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Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit

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Abstract The seasonal savannas (cerrados) of Central Brazil are characterized by a large diversity of evergreen and deciduous trees, which do not show a clear differentiation in terms of active rooting depth. Irrespective of the depth of the root system, expansion of new foliage in deciduous species occurs at the end of the dry season. In this study, we examined a suite of leaf traits related to C assimilation, water and nutrients (N, P) in five deciduous and six evergreen trees that were among the dominant families of cerrado vegetation. Maximum CO_2 assimilation on a mass basis (A_{mass}) was significantly correlated with leaf N and P, and specific leaf area (SLA; leaf area per unit of leaf mass). The highest leaf concentrations of both nutrients were measured in the newly mature leaves of deciduous species at the end of the dry period. The differences in terms of leaf N and P between evergreen and deciduous species decreased during the wet season. Deciduous species also invested less in the production of non-photosynthetic leaf tissues and produced leaves with higher SLA and maintained higher water use efficiency. Thus, deciduous species compensated for their shorter leaf payback period by maintaining higher potential payback capacity (higher values of A_{mass}) and lower leaf construction costs (higher SLA). Their short leafless period and the capacity to flush by the end of the dry season may also contribute to offset the longer payback period of evergreen species, although it may involve the higher cost of maintaining a deep-root system or a tight control of plant water balance in the shallow-rooted ones.

Keywords Carbon isotope discrimination · Leaf level traits · Photosynthesis · Stable isotope ratios · Water use efficiency

Introduction

The central plains of Brazil are occupied by a complex of seasonal savannas, known locally as “cerrado.” The cerrados of central Brazil are the second most extensive plant formation in South America and cover 2.0×10^6 km^2 of land area (Eiten 1972). Like other Neotropical savannas, the cerrado is characterized by strong rainfall seasonality, coupled with constantly high diurnal air temperatures. The soils are generally deep and well drained. Superficial soil layers dry out during the dry season that extends from May to September, while deeper soil layers exhibit a much higher degree of water constancy throughout the year (Franco 2002). The nutrient-poor, acid soils represent an additional limiting factor for plant growth in this region. P is particularly limiting in these ecosystems (Haridasan 2000, 2001).

The upper canopy of cerrado vegetation typically consists of 6- to 8-m-tall, deciduous and evergreen trees (Eiten 1972). The coexistence of tree species with contrasting phenological behaviors in savanna ecosystems has been taken as an indication of differences in depth of the root systems, whereby drought-deciduous species are expected to have

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more superficial root systems and a tight stomatal regulation of transpiration. Deep-rooted evergreen trees would be able to supply enough water to maintain high rates of transpiration and CO_2 assimilation during the dry period (Goldstein et al. 1989). On the other hand, one could expect that deciduous species should have a less conservative strategy for water use because of the short payback interval (short leaf life-span), while evergreen species should have a more conservative strategy of water use (Lloyd and Farquhar 1994). Deciduous species could overcome this limitation if they are able to sustain higher photosynthetic rates per unit of water loss in relation to evergreen species. However, evergreen and deciduous cerrado trees may not show such contrasting strategies of water use and leaf C balance in response to the seasonal drought. Comparisons of hydrogen isotope composition of xylem water and soil water samples collected at different depths do not suggest a clear differentiation in terms of active rooting depth between deciduous and evergreen trees in the Cerrado (Table 1; Jackson et al. 1999). High atmospheric evaporative demand and hydraulic constraints result in strong stomatal limitation of transpiration and a prolonged midday depression of photosynthetic rates in both evergreen and deciduous species during both the wet and the dry seasons (Johnson et al. 1983; Franco 1998; Moraes and Prado 1998; Meinzer et al. 1999; Naves-Barbiero et al. 2000; Franco and Lüttge 2002). Indeed, evergreen and deciduous cerrado trees showed similar stomatal responses to changes in air saturation deficit (Bucci et al. 2004). Moreover, many deciduous trees remain leafless for only short periods, and are able to flush new leaves during the dry season (Rivera et al. 2002).

Photosynthesis is strongly affected by N availability. This reflects a combination of the larger proportional investment of N in photosynthetic machinery and the widespread N limitation in natural ecosystems. Studies in a range of ecosystems have shown that deciduous species generally have higher N concentrations per unit leaf mass and photosynthetic rates than evergreen species (Mooney and Gulmon 1982; Field and Mooney 1986; Sobrado 1991, 1994; Eamus and Cole 1997; Reich et al. 1992, 1997). On the other hand, some field studies have reported that photosynthesis is more limited by P availability in P-deficient soils (Reich and Schoettle 1988; Cordell et al. 2001). A detailed assessment of the nutrient relations of the selected species was beyond the scope of this study. However, measurements of leaf N and P content and specific leaf area (SLA; leaf area per unit of leaf mass) coupled with gas exchange measurements allowed us to address questions related to leaf C balance, patterns of leaf phenology and nutrient allocation in cerrado trees. We also measured seasonal changes in leaf δ^{13}C, N and P, predawn and midday leaf water potential, as well as patterns of leaf phenology and leaf life-span. Foliar δ^{13}C values of plants obtaining their CO_2 from the same sources are considered to be an integrated, long-term estimate of intrinsic water use efficiency (WUE) (Ehleringer and Cooper 1988; Meinzer et al. 1990). Lower values of SLA generally reflect more investment of N in non-photosynthetic components (Field and Mooney 1986). Deciduous species are constrained by the shorter leaf life-span. Thus, we expected that deciduous species would invest less in the production of non-photosynthetic tissues and would produce leaves with higher SLA and higher N and P concentrations. Deciduous species should also have higher photosynthetic rates and WUE than evergreen species, because of the well-known linear relationship between photosynthesis and leaf N and the close correlation between N and P concentrations.

Materials and methods

Study site, plant material and leaf phenology

The study was carried out at the ecological reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE), located approximately 33 km south of Brasilia. The study site (15°56′S, 47°53′W, altitude 1,100 m) is a seasonal savanna having a relatively continuous layer of perennial grasses with a discontinuous layer of deciduous and evergreen trees with a low and almost shrubby growth form. Most trees and shrubs have a thick bark, twisted trunks and scleromorphic leaves. Soils are deep, well-drained, strongly acid dystrophic latosols, with high Al content. The climate is Aw by Köppen's classification and according to the weather station records of the IBGE ecological reserve, the average rainfall is 1,483 mm (1980–1997) with a distinct dry season from May to September. The dry season of 1995 was particularly severe. Although annual rainfall was 1,684 mm, it rained only 37 mm from May to September. Annual rainfall was 1,384 mm in 1996, but it rained a total of 112 mm from May to September. Average (diurnal) relative humidity is around 80% during the rainy season and drops to 55% during the dry season when daily minimum relative humidity reaches values as low as 15%. Mean annual temperature is about 22°C.

A total of 11 woody species were selected based on their phenology and abundance among dominant families of cerrado vegetation (Table 1). These species are commonly found throughout the cerrado domain. In a study of the floristic composition of 98 sites of cerrado and Amazonian savanna, encompassing most of the area of such vegetation in Brazil, these species occurred in 15% (*Miconia ferruginata*) to 82% (*Qualea grandiflora*) of the sites (Ratter et al. 1996).

Starting in September, 1995, branches or twigs of five individuals of each species were marked in such a way that individual leaves could be identified, their abscission noted and the formation of new mature leaves recorded. Five twigs or branches were marked on each individual where possible, since the growth habit of some species, with limited branching, provides few growing points. This was the case with *Schefflera macrocarpa* and *Kielmeyera coriacea*, for example. Monthly observations were carried out from September 1995 to November 1998. In order to define the duration of the leafless period, observations were made on a weekly basis from the end of June to the end of October, when four individuals of *Dalbergia miscolobium*

Table 1 Characteristics of woody species used in this study; data are expressed as mean±SE. A_{CO_2} Maximum CO_2 assimilation (μmol m^{-2} s^{-1}), *SLA* specific leaf area (leaf area per unit of leaf mass; m^2 kg^{-1}) (*n*=number of leaves)

Species	Family	Leafless[a]			Leaf flush	Root depth[b]	A_{CO_2}	SLA
		1996	1997	1998				
Evergreen								
Schefflera macrocarpa	Araliaceae	0	0	0	Throughout the year	Shallow	16.3±0.5	3.50±0.07 (35)
Miconia ferruginata	Melastomataceae	0	0	0	Wet season	Shallow	12.5±0.5	4.97±0.12 (26)
Roupala montana	Proteaceae	0	0	0	End of dry season	Shallow	9.9±0.5	4.12±0.12 (22)
Evergreen leaf-exchanger[c]								
Sclerolobium paniculatum	Leguminosae–Caesalpinioideae	0	0	0	Wet season	Shallow	13.7±0.6	6.84±0.30 (36)
Vochysia elliptica	Vochysiaceae	0	0	0	End of dry season	Deep	8.8±0.7	5.97±0.40 (7)
Ouratea hexasperma	Ochnaceae	0	0	0	End of dry season	Shallow[e]	9.7±0.4	7.29±0.17 (9)
Briefly deciduous[d]								
Dalbergia miscolobium	Leguminosae–Papilionoideae	–	17±0	13±0	End of dry season	Deep	9.8±0.9	8.67±0.14 (30)
Pterodon pubescens	Leguminosae–Papilionoideae	15±4	18±8	14±12	End of dry season	Shallow	12.5±1.4	11.82±0.16 (25)
Deciduous								
Kielmeyera coriacea	Clusiaceae	41±9	26±7	41±8	End of dry season	Deep	11.5±0.6	6.42±1.65 (42)
Qualea grandiflora	Vochysiaceae	23±5	27±9	38±16	End of dry season	Deep	11.9±0.9	7.77±0.40 (26)
Qualea parviflora	Vochysiaceae	26±7	32±12	31±10	End of dry season	Intermediate	10.4±0.5	8.18±1.14 (42)

[a] Average number of days±SD that the plants were without leaves of any type, including young and senescent leaves, in three successive dry periods (1996, 1997, 1998)

[b] From Jackson et al. (1999) and based on comparisons of stable hydrogen isotope composition of stem xylem water and soil water that was collected at different depths in the dry season

[c] Simultaneously sheds leaves and produces new ones

[d] Remain leafless for short periods of time during the dry season

[e] Based on unpublished measurements of stable hydrogen isotope composition

were included, starting in June 1997. Based on these observations, pattens of leaf phenology were obtained, as well as estimates of leaf longevity.

Measurements of leaf gas-exchange and leaf water potential

Maximum CO_2 assimilation (A_{CO_2}), stomatal conductance at A_{CO_2} (g_{wv}), intrinsic WUE (A_{CO_2}/g_{wv}) and the ratio of intercellular to ambient CO_2 partial pressure (p_i/p_a) were determined under ambient conditions with a portable photosynthesis system (301-PS CID, Vancouver, Wash.). The 301-PS was configured in the open system mode. Gas exchange measurements were carried out towards the end of the dry season (August) of 1996 and at the peak of the wet season (January and February) of 1997. Because of the small compound leaves, we used a LI-6200 (Li-Cor, Lincoln, Neb.) to measure gas exchange in *Pterodon pubescens* and *D. miscolobium*. These measurements were made only in January 1996 and problems with the humidity sensor prevented the calculation of g_{wv} and p_i/p_a. Leaf gas exchange was measured in two or three sunlit leaves of four (*Q. grandiflora* in 1996) to six (all others) pre-marked individuals during a 2- to 4-h period between 0800 hours and 1200 hours.

predawn and midday leaf water potentials were used as indicators of plant water status. Leaf water potential was measured with a pressure chamber (model 3005-14442; Soil Moisture, Santa Barbara, Calif.) in August of 1996 and February of 1997. One leaf of three to six individuals was sampled at each time. Measurements were done in the same individuals used in the gas exchange measurements.

Isotopic and nutrient analysis

Several adult leaves per individual were selected and pooled by individual. The leaves were then transported to the laboratory where their area was determined. They were then oven-dried at 70°C and their dry leaf mass determined for calculation of SLA (ratio of leaf area to leaf dry mass). The dried leaves were finely ground and a subsample was taken for total N and P determinations. N was determined in diluted acid digests according to the micro-Kjeldhal procedure (Bataglia et al. 1978). Total extractable P was determined colorimetrically by complex formation with molibdovanadate according to Bataglia et al. (1978). An additional subsample was taken for $\delta^{13}C$ determination. Samples were sent to Mountain Mass Spectrometry (Evergreen, Colo.), where the relative abundance of ^{13}C and ^{12}C in the CO_2 produced from combustion of the samples was analyzed by mass spectrometry. C isotopic discrimination (Δ) was calculated as $(\delta^{13}C_{air}–\delta^{13}C_{plant})/(1+\delta^{13}C_{plant})$, where $\delta^{13}C_{plant}$ is the C isotope ratio of the plant material and $\delta^{13}C_{air}$ is that of the air (−8‰), as described by Farquhar and Richards (1984).

Samples for C isotope and nutrient analysis were taken in September and November 1995, and March 1996. To relate leaf N and P to CO_2 assimilation, additional samples for nutrient analysis were taken in January 1996 (*P. pubescens* and *D. miscolobium*) and January 1997 (all other species), when gas exchange measurements were performed.

Data analysis

Although we examined a large number of species, we recognise that we do not have enough species to clearly distinguish the four different phenological groups depicted in Table 1. Thus, we pooled briefly deciduous and deciduous species in a single functional group, as leaf life-span in all of them is <1 year and they remain leafless for at least several days. New leaves emerge after leaf abscission. The other six species were grouped as evergreens. They always maintain a green canopy and leaf life-span is at least 1 year. However, we kept all four phenological groups separated in most figures and tables and clear differences among them were highlighted.

The statistical package Statview for Windows 5.0 (SAS Institute) was used to analyze the data. A multivariate ANOVA (MANOVA) followed by the Fisher's protected least significant difference multiple comparison test (Fisher's) was applied to analyze the effects of leaf phenology and season on leaf N, P and Δ. Because the interaction term was significant, the variables were first $\log_{10}$ transformed to restore the additivity of the data (Sokal and Rohlf 1995). We did not have a complete C isotope data set for *P. pubescens* and *Q. grandiflora*. Thus, these two species were not included in the analyses. However, all the available data for these two species were included in the figures.

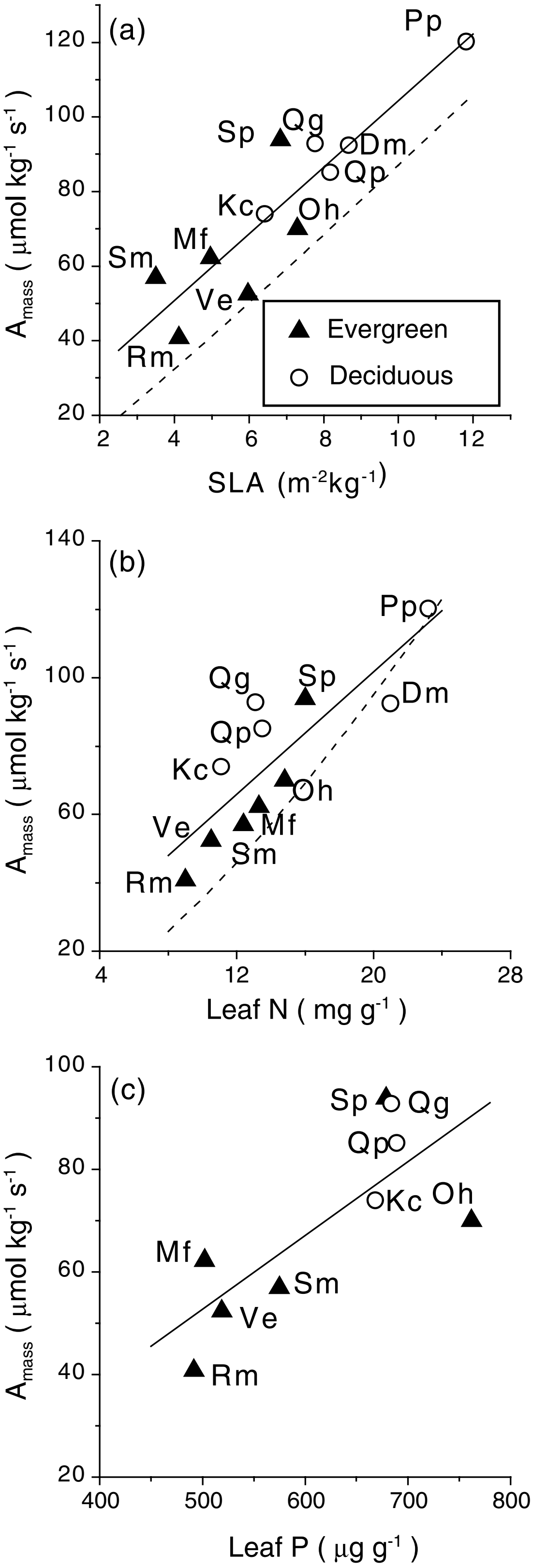
We used unpaired *t*-tests or Mann-Whitney *U*-tests to evaluate the differences between evergreen and deciduous in regard to SLA and A_{CO_2} on a mass and leaf area basis and paired *t*-tests to evaluate the effect of drought on gas exchange parameters and leaf water potential of evergreen species. Significance was determined as $P<0.05$ unless otherwise noted.

Results and discussion

The timing of bud break was variable among evergreen species, while all deciduous species flushed by the end of the dry season (Table 1). Evergreen leaf-exchangers simultaneously shed the leaves and produced new ones, while the briefly deciduous species remained leafless for short periods of time of <3 weeks. The other deciduous species remained leafless for periods of about 3–6 weeks (Table 1). There was variation between the evergreen species with regard to leaf longevity. *M. ferruginata* retained its leaves for approximately 24 months, while *Schefflera macrocarpa* and *Roupala montana* tended to retain their leaves for approximately 18 months. Leaf lifespan was about 12 months for the three evergreen leaf-exchangers and 10–11 months for the deciduous species. Although there was not a sharp separation in terms of active rooting depth between the two phenological groups in the dry season, most deciduous species were apparently extracting water from deeper soil layers than the evergreens (Table 1).

Deciduous and evergreen species had similar rates of A_{CO_2} at the peak of the wet season (Table 1). g_{wv}s were also similar between the two phenological types, ranging from 133 mmol m^{-2} s^{-1} to 228 mmol m^{-2} s^{-1}. Differences in maximum CO_2 assimilation and stomatal conductance between evergreen and deciduous trees are frequently small in savannas and dry deciduous forests (Goldstein et al. 1989; Sobrado 1991, 1994; Eamus and Cole 1997). Deciduous species invested less in the production of non-photosynthetic leaf tissues and produced leaves with higher SLA (*t*-test; P=0.016; Table 1). These differences were reflected in CO_2 assimilation rates on a mass basis (A_{mass}). Values of maximum A_{mass} of deciduous and evergreen species averaged 92.9 µmol kg^{-1} s^{-1} and 62.7 µmol kg^{-1} s^{-1}, respectively. These differences were statistically significant (*t*-test; P=0.019). Thus, deciduous species compensated their shorter leaf pay back period by an increase in the potential payback capacity (maximum A_{mass}), when soil water was not limiting. Prado and Moraes (1997) reported A_{mass} values within this range for 20 cerrado woody species at a site near the southern limit of cerrado vegetation, but they did not include information on leaf phenology. A_{mass} increased with SLA for both evergreen and deciduous species (Fig. 1a). The relationship was similar to the general one fitted for data across biomes (Reich et al. 1999).

Photosynthesis is strongly affected by N availability and it is well known that photosynthetic capacity increases linearly with leaf N concentration (Field and Mooney 1986; Reich et al. 1995). Indeed, Eamus and Prior (2001) showed that, for a range of tree species from different seasonally dry ecosystems, leaf N increases with light-saturated A_{CO_2}, with no clear distinction between evergreen and deciduous species. This was also found in the present study. Maximum CO_2 assimilation was significantly correlated with leaf N and leaf P on a mass basis (Fig. 1b, c) but not on an area basis (not shown). The close correlation between A_{mass} and both leaf SLA and N suggests that decreasing SLA is associated with greater allocation of biomass to structural components of the leaf rather than metabolic components (Field and Mooney 1986; Reich et al. 1998).



◀ **Fig. 1** Relationships between **a** maximum CO_2 assimilation on a mass basis (A_{mass}) and specific leaf area (SLA); **b** A_{mass} and leaf N concentration; **c** A_{mass} and leaf P concentration. *Each point* is the mean of two to six trees per species. The *lines* are regressions fitted to the data: **a** A_{mass}=15.108+8.9262(SLA), r=0.901, P<0.001, n=11; **b** A_{mass}=12.132+4.4782(leaf N), r=0.841, P=0.001, n=11; **c**A_{mass}=−19.221+0.1438(leaf P), r=0.766, P=0.016, n=9. The *dotted line* describes the log–log relationship between A_{mass} and SLA ($\log A_{mass}$=−0.22+1.08$\log_{10}$SLA; Reich et al. 1999) and between A_{mass} and leaf N [$\log A_{mass}$=0.13+1.42$\log_{10}$(leaf N); Reich et al. 1999] fitted to data from six biomes. *SmSchefflera macrocarpa*, *MfMiconia ferruginata*, *RmRoupala montana*, *SpSclerolobium paniculatum*, *VeVochysia elliptica*, *OhOuratea hexasperma*, *DmDalbergia miscolobium*, *PpPterodon pubescens*, *QpQualea parviflora*, *QgQ. grandiflora*, *KcKielmeyera coriacea*

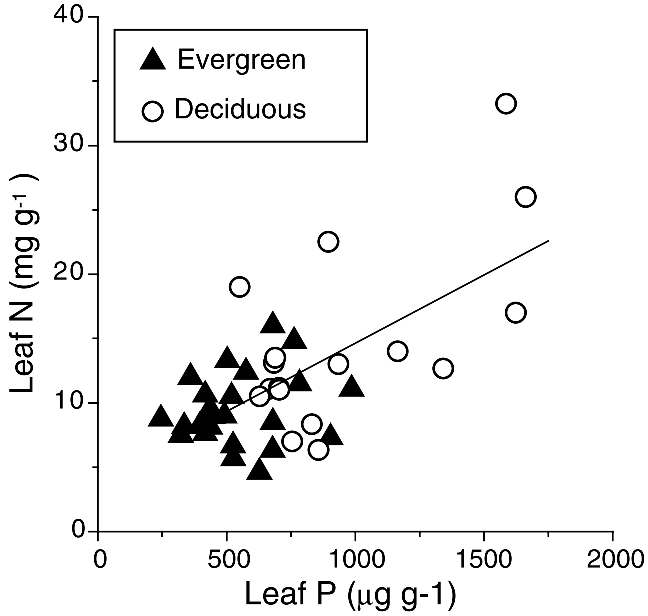


Fig. 2 Relationship between leaf N and P based on measurements taken in the dry and the rainy season. The *line* is the regression fitted to the data: leaf N=4.0398+0.0106(Leaf P), r=0.653, P<0.0001, n=41

Indeed, using multiple linear regression, A_{mass} was highly significantly related to the combination of leaf N and SLA (r=0.92, P=0.0006). As expected, there was also a significant correlation between leaf N and leaf P (Fig. 2) across species. Thus, deciduous and evergreen trees shared common relationships between leaf traits, which suggests that selective pressures impose strong constraints on functional trait variability in cerrado environments. On the other hand, the results of the MANOVA gives support to the hypothesis that evergreen and deciduous species have different combinations of leaf traits, at least in terms of leaf N, P and Δ and that these combinations are influenced by seasonality (Table 2).

Soil water availability is generally not a limiting factor during the wet season in cerrado ecosystems (Franco 2002). However, high atmospheric evaporative demand and hydraulic constraints impose a strong stomatal limitation of transpiration and a prolonged midday depression of photosynthesis during both the wet and the dry seasons (Franco 1998; Moraes and Prado 1998; Meinzer et al. 1999; Naves-Barbiero et al. 2000; Franco and Lüttge 2002). This would be particularly critical during the dry season, which is characterized by very low values of relative humidity (Franco 2002). Most evergreen species showed a decline in the maximum CO_2 assimilation rates and stomatal conductances in the dry season, while leaf-to-air vapour pressure deficit (VPD) increased substantially (Fig. 3). The magnitude of the decrease was larger for stomatal conductance; as a result three species had a significant increase in A_{CO_2}/g_{wv}. On the other hand, p_i/p_a remained constant for five out of the six species. The only exception was *Vochysia elliptica*, where p_i/p_a showed a small, but significant increase by the end of the dry season. This deep-rooted species had the least variation in both predawn and midday leaf water potential (Fig. 4). Although statistically significant (t-test; $P \leq 0.02$), these seasonal differences in predawn and midday water potential were relatively small, when compared to trees of Venezuelan dry forests (Sobrado 1986) but similar to those of evergreen species of Australian savannas (Duff et al. 1997; Myers et al. 1997). Seasonal variations in predawn and midday water potential in evergreen cerrado species may partially reflect nocturnal transpiration that would limit plant recharge during night-time (Bucci et al. 2004).

Table 2 Results of the multivariate ANOVA for the effects of leaf phenology and time of the year on leaf traits (leaf N, P and C isotopic discrimination)

Source of variation	F-value	P-value
Phenology		
Wilks' λ	9.968	0.0004
Pillai trace	9.968	0.0004
Season		
Wilks' λ	9.805	<0.0001
Pillai trace	8.989	<0.0001
Phenology × season		
Wilks' λ	1.997	0.0903
Pillai trace	1.791	0.1256

We do not report measurements of gas exchange and of leaf water potential in deciduous species because they were leafless or had only very young leaves when we took the dry season measurements. However, other studies have reported that stomatal conductance in deciduous cerrado species also declined significantly during the dry season, while seasonal variations in leaf water potential were relatively small (Cardinot 1998; Maia 1999; Naves 2000; Bucci et al. 2004). This decrease in stomatal conductance in both phenological groups is mostly a response to the strong increase in air saturation deficit during the dry season (Bucci et al. 2004). Indeed, evergreen and deciduous cerrado species showed similar stomatal responses to changes in air saturation deficit (Bucci et al. 2004).

These seasonal changes in maximum A_{CO_2} and g_{wv} could affect WUE (CO_2 assimilation/transpiration) of evergreen and deciduous species. Although WUE can be calculated from diurnal cycles of A_{CO_2} and transpiration, we did not follow this approach because of the uncertainties involved in attempting to integrate instantaneous measurements to represent a whole season. Instead, we used changes in leaf Δ to assess WUE on a seasonal basis. Eleven of the 13 species studied by Mattos et al. (1997) in a cerrado area in southern Brazil showed a decrease in leaf Δ (higher WUE) during the dry season. The decrease ranged from 0.3‰ to 4‰ and it was statistically significant at the community level. They related their results to a larger decrease in g_{wv} in comparison to A_{CO_2}. However, they based this conclusion on gas exchange results for only two of the 13 species. Although we were not able to detect a seasonal variation

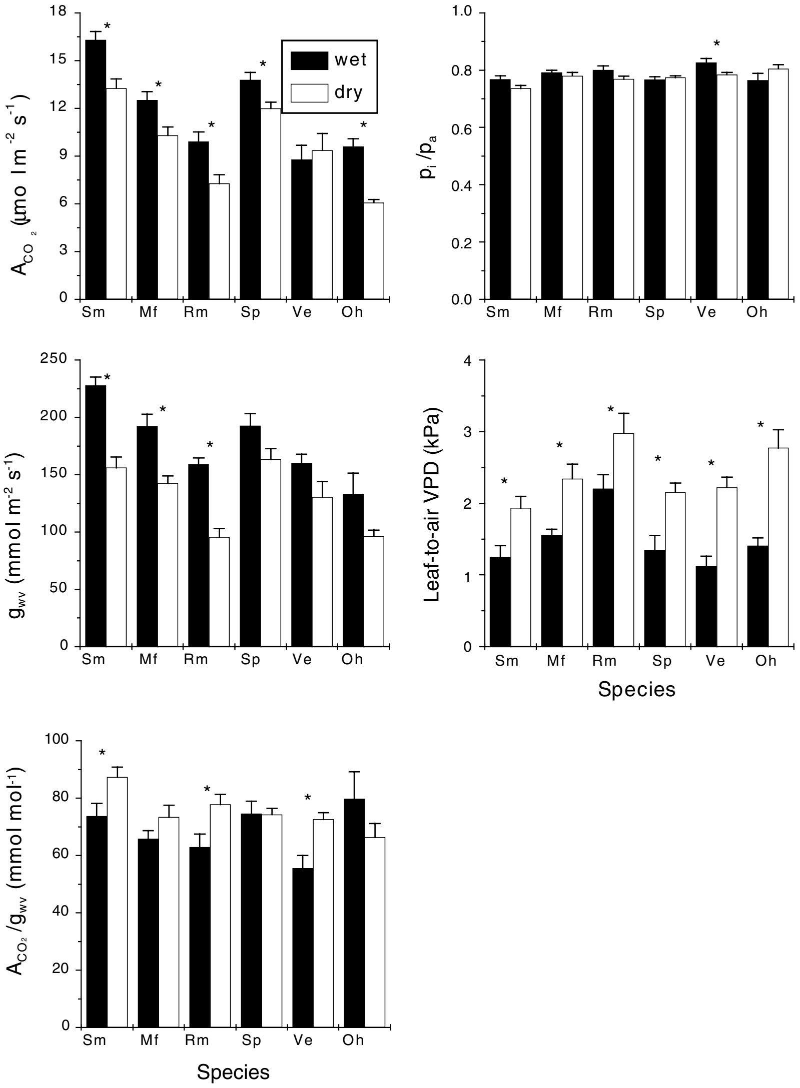


Fig. 3 Seasonal changes in maximum CO_2 assimilation (A_{CO_2}), stomatal conductance atA_{CO_2} (g_{wv}), intrinsic WUE (A_{CO_2}/g_{wv}), the ratio of intercellular to ambient CO_2 partial pressure (p_i/p_a) and leaf-to-air vapour pressure deficit (*VPD*) for six evergreen cerrado trees. Data were collected at the peak of the rainy season (*wet*) and at the end of the dry season (*dry*). Each *bar* represents the mean+1 SE (n=6 trees per species). For other abbreviations, see Fig. 1

in leaf Δ at the community level, leaf Δ was significantly higher for deciduous species (Fig. 5a).

C isotope discrimination is largely dependent on the ratio of intercellular to ambient CO_2 concentrations prevailing when the leaf C is assimilated (Farquhar et al. 1982, 1989). Thus a decrease in p_i/p_a should reflect diffusional limitations to CO_2 uptake from reductions in stomatal conductance and/or an increase in carboxylation efficiency (higher CO_2 assimilation rates; Ehleringer 1994). Higher foliar δ^{13}C values were reported in shallow-rooted deciduous species of a Venezuelan seasonally tropical dry forest, when compared to foliar δ^{13}C values of deep-rooted evergreen species (Sobrado and Ehleringer 1997). They related their results to a stronger stomatal control in the shallow-rooted deciduous species. On the other hand, Medina and Francisco (1994) observed an increase in foliar δ^{13}C values toward the end of the dry season in both the evergreen *Curatella americana* and the deciduous *Godmania macrocarpa* in a Venezuelan savanna. They concluded that the similarity of WUE in both species were the result of higher photosynthetic capacity in *G. macrocarpa* and lower stomatal conductances in *C. americana*. The effects of drought on stomatal conductance are apparently similar for deciduous and evergreen cerrado trees (Bucci et al. 2004). Thus, differences between evergreen and deciduous cerrado trees in terms of WUE are probably the result of an increase in carboxylation efficiency, which could be achieved by producing new leaves with a higher N concentration. Indeed, there was a significant difference in leaf N and P between deciduous and evergreen species and a significant seasonal variation (Fig. 5b, c). The highest leaf N and P concentrations were measured in the newly mature leaves of deciduous plants that were produced at the peak of the dry season. It was also the period when the largest differences between deciduous and evergreen species were measured. The differences in terms of leaf N and P between the two phenological groups decreased during the wet season. There was also a significant relationship between leaf values of Δ and leaf N (r=0.41; P=0.026), as well as between Δ and P (r=0.48; P=0.007).

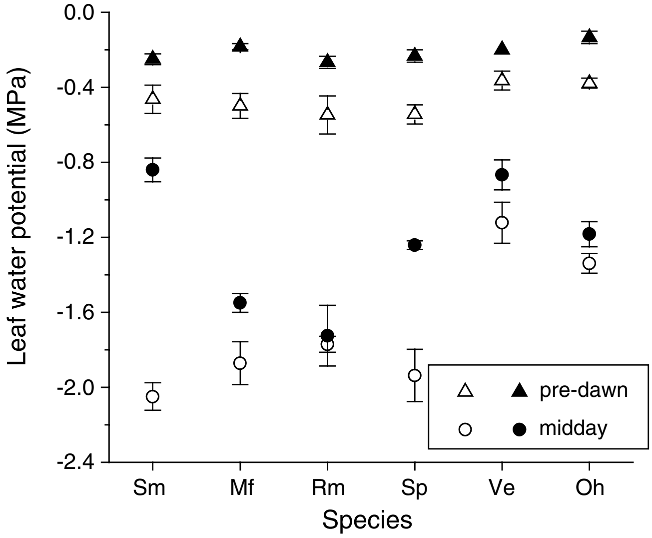


Fig. 4 Midday and predawn leaf water potentials during the dry (August 1996) and rainy season (February 1997) for six evergreen cerrado trees. Data expressed as means±1 SE (n=3–6 trees per species). *Open symbols* Measurements taken in the dry season, *solid symbols* measurements taken in the dry and wet seasons. For abbreviations, see Fig. 1

The use of leaf δ^{13}C or Δ values as an integrated measure of WUE has to be examined with caution because it depends on assumption that CO_2 concentration of the air (p_a) and leaf-to-air VPD ($e_i - e_a$) will not change seasonally:

$$\mathrm{WUE} = [p_a(1 - p_i/p_a)]/[1.6(e_i - e_a)] \qquad (1)$$

and

$$\Delta = [a + (b - a)p_i/p_a]10^{-3} \qquad (2)$$

where a and b are 4.4‰ and 27‰, respectively (Farquhar et al. 1989).

Although one can perhaps assume small seasonal variations in p_a, $e_i - e_a$ increased substantially during the drought, from about 1.48 kPa to 2.40 kPa (Fig. 3). Deciduous species would still maintain higher WUE than evergreens at the end of the dry season, if we assume that both phenological groups would have similar values of leaf-to-air VPD.

One could still expect that C return per unit dry weight invested N and C should be higher in evergreens because leaves are photosynthetically active for longer periods (Sobrado 1991) and lower amortized leaf construction costs to replace the tree crown, provided that the leaves are held by more than a year (Givnish 2002). However, maximum C return in evergreens is greatly constrained by the combined effects of partial leaf loss and reductions in photosynthetic rates during the dry season (Franco 1998) and leaf damage by herbivores and pathogens (Marquis et al. 2002). Deciduous species and several evergreens flush leaves before the rains begin (Table 1), so that the most vulnerable stage of development (the new leaf stage) has already passed by the time the herbivorous insect activity begins (Marquis

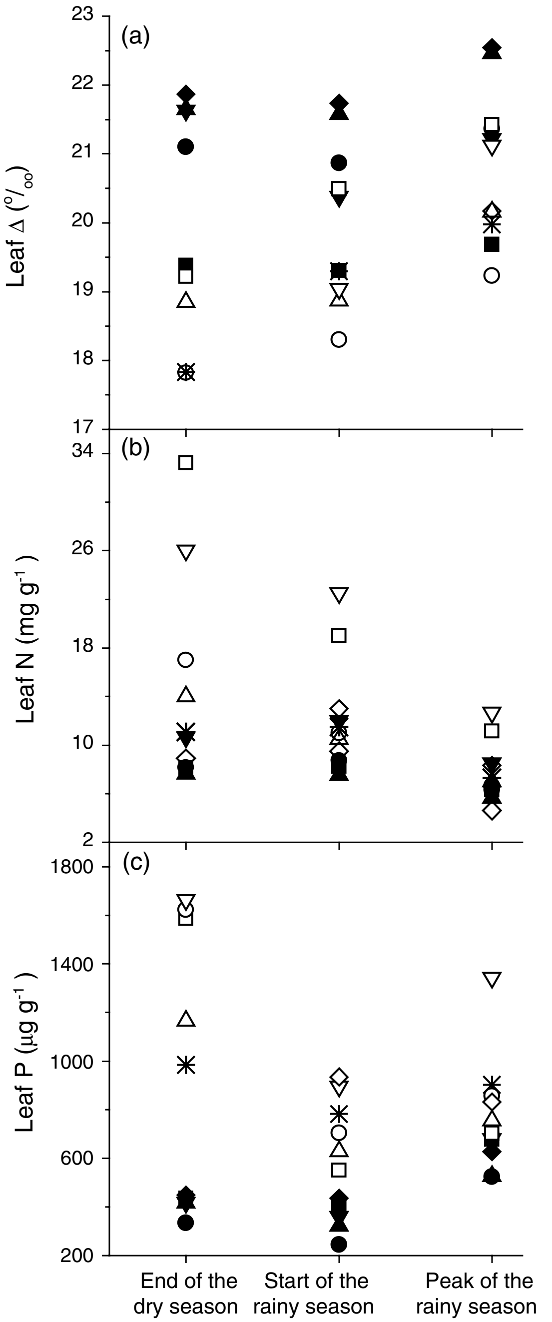


Fig. 5 Seasonal changes in leaf **a** C isotopic discrimination Δ, **b** N and **c** P concentrations for evergreen and deciduous species growing in a cerrado site at the Instituto Brasileiro de Geografia e Estatística reserve. Leaf samples were collected on 17 September or 6 October 1995 (end of dry season), 2 November 1995 (start of rainy season) and 7 March 1996 (peak of rainy season). Evergreen species: ■ *S. macrocarpa*, ● *M. ferruginata*, ▲ *R. montana*, ▼ *S. paniculatum*, *filled diamondV. elliptica*, *asteriskO. hexasperma*. Deciduous species: □ *D. miscolobium*, ○ *P. pubescens*, △ *Q. grandiflora*, ▽ *K. coriacea* ◊ *Q. parviflora*. There were statistically significant differences (P<0.05; Fisher's PSLD test) between evergreen and deciduous species in terms of leaf Δ, N and P. At the community level, leaf N concentrations were significantly different between the end of the dry period and the peak of the rainy period and between the start and the peak of the rainy period. In terms of leaf P concentrations, there were significant differences between the end of the dry and the start of the rainy season and between the start and the peak of the rainy season. There was no significant effect of seasonality on leaf Δ

et al. 2002). However, leaf damage by pathogen attack is much higher than damage by herbivores in cerrado ecosystems and fully expanded leaves continued to accrue damage throughout their lives (Marquis et al. 2001, 2002). The lower SLA of the evergreen species also suggests larger leaf construction and maintenance costs and this should also be considered (Sobrado 1991; Eamus and Prior 2001).

Total daily water loss of deciduous and evergreen species showed little seasonal variation (Meinzer et al. 1999; Bucci et al. 2004). In the case of evergreens, partial leaf loss and partial stomatal closure was enough to compensate for the increase in evaporative demand of the air during the drought period. On the other hand, this would result in a significant decrease in daily C gain at the crown level. Thus, the effect of drought on plant WUE would be even more substantial, as the tree would not reduce water loss in the dry season, but it would fix less C. On the other hand, deciduous species would have to face the higher belowground costs associated with maintaining a deep-root system that characterizes most of them (Table 1). However, deciduous species remain completely leafless for only short periods (a few weeks to <2 months) and leaf flushing occurs primarily in the late dry season (Table 1; Maia 1999; Naves 2000; Rivera et al. 2002). This allows them to quickly achieve full crown development and maximal C gain when the rains begin. Moreover, the higher leaf N and P concentrations of the newly developed crown of deciduous species would potentially allow higher photosynthetic rates than evergreen trees at the end of the dry season and during the transition from the dry to the wet period.

Some shallow-rooted deciduous and evergreens are also able to flush before the onset of the rainy season (Table 1). In this case, a tight control of transpiration by reductions in stomatal conductance and partial or total leaf shedding coupled with osmotic adjustment and internal water storage may allow the plant to stabilize water balance (Bucci 2001; Eamus and Prior 2001). It has to be pointed out that only the upper soil layers are really depleted of water (Franco 2002). On the other hand, one could expect that the onset of leaf flush in these species would be greatly constrained in dry years and that small differences in root distribution may play a critical role.

In conclusion, A_{mass} was significantly positively correlated with SLA, leaf N and P, which were higher in leaves of deciduous species. Thus, deciduous species compensated for their shorter leaf pay back period by maintaining higher potential payback capacity (higher values of maximum A_{mass}) and lower leaf construction costs (higher SLA). The short leafless period of deciduous species may also partially offset the longer payback period of evergreen species, although it may involve the higher cost of maintaining a deep-root system or a tight control of plant water balance. On the other hand, evergreens may be greatly constrained in terms of producing leaves with a long life-span, because of accrued leaf damage by herbivores and pathogens and substantial reductions in stomatal conductance and partial leaf loss to stabilise water balance during the dry season.

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