration of calcium.

Accordingly to Loveless (1961, 1962) the roles of P and N in plant metabolism are interrelated in a number of ways, as they are among the essential nutrients for the synthesis of proteins. It would be expected that intermediate products of metabolism which otherwise might have formed protein should, in the absence of adequate phosphate, be diverted along alternative metabolic pathways to form other end products, including that estimated as fibre (cellulose and lignin). Thus, the carbon metabolism is deviated for the formation of other products and sclerophylly would be the expression of a metabolism found in plants that can tolerate low levels of phosphate (Loveless 1962; Groom and Lamont 1999). Also, Roderick et al. (1999) found that there was a decline in leaf N as thickness declined from 350 μm, suggesting that much of the N is located within the mesophyll cells.

Conclusions

We did not find any significant relationship between sclerophylly with herbivory or water status, therefore not corroborating the hypotheses that predict sclerophylly is an adaptation to anti herbivore defense in *Q. parviflora* or is an adaptation to seasonal water deficits for savannas. Our results corroborate the findings of other authors (e.g, Arens, 1958a, b; Loveless 1961, 1962; Sobrado and Medina 1980) and the hypothesis that predicts sclerophylly as an adaptation to low rates of essential nutrients supply, such as P and K, from soil. This efficiency of nutrient use by *Q. parviflora* allows this species to survive in nutrient poor-soil habitats in the Brazilian cerrado.

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