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Apparent carboxylation efficiency and relative stomatal and mesophyll limitations of photosynthesis in an evergreen cerrado species during water stress

J.A.F. MONTEIRO* and C.H.B.A. PRADO*,**

Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde,
Laboratório de Fisiologia Vegetal, Departamento de Botânica, 13565-905, São Carlos, SP, Brasil

Abstract

Miconia albicans, a common evergreen cerrado species, was studied under field conditions. Leaf gas exchange and predawn leaf water potential (Ψ_{pd}) were determined during wet and dry seasons. The potential photosynthetic capacity (P_{Npmax}) and the apparent carboxylation efficiency (ε) dropped in the dry season to 28.0 and 0.7 %, respectively, of the maximum values in the wet season. The relative mesophyll (L_m) and stomatal (L_s) limitations of photosynthesis increased, respectively, from 24 and 44 % in the wet season to 79 and 57 % at the peak of the dry season when mean Ψ_{pd} reached –5.2 MPa. After first rains, the P_{Npmax}, ε, and L_m recovered reaching the wet season values, but L_s was maintained high (63 %). The shallow root system growing on stonemason limited by lateral concrete wall to a depth of 0.33 m explained why extreme Ψ_{pd} was brought about. Thus *M. albicans* is able to overcome quickly the strains imposed by severe water stress.

Additional key words: dry and wet seasons; leaf water potential; net photosynthetic rate; root distribution; stomatal conductance.

Introduction

The Cerrado domain area extending 23 % of Brazilian territory (Ribeiro and Walter 1998) has the richest flora of the neotropical savanna woody species (Sarmiento and Monasterio 1983, Castro *et al.* 1999). The mean annual air temperature in cerrado area is between 22–26 °C, and total annual rainfall 800–1 800 mm (Nix 1983). The core region shows 2–3 months without rainfall (Franco *et al.* 1996, Franco 2002) and a maximum of 2 months free of rains take place in the Southeast area (Mattos *et al.* 1997, Prado *et al.* 2004). Most of rainfalls are distributed in October–March (Ribeiro and Walter 1998).

Evergreen, deciduous, semi-deciduous, and brevi-deciduous woody species (*sensu* Williams *et al.* 1997) co-occur in the cerrado area (Paula 2002). Despite their different deciduousness, the assimilation rate and the stomatal conductance of cerrado woody species decrease during dry season (Franco 1998, Moraes and Prado 1998, Prado *et al.* 2004). However, there are no data on carboxylation efficiency of CO_2 assimilation during dry season. At the peak of dry season the soil water potential at core area of Cerrado reaches –1.7 MPa at 0.85 m, –3.8 MPa at 0.30 m, and –6.2 MPa at 0.05 m far from the surface (Franco 2002). Jackson *et al.* (1999) showed that most of the evergreen Cerrado species could have shallow root system while the deciduous species had a deep one. In addition, the foliage that persists during Cerrado dry season must deal with high vapour pressure deficit, irradiance, and air temperature (Prado *et al.* 2004). We supposed that evergreen *Miconia albicans* (Sw) Triana, a common evergreen species of cerrado (Ratter *et al.* 1996), tolerates intense drought stress due to its leaf persistence and widespread distribution in cerrado domain. The root size and distribution of *M. albicans* were considered and related to leaf gas exchange and predawn leaf water potential during dry and wet seasons.

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**Corresponding author: fax: +55-16-33518308 e-mail: caique@power.ufscar.br

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Materials and methods

Study area: *M. albicans* usually grows in sunny areas as small tree up to 3.0 m tall. Three adult individuals (4-y-old) were considered. The experiments were carried out in the garden of the Botany Department in São Carlos Federal University (UFSCar, 22°00'S–47°30'W, 850 m a.s.l.). The individuals were cultivated on a stonemason using cerrado soil (oxisols). The area of the stonemason was 2.16 m^2 (0.9×2.4 m) limited by lateral concrete wall to a depth of 0.33 m below the soil surface. The vertical root growth was brought about free of obstruction.

Meteorological data of the National Institute of Meteorology (INMET) were obtained in station 83726 (1.0 km far from the study area).

Gas exchange measurements were carried out during 2001 at the peak (February) and at the end (May) of the rainy season; at the beginning (June) middle (July) and at the peak (August) of the dry season; and at the beginning of the following rainy season (August and October). Net photosynthetic rate (P_N) was measured as a function of the photosynthetic photon flux density, PPFD (P_N-PPFD curve) and of the external, C_e, CO_2 concentration (P_N-C_e curves). P_N as a function of sub-stomatal (internal, C_i) CO_2 concentration was calculated from P_N-C_e curves. The apparent carboxylation efficiency (ε) was determined from P_N-C_i curves, and both P_N-C_e (not shown) and P_N-C_i curves were similar. P_N was measured under PPFD = 1 600 μmol m^{-2} s^{-1} in nine leaves totally expanded (three leaves from each individual) before P_N-PPFD or P_N-C_i determinations. The leaf showing the highest P_N was chosen to perform the P_N-PPFD and the P_N-C_i curves during the morning (between 09:00–10:00 h). PPFD, C_e, C_i, leaf temperature, P_N, stomatal conductance to water vapour (g_s), and leaf transpiration rate (E) were measured by a portable infrared gas analyzer (IRGA, model *LCA-4*, *ADC*, Hoddesdon, UK), connected to a chamber (*PLCN-4*, *ADC*) and a dichroic light cannon (*PLU-002*, *ADC*, Hoddesdon, UK). During gas exchange measurements the leaf temperature was kept constant (27.1±1.2 °C) using an *ADC* Peltier system set under the head of *PLCN-4* leaf chamber. PPFD values between 800–2 000 μmol m^{-2} s^{-1} were monitored by the voltage applied (0–12 V). Bellow 800 μmol m^{-2} s^{-1}, PPFD was decreased by glass filters (*Comar Instruments*, Cambridge, UK). The P_N-PPFD curve was obtained before the P_N-C_i ones in order to estimate the saturation irradiance using Prado and de Moraes (1997) equation:

$$P_N = P_{Nmax}\,(1 - e^{-k(\mathrm{PPFD} - \mathrm{Lc})}) \tag{1}$$

where P_N [μmol m^{-2} s^{-1}], P_{Nmax} = maximum net photosynthesis [μmol m^{-2} s^{-1}], e = Euler constant, k = constant, PPFD [μmol m^{-2} s^{-1}], and L_c = compensation irradiance [μmol m^{-2} s^{-1}].

P_N-C_i curves under constant PPFD (1 600 μmol m^{-2} s^{-1}) were obtained by a gas dilutor (*GD-602*, *ADC*, Hoddesdon, UK) and a cylinder containing around 1 600 μmol mol^{-1} of CO_2 (*White Martins*, Sertãozinho, SP, Brazil) connected to the gas dilutor. *GD-602* was linked to the IRGA *LCA-4*. This set was organized as a half-open system. P_N-C_i curves were carried out under field conditions recording 7–4 values of P_N at each C_e concentration (from 20 to 1 600 μmol mol^{-1}). The initial CO_2 concentration was about 1 600 μmol mol^{-1} and each dilution resulted in 90 % of the prior CO_2 concentration. The C_i values at each external CO_2 concentration were calculated by IRGA using the equation described by Caemmerer and Farquhar (1981):

$$C_i = [(g_c - E/2)\,C'_{an} - P_N]\,(g_c + E/2)^{-1} \tag{2}$$

where C_i [μmol mol^{-1}], g_c = stomatal conductance for CO_2 diffusion [mol m^{-2} s^{-1}], E [mmol m^{-2} s^{-1}], C'_{an} = CO_2 concentration in the analyzed air [μmol mol^{-1}], dilution from transpiration corrected, P_N [μmol m^{-2} s^{-1}].

$$g_c = (1.6\,r_s + 1.37\,r_b)^{-1} \tag{3}$$

where r_s = stomatal resistance to diffusion of water vapour [mol^{-1} m^{-2} s], r_b = boundary layer resistance to diffusion of water vapour (typically 0.40 mol^{-1} m^2 s for *PLCN-4* leaf chamber).

P_N-C_i curves were corrected using the Eq. (1) replacing the component of PPFD to CO_2 component (C_i):

$$P_N = P_{Npmax}\,(1 - e^{-k(Ci - \Gamma)}) \tag{4}$$

where P_{Npmax} = potential photosynthetic capacity [μmol m^{-2} s^{-1}], e = Euler constant, k = constant, Γ = CO_2 compensation concentration [μmol mol^{-1}].

When C_i is equal to 1 600 μmol mol^{-1} (from Eq. 4), the biochemical photosynthetic process is virtually saturated by CO_2 and P_N is named potential photosynthetic capacity (P_{Npmax}, μmol m^{-2} s^{-1}, Larcher 2003). The apparent carboxylation efficiency (ε, mol m^{-2} s^{-1}), represented by the initial slope in P_N-C_i curves (Bota *et al.* 2004), was determined using the first derivation of Eq. (4):

$$\varepsilon = k\,P_{npmax}\,e^{k\Gamma} \tag{5}$$

Relative stomatal limitation of photosynthesis (L_s, %) was calculated as proposed by Farquhar and Sharkey (1982):

$$L_s = 100\,(P_N' - P_N)\,P_N'^{-1} \tag{6}$$

where P_N' = net photosynthetic rate when C_i is equal to the regular atmosphere CO_2 concentration (355 μmol mol^{-1}) in P_N-C_i curves [μmol m^{-2} s^{-1}], P_N = net photosynthetic rate at regular atmosphere CO_2 concentration (355 μmol mol^{-1}) in P_N-C_e curves [μmol m^{-2} s^{-1}]. Regular atmospheric CO_2 concentration was determined using the mean C_e value in P_N-PPFD curves (355±20 μmol mol^{-1}).

The relative mesophyll limitation (L_m, %) of photosynthesis was obtained as proposed by Jacob and Lawlor (1991):

$$L_m = 100\,(P_{NF} - P_{ND})\,P_{NF}^{-1} \qquad (7)$$

where P_{NF} = net photosynthetic rate when C_i was 1 600 μmol mol^{-1} at favourable water status of assimilation [μmol m^{-2} s^{-1}], P_{ND} = net photosynthetic rate when C_i was 1 600 μmol mol^{-1} under drought [μmol m^{-2} s^{-1}].

g_s and E were recorded by IRGA *LCA-4* during measurement of P_N-C_i curves. All g_s and E data were collected (minimum 16 and maximum 31 values per curve) between 290–450 μmol mol^{-1} of C_e during P_N-C_i curves carried out in February 13 and 15, May 28, June 4, July 5, August 13 and 28, and October 19 in 2001. External regular atmospheric CO_2 concentration was 355±20 μmol mol^{-1}. The differences among periods with respect to E and g_s were analysed with Kruskal-Wallis test (nonparametric ANOVA) and Dunn´s multiple comparison was used as posterior test.

Results

Meteorological conditions and the P_N-PPFD curve: Fig. 1 shows monthly air temperature and rainfall. Rainfall and mean air temperatures decreased in June (beginning of dry season) and increased at the end of August. 15.9 mm of rainfalls were registered during dry season between June 26 and July 28. The beginning of the rainy season happened at the end of August 2001 (34.5 mm, from August 22 to August 28). P_{Nmax} was measured in wet season (10.6 μmol m^{-2} s^{-1}, PPFD 1 500 μmol m^{-2} s^{-1}, Fig. 2).

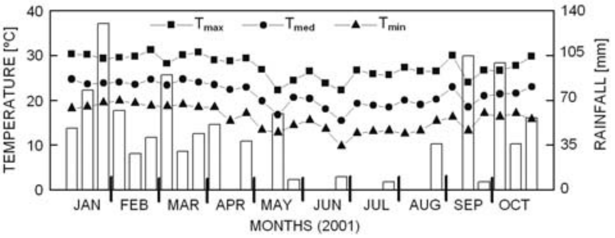

Fig. 1. Main air temperature (*symbols*) and total rainfall (*bars*) at each ten days in 2001.

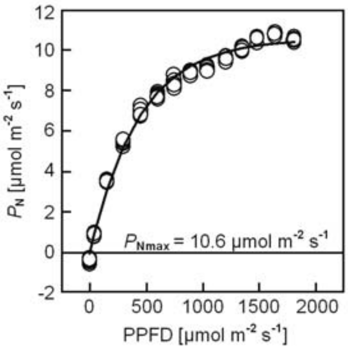

Fig. 2. Net photosynthetic rate (P_N) as a function of photosynthetic photon flux density (PPFD) in *Miconia albicans* in wet season (February 2001). P_{Nmax} = maximum net photosynthetic rate.

Water potential determinations and root system exposition: Predawn leaf water potential (Ψ_{pd}) was measured at the beginning of the rainy season and at the peak of the dry season during 2001 and 2002. Three leaves from three different individuals were used to determine Ψ_{pd} by a pressure chamber model *3005* (*Santa Barbara Soil Moisture*, Santa Barbara, USA). The three individuals of *M. albicans* growing on stonemason were separated from soil by excavation. A hole was realised with same stonemason diameter in front of the individuals in order to facilitate the root system exposition. Roots were separated from soil by water at low intensity. It was necessary to excavate to a depth of 0.50 m for exposing all root system.

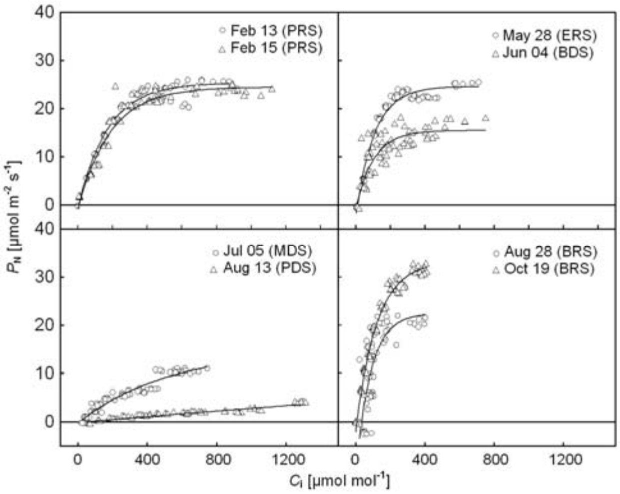

Fig. 3. Net photosynthetic rate (P_N) as a function of sub-stomatal CO_2 concentration (C_i) in *Miconia albicans* leaves during 2001 at the peak (February, PRS) and at the end (May, ERS) of the rainy season; at the beginning (June, BDS), middle (July, MDS), and at the peak (August, PDS) of the dry season; and in the beginning of the next rainy season (August and October, BRS).

Leaf gas exchange and root size: P_N-C_i curves determined during the study period are shown in Fig. 3, and measurements of leaf gas exchange obtained from these curves in Table 1. The influence of water stress and the recovery capacity after the first rains were unmistakable. The P_{Npmax}, g_s, and E were higher between the peak (February) and the end (May) of the rainy season. In June, when rainfall decreased (Fig. 1), P_{Npmax}, g_s, and E decreased (Fig. 3 and Table 1). At the peak of dry season (August 13) P_{Npmax}, g_s, and E reached the lowest values. At the beginning of the new rainy season (August 28), P_{Npmax} (22 μmol m^{-2} s^{-1}) was similar to those values observed in the prior rainy season (24-25 μmol m^{-2} s^{-1}). The

Table 1. Potential photosynthetic capacity (P_{Npmax}), stomatal conductance (g_s, mean±SD), transpiration rate (E, mean±SD), apparent carboxylation efficiency (ε), and relative mesophyll (L_m) and stomatal (L_s) limitations of photosynthesis in leaves of *Miconia albicans* during 2001. BRS = beginning of the rainy season; ERS = end of the rainy season; MDS = middle of the dry season; PDS = peak of the dry season; PRS = peak of the rainy season. Mean values±SD of g_s or E in columns followed by same letter are not significantly different ($p<0.01$).

Month/day	and period	P_{Npmax} [μmol m^{-2} s^{-1}]	g_s [mol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	ε [mol m^{-2} s^{-1}]	L_m [%]	L_s [%]
Feb/13	PRS	25.3	0.121±0.011 ab	1.86±0.11 ab	0.153	24.0	43.5
Feb/15	PRS	24.5	0.094±0.009 abcd	1.58±0.11 abc	0.137	26.4	50.0
May/28	ERS	24.6	0.099±0.009 abc	1.43±0.07 abcd	0.257	26.1	49.0
Jun/04	BDS	15.5	0.058±0.008 cde	1.15±0.12 cde	0.166	53.5	54.5
Jul/05	MDS	14.8	0.019±0.003 efg	0.56±0.07 efg	0.030	55.5	64.6
Aug/13	PDS	7.0	0.004±0.005 g	0.27±0.03 g	0.001	79.0	57.2
Aug/28	BRS	22.4	0.053±0.007 cdef	0.85±0.08 cdef	0.402	32.7	62.9
Oct/19	BRS	33.3	0.124±0.007 a	1.98±0.06 a	0.294	0.0	55.7

Fig. 4. Root system of *Miconia albicans* growing on a stonemason limited by a superficial lateral wall to a depth of 0.33 m from the soil surface. There are many thin and some thicker (indicated by hand) roots grown from central region just under the stem reaching only 0.45 m far from the soil surface.

g_s and E values followed the same P_{Npmax} trend but the recovery was postponed. *M. albicans* had shallow root system that limits its vertical soil exploration to a depth of 0.45 m (Fig. 4). In addition, the concrete wall of stonemason limited water availability to a depth of 0.33 m.

ε, L_m, and L_s limitations of photosynthesis: A great decrease of ε (from 0.17 in June to 0.03 in July) was observed only when P_{Npmax} was largely reduced under the highest L_s (65 %) amidst the dry season (Table 1). Higher values of L_m were obtained when ε decreased according to water stress. It was possible to infer from ε values that impairment of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity did not limit photosynthesis until drought was very severe.

Table 2. Mean values±SD of predawn (Ψ_{pd}) leaf water potential in *Miconia albicans* at different periods during 2001–2002. BRS = beginning of the rainy season; PDS = peak of the dry season.

Ψ_{pd} [MPa]	Month/day/year	Period
–5.20±0.50	Aug/17/2001	PDS
–0.40±0.21	Aug/30/2001	BRS
–0.60±0.15	Oct/25/2001	BRS
–4.50±0.50	Aug/23/2002	PDS
–4.70±0.90	Aug/25/2002	PDS

Ψ_{pd} and root size: *M. albicans* individuals showed striking alterations of leaf shape (data not shown). In August 17 (Ψ_{pd} = –5.2 MPa) most leaves were curled behind first rains in August 30 (Ψ_{pd} = –0.40 MPa) but these leaves returned to straight normal shape after first rains. Despite the amazing Ψ_{pd} values around –5.0 MPa at the peak of dry season in 2001–2002 (Table 2), leaves of *M. albicans* were not shed during water stress even when external factors promoting leaf abscission took place in dry season such as low temperature, water stress, and short daylight (1.5 h shorter in August than in February at 22°00'S). Individuals of *M. albicans* had a thin homogeneous root system without a central large pivot. These roots reached only to depth of 0.45 m (Fig. 4).

Discussion

Stomatal behaviour after relief of water stress was the first indication (Fischer *et al.* 1970) that g_s and E do not depend simply on immediate turgor and leaf water potential. Typically, g_s and E behaviour are strongly linked to prolonged drought (*e.g.* from February to August 13, Table 1) rather than short-term (August 13–August 28) variation in plant water status (Lösch and Schulze 1995). It means that after water stress relief the plentiful autotrophy is quickly resumed prior the maximal water expenditures. This behaviour represents great advantage to evergreen species such as *M. albicans* in the beginning of the rainy season, when they are able to use quickly the whole foliage at full assimilation capacity under limited water availability after first light rains.

The reduction of leaf gas exchange capacity by narrowing stomatal pore (lower g_s values under higher atmosphere vapour pressure deficit) was recorded under natural conditions in cerrado (Mattos *et al.* 1997, Franco 1998, Moraes and Prado 1998, Prado *et al.* 2004) and in Australian savanna woody species (Myers *et al.* 1997, Prior *et al.* 1997, Eamus 1999). In three evergreen woody species of Australian savanna the assimilation rate was reduced 10–20 % during dry season (Eamus 1999). The dominant evergreen species (*Eucalyptus miniata* A.Cunn.) in wet-dry savanna in Northern Australia had high maximum g_s value (>0.40 mol m^{-2} s^{-1}) throughout the dry season, suggesting that its roots had access to groundwater (Myers *et al.* 1997). Contrastingly, adult individuals of *M. albicans* under natural condition showed severe midday leaf gas exchange depression after 18 d of rain-free period during dry spell amidst the rainy season (Mattos *et al.* 2002). Shallow roots of this species were probably affected by superficial soil dehydration during the spell, decreasing the water uptake. On the other hand, the shallow root system is the first one to receive water supply from light rain. Prompt absorption of this water by superficial roots makes clear the rapid recovering of photosynthesis in *M. albicans* such as in August 28.

The L_m values increased in June, reached the peak value in August 13, and dropped at the first rains in August 28. With exception of August 13, the L_s values were always higher than L_m. The L_s increased slowly during dry season and it did not return to prior wet season values even in October ($L_s = 56$ %), when the highest P_{Npmax} was recorded. Stomatal limitation of photosynthesis after first rains in August 28 was a result of lower values of g_s (0.05 mol m^{-2} s^{-1}). Using Eq. (3) to calculate g_c, the mean stomatal conductance to CO_2 was two times greater in February (0.065 mol m^{-2} s^{-1}) than in August 28 (0.033 mol m^{-2} s^{-1}) after first rains. The mesophyll of *M. albicans* foliage did not represent the principal limitation of photosynthesis during the most of the dry season recovering assimilation capacity quickly after the water stress relief. Therefore, lower g_s value was the principal limitation of P_N during most part of the drought-stressed period.

Values of ε in February were similar to those from P_N-C_i curves determined by Tezara *et al.* (1998) on potted shrub *Ipomoea c*The stomatal pore narrowing with other physiological alterations in foliage were able to protect and kept working the mesophyll carboxylation at morning during great part of the dry season. *arnea* (Jacq.) free of water stress growing at the field site (0.120 mol m^{-2} s^{-1}) and between those obtained by Prado *et al.* (2005) in two young cerrado woody species growing under full solar irradiance: *Cybistax antisyphilitica* (Mart.) Mart. (0.085 mol m^{-2} s^{-1}) and *Tabebuia chrysotricha* (Mart. *ex* DC) Mart. (0.160 mol m^{-2} s^{-1}). Apparent carboxylation efficiency usually correlates with RuBPCO activity (Caemmerer 2000) and it was observed in five species with different characteristics of photosynthetic and water relations during drought-induced depression of photosynthesis (Bota *et al.* 2004). The RuBPCO activity did not change even when Ψ_{pd} reached –2.5 MPa in *Rhamnus alaternus* L., and the activity of this enzyme was 60 % at Ψ_{pd} = –3.5 MPa in *Rhamnus ludovici-salvatoris* R. Chodat (Bota *et al.* 2004). Warren and Adams (2004) argued that some evergreen trees contain more RuBPCO than required to support photosynthesis activity. It would be a manner to accumulate nitrogen without adverse osmotic or toxic effects in evergreen foliage. This assimilated nitrogen could be utilized for herbivore deterrence, growth, and photosynthesis under stress condition. Thus, ε was maintained high till the beginning of the dry season (July), or it increased quickly (after first rains, August 28) offsetting the stomatal limitations of photosynthesis by activating the excess of RuBPCO in evergreen leaves as supposed by Warren and Adams (2004).

The minimum Ψ_{pd} value obtained (–5.2 MPa) can be compared to others in evergreen species during dry season under natural conditions in cerrado vegetation such as –0.50 MPa in *Annona coriacea* Mart. and –0.70 MPa in *Rapanea umbellata* Mart. *ex* A.DC. (Mattos *et al.* 1997), or –0.47 MPa for individuals 1.1–3.4 m tall of *Roupala montana* Aubl. (Naves-Barbiero *et al.* 2000). Average value of Ψ_{pd} for 22 woody species of cerrado vegetation showing different deciduousness under natural condition recorded by Prado *et al.* (2004) was –0.35±0.21 MPa in dry season. Average leaf water potential value at midday in daily course of *Attalea exigua* Drude, a palm 1.0 m tall in Brazilian cerrado, was –3.3±0.15 MPa (Moraes *et al.* 1989); it is the lowest value of leaf water potential obtained in a cerrado woody species under natural conditions. Tree water status was considered one of the most important factors determining leaf abscission in wet-dry tropical areas (Reich and Borchert 1984). Despite external factors and striking adverse leaf water status (Ψ_{pd} around –5.0 MPa), the leaf abscission or senescence did not start in *M. albicans* during the water stress. It means that strong endogenous processes, probably involving growth regulators, were making ineffective all external (climatic factors) and some internal (leaf water status) conditions for shedding leaves during water stress. Jackson *et al.* (1999) pointed out that evergreen cerrado woody species acquired water primarily in the upper soil layer (above 0.20 m). Being evergreen and showing shallow root system *M. albicans* might be able to maintain net photosynthesis under more intense water stress. Scholz *et al.* (2002) detected negative sap flow (from the roots to the soil) during dry season in cerrado woody species with shallow roots. It also could explain why *M. albicans* reached Ψ_{pd} values as negative as –5.2 MPa at the peak of the dry season growing on stonemason.

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