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PHOTOSYNTHESIS AND WATER RELATIONS IN CERRADO VEGETATION

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Resumo:

“Fotossíntese e relações hídricas em vegetação de cerrado”

Neste artigo são discutidos alguns aspectos das relações hídricas e das trocas do CO_2 em plantas de cerrado e cerrado *stricto sensu*. A capacidade fotossintética sob condições de campo em plantas lenhosas de cerrado, expressada tanto em função da área foliar (A_{max}/A) como em função do peso específico foliar (A_{max}/W), é comparada com outros tipos de vegetação, e um possível valor de referência de A_{max}/W para esclerófilas é sugerido. Comparando-se valores da fotossíntese líquida (A), condutância estomática (g_s) e taxa de transpiração (E) nas estações seca e chuvosa, verifica-se que há uma severa restrição das trocas gasosas no período seco de inverno. Além da restrição nas trocas gasosas, as plantas perdem parcialmente as folhas (brevideciduidade), havendo diminuição do potencial osmótico das folhas remanescentes (ajuste osmótico). Plantas jovens cultivadas em vasos, quando submetidas a déficit hídrico induzido pela suspensão da rega, suportam valores relativamente baixos de potencial hídrico foliar antes de fechar os estômatos e também se ajustam osmoticamente. Fatores como a baixa umidade do ar e a ocorrência de geadas esporádicas de inverno provavelmente afetam as trocas gasosas dessas plantas, diminuindo principalmente a condutância estomática e a fotossíntese líquida.

Abstract:

We discuss some aspects of water relations and CO_2 exchange in plants of two physiognomic types of neotropical savanna called *cerrado*: *cerradão* and *cerrado stricto sensu*. Photosynthetic capacity under field conditions in *cerrado* woody plants, expressed on the basis of leaf area (A_{max}/A) and weight (A_{max}/W), is compared to that of other types of vegetation. A possible A_{max}/W reference value for sclerophylls is proposed. Comparing the values of net photosynthesis (A), stomatal conductance (g_s) and transpiration rate (E) in dry season and wet season, we observed a severe restriction of gas exchange during the dry period in the winter. Additionally, there is partial leaf fall and a decrease of osmotic potential of the remaining leaves (osmotic adjustment) in response to water stress. Young potted plants when submitted to water stress, by suppression of watering, can stand relatively low values of leaf water potential before the closure of stomata and are also able to adjust osmotically. Low air humidity and the occurrence of sporadic frosts in winter probably affect gas exchange in these plants, reducing stomatal conductance and photosynthesis.

Introduction

The *cerrado* vegetation is a neotropical savanna which originally covered approximately 1,800,000 Km² of the Brazilian territory. According to Coutinho (1978), this vegetation is formed by a mosaic of physiognomic types: *campo limpo* (low biomass type), *campo sujo*, *campo cerrado*, *cerrado stricto sensu* and *cerradão* (high biomass type). The soil is oligotrophic with high aluminium content (Goodland & Pallardy, 1983) and drought occurs seasonally (Nix, 1983) from June to September.

In this article we discuss some aspects of water relations and CO₂ gas exchange in *cerradão* and *cerrado stricto sensu* species with the following objectives: (a) determination of the photosynthetic capacity under field conditions and comparison of these values with other vegetation types; (b) determination of daily courses of net photosynthesis, stomatal conductance, transpiration rate, water potential and a comparison of these values between rainy and dry seasons; and (c) CO₂ gas and water vapor exchange in young potted plants under water stress conditions.

Photosynthetic capacity

According to Larcher (1995) the maximal rate of CO₂ uptake under natural conditions of atmospheric CO₂ concentration and optimal conditions with respect to all other environmental factors is a constitutional characteristic of certain groups and species of plants. This capability for net photosynthesis is termed photosynthetic capacity and can be expressed quantitatively by specific maximal values (A_{max}) under natural conditions of CO₂ supply.

Prado (1994) determined the curve of photosynthesis as a function of photosynthetic active radiation (PAR) in 20 woody *cerrado* species under field conditions during clear days in the rainy season. Table 1 shows the values of photosynthetic capacity expressed on a leaf area basis (A_{max}/A), PAR for saturation of 90% of A_{max} , light compensation point (LCP) and leaf temperature at light compensation point (T). Most values of LCP and PAR for saturation of 90 % of A_{max} are between 20 - 40 mmol m⁻² s⁻¹ and 600 - 900 mmol m⁻² s⁻¹ respectively, and are similar to those found in sunleaves of deciduous species cited by Larcher (1995).

The A_{max}/A values are 90 % between 6 - 14 mmol m⁻² s⁻¹. This range is similar to that (3.8 - 15.5 mmol m⁻² s⁻¹) found in 11 *cerrado* species by several authors (Franco, 1983; Johnson *et al.*, 1983; Netto & Hay, 1986; Mattos, 1992; Kanno, 1993). Studies of 6 savanna species (San José, 1977; Ferrar, 1980; Cresswell *et al.*, 1982; Sarmiento *et al.*, 1985) showed similar A_{max}/A values (3.6 - 11.7 mmol m⁻² s⁻¹).

Table 1. Photosynthetic capacity expressed on a leaf area basis (A_{max}/A) and on a leaf weight basis (A_{max}/W), photosynthetic active radiation (PAR) for saturation of 90% of A_{max} , light compensation point (LCP) and leaf temperature at light compensation point (T) in 20 woody cerrado species (data from Prado, 1994).

Species	A_{max}/A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	A_{max}/W ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	LCP/T ($\mu\text{mol m}^{-2} \text{s}^{-1}$)/ $^{\circ}\text{C}$
<i>Aegiphyla lhotzkiana</i>	9.4	0.079	868	46 / 29.1
<i>Annona coriacea</i>	9.3	0.062	1079	33 / 28.0
<i>Aspidosperma tomentosum</i>	10.2	0.072	637	15 / 29.7
<i>Bauhinia holophylla</i>	10.4	0.073	803	36 / 28.0
<i>Bowdichia virgilioides</i>	9.2	0.055	718	21 / 24.4
<i>Campomanesia aromatica</i>	10.5	0.070	646	24 / 28.5
<i>Caryocar brasiliense</i>	9.4	0.079	782	40 / 30.4
<i>Connarus suberosus</i>	12.2	0.082	817	24 / 28.0
<i>Davilla rugosa</i>	10.2	0.062	802	35 / 27.9
<i>Didymopanax vinosum</i>	17.6	0.119	1250	39 / 28.6
<i>Duguetia furfuracea</i>	9.7	0.060	668	29 / 25.8
<i>Gochnatia floribunda</i>	16.2	0.096	878	26 / 27.9
<i>Kielmeyera coriacea</i>	10.5	0.051	1185	34 / 26.0
<i>Miconia albicans</i>	12.9	0.084	817	24 / 25.5
<i>Miconia ligustroides</i>	14.0	0.107	804	11 / 28.0
<i>Piptocarpha rotundifolia</i>	12.3	0.077	696	39 / 29.4
<i>Qualea dichotoma</i>	10.9	0.076	801	34 / 26.9
<i>Styrax camporum</i>	8.1	0.039	692	35 / 33.2
<i>Tibouchina stenocarpa</i>	19.8	0.145	1224	13 / 27.2
<i>Tocoyena formosa</i>	6.5	0.041	753	11 / 30.1
Mean Values	11.5	0.076	846	28 / 28.1

Cerrado species are sclerophyllous (Goodland & Ferri, 1979) and have higher A_{max}/A values than those of sclerophyllous plants of periodically dry regions ($4 - 10 \text{ mmol m}^{-2} \text{ s}^{-1}$; Larcher, 1995). The range of $6 - 14 \text{ mmol m}^{-2} \text{ s}^{-1}$ is similar to that of woody deciduous species (Korner *et al.*, 1979; Larcher, 1995). On the other hand, these A_{max}/A values for woody cerrado plants are higher than those of woody evergreen species (Korner *et al.*, 1979; Salisbury & Ross, 1992; Larcher, 1995), and lower than those of C_3 annuals (Mooney *et al.*, 1981; Hull & Mooney, 1990). Fig. 1 shows a comparison of the average values of A_{max}/A between these phenological groups. The average values of A_{max}/A decrease in the following order: C_3 annuals, cerrado, deciduous and evergreen species.

Expressing A_{max} on a weight basis (A_{max}/W) by dividing A_{max}/A by the specific leaf weight (SLW), it appears that 80% of these values are between $0.030 - 0.040 \text{ mmol g}^{-1} \text{ dw s}^{-1}$ (Table 1). When compared with those of evergreen sclerophyllous species (Mooney, 1981; Field *et al.*, 1983; Mooney *et al.*, 1983; Wagner *et al.*, 1993), these values are still higher. But a comparison of the A_{max}/W of the four phenological groups previously mentioned shows that these values are lower than those of woody deciduous plants (Fig. 2).

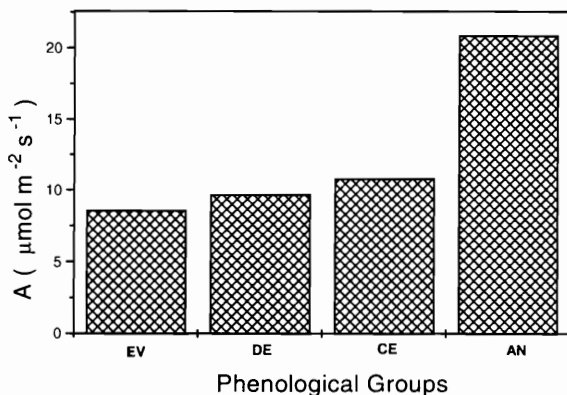


Fig. 1. Average values of photosynthetic capacity expressed on a leaf area basis (A_{max}/A) for 61 evergreen sclerophyllous species (EV); 46 deciduous species (DE); 28 cerrado species and 20 C_3 annual species (AN). Data of cerrado species from Kanno (1993) and Prado (1994). Data of EV, DE and AN compiled by Prado (1994) from several authors.

Considering that cerrado woody species are sclerophyllous and that A_{max}/W is between sclerophyllous evergreen and deciduous species, we can corroborate observations on the brevideciduousness of woody neotropical savanna species (Sarmiento & Monasterio, 1983) and leaf fall in cerrado vegetation during the dry season (Rizzo *et al.*, 1971; Barros & Caldas, 1980; Mantovani, 1983; Mattos, 1992; Paulilo & Felipe, 1992), suggesting that these woody cerrado plants could be considered as sclerophyll-brevideciduous.

Fig. 2 shows that there is a negative relationship between leaf lifespan (2, 6, 16 months for annuals, deciduous and evergreen species, respectively, according to Mooney & Gulmon (1982) and 12 months for neotropical savanna woody species, according to Sarmiento & Monasterio (1983)) and A_{max}/W in the four phenological groups. Fig. 2 also shows a positive relationship between leaf lifespan and SLW. These results suggest a possible relationship between SLW and A_{max}/W : as SLW increases (higher sclerophyllly) A_{max} decreases, as demonstrated by Reich & Walters (1992) for a broad range of different species and plant life forms.

Fig. 3 correlates A_{max}/W with sclerophylly (SLW) by showing a compilation of 84 values including C_3 annuals, deciduous, sclerophyllous evergreen and cerrado species. As expected, A_{max}/W is negatively related to SLW.

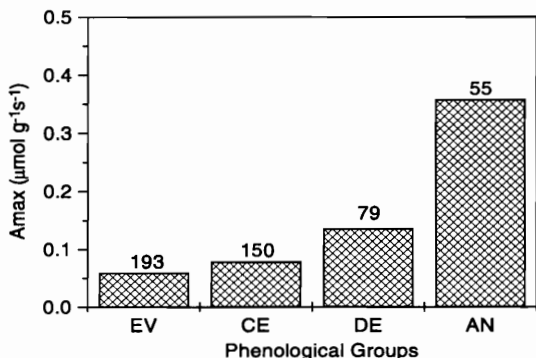


Fig. 2. Average values of photosynthetic capacity expressed on a leaf dry weight basis (A_{max}/W) for 18 evergreen sclerophyllous species (EV); 23 cerrado species (CE); 25 deciduous species (DE) and 13 C_3 annual species (AN). Values of average SLW (Specific Leaf Weight) for each phenological group are shown above the columns. Data on cerrado vegetation from Kanno (1993) and Prado (1994). Data on EV, DE and AN compiled by Prado (1994) from several authors.

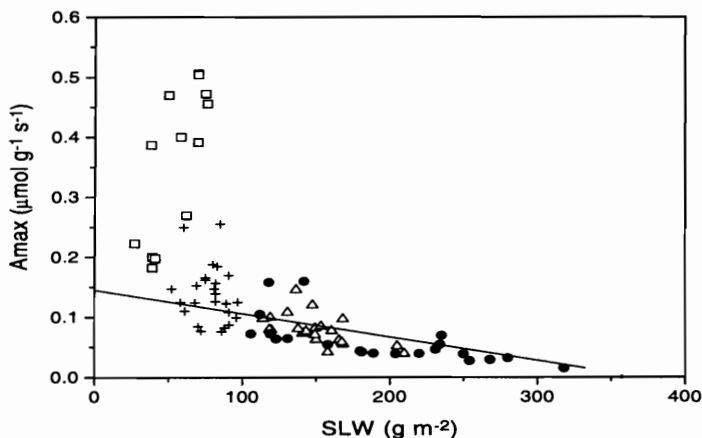


Fig. 3. Relationship between photosynthetic capacity expressed on a leaf dry weight basis (A_{max}/W) and specific leaf weight (SLW) in 21 evergreen sclerophyllous species (●); 23 cerrado species (Δ); 25 deciduous species (+) and 13 C_3 annual species (□). A_{max}/W reference value for sclerophylly ($0.143 \text{ mmol g}^{-1} \text{ s}^{-1}$) was determined by extrapolating the linear regression of the points corresponding to the values of SLW from 131 to 320 g m^{-2} to the Y axis. Data on cerrado vegetation from Kanno (1993) and Prado (1994). Data on EV, DE and AN compiled by Prado (1994) from several authors. $A_{max}/W = -0.004\text{SLW} + 0.143$; $n = 34$, $r^2 = 0.439$, $P < 0.01$. See text for explanation.

Prado (1994) established a possible A_{max}/W reference value for sclerophyllly using the values of photosynthetic capacity of Fig. 3. This value represents a critical point: above this value we have the species with lower SLW and higher A_{max}/W (C_3 annuals and most deciduous plants); below this value we have the species with higher SLW and lower A_{max}/W (evergreen sclerophyllous and most woody cerrado plants). This reference value ($0.143 \text{ mmol g}^{-1} \text{ dw s}^{-1}$) was determined in Fig. 3 by extrapolating the linear regression of the points corresponding to the lowest mean value of SLW for sclerophyllous species described (131 g m^{-2} ; Medina *et al.*, 1990) and the highest one (320 g m^{-2} ; Mooney & Gulmon, 1982) to the Y axis. According to this interpretation, A_{max}/W in sclerophyllous species would probably be lower than $0.143 \text{ mmol g}^{-1} \text{ w s}^{-1}$ and higher in non-sclerophyllous species.

These four phenological groups are also characterized by the relationship between leaf nitrogen (% of dry weight) and SLW (Fig. 4). The degree of sclerophyllly has been related to the nutritional status of the leaf (Arens, 1958a,b; Loveless, 1961; 1962; Goodland & Ferri, 1979; Sobrado & Medina, 1980): the lower the nutritional status of the leaf the higher the degree of sclerophyllly.

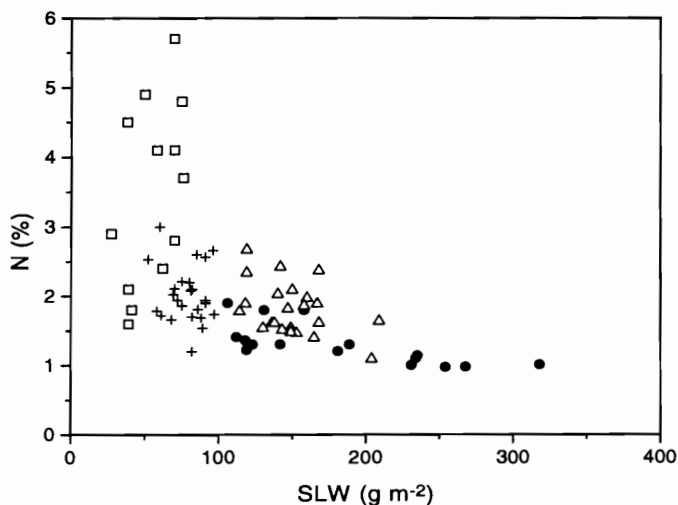


Fig. 4. Relationship between leaf nitrogen (% of dry weight) and specific leaf weight (SLW) in 16 evergreen sclerophyllous species (●); 23 cerrado species (Δ); 24 deciduous species (+) and 13 C_3 annual species (□). Data on cerrado vegetation from Kanno (1993) and Prado (1994). Data on EV, DE and AN compiled by Prado (1994) from several authors. $N (\%) = 3.35 * e^{0.0067 * SLW} + 0.129$, $n = 79$, $r^2 = 0.341$, $P < 0.01$.

Daily and seasonal courses of gas exchange and water potential

Using different approaches Moraes *et al.* (1989) and Perez & Moraes (1991a, b) (Diffusion Porometer) and Mattos (1992) (Infrared Gas Analyzer) studied daily and seasonal courses of net photosynthesis (A), water potential (Ψ), osmotic potential (π), stomatal conductance (gs), transpiration rate (E) and relative water content (RWC) in several species of cerrado vegetation. These authors observed a marked decrease in A, gs, π , E and RWC during the dry season (from June to September). Minimum water potential values also decreased during the dry period, with the exception of *Oxalis hirsutissima* where these values were practically unchanged during the whole year. Kanno (1993) also observed a pronounced decrease of A, gs and E in three cerrado *stricto sensu* species during the dry season, but did not observe seasonal variations in the values of Ψ . These values are summarized in Table 2, where percent decrease of these parameters in the dry season, in relation to the wet season, was calculated.

Table 2. Decrease (%) of the average values of net photosynthesis (A), stomatal conductance (gs), osmotic potential (π), water potential (Ψ) and relative water content (RWC) in daily courses during the dry season (June - September) in relation to the rainy season (October - March) from 8:00 to 16:00 h in cerrado plants. Data calculated from: Moraes *et al.* (1989*); Perez & Moraes (1991a, b**); Mattos (1992***) for cerrado species and Kanno (1994****) for cerrado *stricto sensu* species.

Species	A	gs	Ψ	π	RWC
<i>Attalea exigua</i> *	-	25.0	25.3	-	30.2
<i>Didymopanax vinosum</i> *	-	76.5	72.4	-	6.2
<i>Oxalis hirsutissima</i> *	-	56.1	0	-	11.9
<i>Pterodon pubescens</i> *	-	77.8	33.2	-	11.3
<i>Serjania lethalis</i> *	-	82.8	33.8	-	14.1
<i>Xylopia aromatica</i> *	-	77.0	19.0	-	13.6
<i>Byrsonina intermedia</i> **	-	27.3	84.7	-	-
<i>Copaifera langsdorfii</i> **	-	40.0	77.6	45.0	29.1
<i>Erythroxylum suberosum</i> **	-	36.4	156.5	61.0	-
<i>Lippia lupulina</i> **	-	53.8	127.5	-	-
<i>Miconia stenostachia</i> **	-	61.5	30.6	-	-
<i>Ocotea pulchella</i> **	-	20.0	103.6	-	36.0
<i>Panicum sp</i> **	-	93.3	138.7	-	-
<i>Psychotria capitata</i> **	-	50.0	129.4	53.0	-
<i>Rapanea guianensis</i> **	-	58.3	28.6	-	11.6
<i>Copaifera langsdorfii</i> ***	19.3	59.1	-	-	-
<i>Rapanea umbellata</i> ***	41.1	72.7	-	-	-
<i>Xylopia aromatica</i> ***	44.9	74.4	-	-	-
<i>Anacardium nanum</i> ****	19.0	64.2	-	-	-
<i>Andira humilis</i> ****	62.3	90.3	-	-	-
<i>Eriotheca gracilipes</i> ****	35.12	66.7	-	-	-

J.A.P.V. Moraes & C.H.B.A. Prado (unpubl. data) studied diurnal courses of net photosynthesis, stomatal conductance and transpiration rate in 17 species of cerrado *stricto sensu* in September (peak of the dry season), October (beginning of the rainy season) and March (peak of the rainy season) utilizing an infrared gas analyzer. Selected examples (*Bauhinia holophylla* and *Eriotheca gracilipes*) are shown in Fig. 5. Table 3 shows the average values obtained between 8:00 and 14:00 h for each species in the three periods of the year. There is a pronounced decrease of A, gs and E values during the dry season. In October, even after the beginning of the rainy period, the values of A, gs and E, although higher than those of the dry season, are still lower than those of the rainy season. By comparing the means of these average values, it appears that for the 17 studied species, net photosynthesis, stomatal conductance and transpiration rates are statistically higher in the rainy season, lower in the dry season and intermediary at the beginning of the rainy season. In Table 4, the average values of these parameters were selected in relation to morning values (from 8:00 to 11:00 h) and midday values (from 12:00 to 15:00 h) both in the rainy and in the dry season. A, gs and E decrease during the midday period when temperature is higher and air humidity is lower (Moraes *et al.*, 1989; Perez & Moraes (1991a, b), as observed in many trees (Larcher, 1995). The midday depression is more accentuated in the dry season. Photosynthesis and stomatal conductance are more affected than transpiration. In the rainy season, only the mean values of E were not statistically different between morning and midday values, due to higher water saturation deficit in the atmosphere at this time, counterbalancing lower values of gs.

Low temperature stress can also occur during the dry season in the cerrado vegetation in southeastern Brazil. Perez & Moraes (1983) observed that water-vapor exchange in 3 woody cerrado species (*Didymopanax vinosum*, *Xylopia aromatica* and *Pterodon pubescens*) was strongly affected by a severe frost that occurred in July, 1981 (minimal temperature: -2.3°C). Stomatal conductance was practically null during several days. With the exception of *X. aromatica* that lost all leaves, the stomata became functional again, about 15 days later. So, chilling effects can sometimes superimpose the effects of drought stress.

The above results indicate that there are substantial changes in leaf water status during the dry season in several cerrado species. Brevideciduousness of woody species is also probably due to water stress. Furthermore, restrictions on net photosynthesis, transpiration, and stomatal conductance found during the dry season disagree with results obtained by Ferri (1979), who did not observe transpiration restriction in cerrado species in any period of the year.

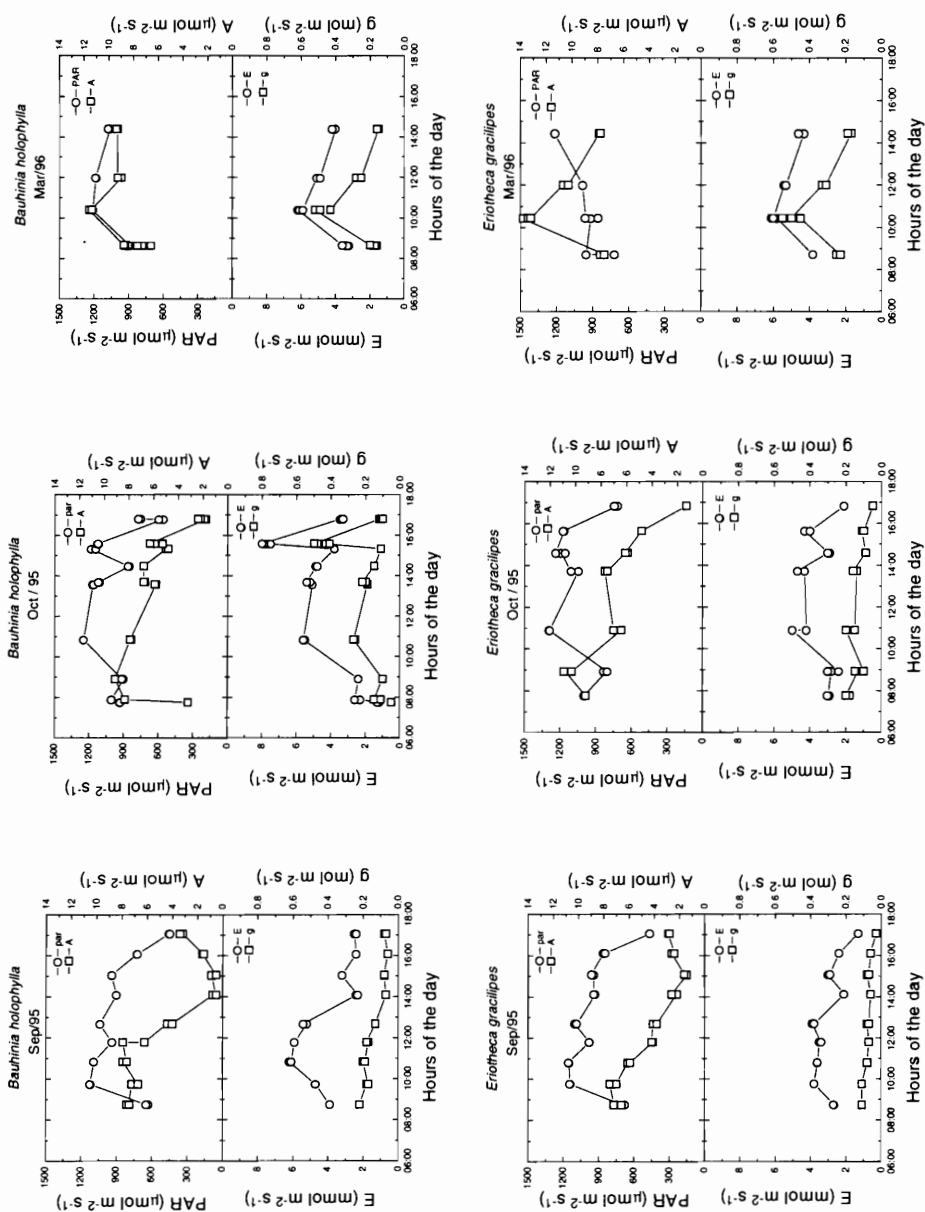


Fig. 5 - Diurnal courses of net photosynthesis (A), stomatal conductance (g), transpiration rate (E) and photosynthetic active radiation (PAR) in "cerrado" species in September (peak of dry season), October (beginning of rainy season) and March (peak of rainy season).

Table 3. Comparison of the average values (from 8:00 to 14:00 h) of net photosynthesis (A), stomatal conductance (gs) and transpiration rate (E) of cerrado species during the months September (peak of dry season), October (beginning of the rainy season) and March (peak of the rainy season). Means of these average values for all 17 plants are shown in each column. All means (different letters) are statistically different at the 5 % level (J.A.P.V. Moraes & C.H.B.A. Prado, unpubl. data).

Species	A ($\mu\text{mol m}^{-2}\text{s}^{-1}$)			gs ($\text{mol m}^{-2}\text{s}^{-1}$)			E ($\text{mmol m}^{-2}\text{s}^{-1}$)		
	Sep	Oct	Mar	Sep	Oct	Mar	Sep	Oct	Mar
<i>Anacardium nanum</i>	3.23	5.59	9.55	0.092	0.132	0.364	2.85	3.63	4.91
<i>Annona coriacea</i>	5.51	5.11	9.05	0.190	0.128	0.326	5.16	3.78	5.19
<i>Bauhinia holophylla</i>	4.54	6.41	9.02	0.138	0.208	0.255	4.24	4.63	4.35
<i>Campomanesia aromatica</i>	5.09	6.02	10.74	0.109	0.104	0.479	3.11	3.23	5.11
<i>Casearia silvestris</i>	1.48	4.85	6.04	0.036	0.128	0.151	1.55	3.80	4.30
<i>Diospyrus sp.</i>	1.84	3.07	3.44	0.139	0.182	0.389	3.98	4.49	5.95
<i>Duguetia furfuracea</i>	4.59	3.94	9.24	0.105	0.103	0.412	3.68	3.38	5.35
<i>Eriotheca gracilipes</i>	4.33	7.27	10.27	0.080	0.132	0.331	3.11	3.56	5.01
<i>Heteropterys byrsonimifolia</i>	2.20	3.52	7.99	0.074	0.170	0.240	2.87	4.31	4.48
<i>Kielmeyera coriacea</i>	3.29	8.92	9.40	0.141	0.182	0.290	3.49	4.19	5.16
<i>Miconia albicans</i>	4.96	4.35	11.34	0.048	0.096	0.369	1.68	3.08	4.44
<i>Miconia ligustroides</i>	6.57	7.52	6.36	0.086	0.137	0.112	3.59	3.70	2.88
<i>Myrcia rufipes</i>	2.30	4.39	9.77	0.059	0.181	0.217	2.33	4.65	4.35
<i>Ouratea spectabilis</i>	3.39	5.99	6.36	0.095	0.159	0.194	2.81	3.89	3.89
<i>Piptocarpha rotundifolia</i>	7.29	8.85	9.97	0.288	0.476	0.434	5.56	5.51	4.96
<i>Stryphnodendron barbadetiman</i>	2.56	6.24	6.75	0.083	0.213	0.390	2.71	4.45	6.18
<i>Tibouchina stenocarpa</i>	3.26	7.07	7.32	0.099	0.350	0.705	2.86	5.66	5.62
MEAN VALUES	3.91a	5.83b	8.39c	0.110a	0.181b	0.333c	3.27a	4.11b	4.83c

Table 4. Comparison of the average values of net photosynthesis (A), stomatal conductance (gs) and transpiration rate (E) in cerrado species in two periods of the day (from 8:00 h and from 12:00 to 15:00 h) during the rainy and during the dry season. Means of these average values for all 17 plants are shown in each column. Different letters indicate that the means are statistically different at the 5% level (J.A.P.V. Moraes & C.H.B.A. Prado, unpubl. data).

Species	March (Rainy Season)						September (Dry Season)					
	A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		gs ($\text{mol m}^{-2} \text{s}^{-1}$)		E ($\text{mmol m}^{-2} \text{s}^{-1}$)		A ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		gs ($\text{mol m}^{-2} \text{s}^{-1}$)		E ($\text{mmol m}^{-2} \text{s}^{-1}$)	
	8-11h	12-15h	8-11h	12-15h	8-11h	12-15h	8-11h	12-15h	8-11h	12-15h	8-11h	12-15h
<i>Anacardium nanum</i>	9.75	9.35	0.38	0.35	4.28	5.55	6.00	1.57	0.14	0.07	3.40	2.60
<i>Annona coriacea</i>	9.97	7.94	0.36	0.29	5.10	5.30	9.13	4.35	0.20	0.20	6.10	5.40
<i>Bauhinia holophylla</i>	9.97	9.25	0.33	0.21	4.75	4.55	7.40	2.43	0.20	0.10	4.92	3.83
<i>Campomanesia aromatica</i>	11.62	9.99	0.53	0.43	4.87	5.31	6.95	3.45	0.14	0.10	3.10	3.10
<i>Casearia silvestris</i>	6.80	5.53	0.22	0.10	5.38	3.58	3.55	1.05	0.07	0.03	2.10	1.55
<i>Diospyrus sp.</i>	4.68	2.62	0.55	0.28	6.15	5.82	6.85	0.75	0.12	0.12	3.45	3.68
<i>Duguetia furfuracea</i>	9.85	8.33	0.47	0.32	5.25	5.50	6.33	4.80	0.13	0.11	4.23	4.20
<i>Eriotheca gracilipes</i>	11.14	9.18	0.40	0.25	5.10	4.90	6.72	3.18	0.10	0.07	3.37	2.98
<i>Heteropterys byrsonimifolia</i>	10.72	6.04	0.30	0.20	4.88	4.19	4.40	0.76	0.12	0.05	4.40	2.16
<i>Kielmeyera coriacea</i>	10.28	8.53	0.40	0.18	5.73	4.60	3.68	2.80	0.31	0.08	5.28	2.70
<i>Miconia albicans</i>	13.40	10.90	0.61	0.25	5.65	4.37	9.38	3.75	0.08	0.04	2.25	1.54
<i>Miconia ligustroides</i>	5.67	6.55	0.13	0.10	2.73	2.87	8.38	5.04	0.10	0.07	4.08	3.12
<i>Myrcia rufipes</i>	10.20	9.26	0.23	0.20	4.20	4.54	4.55	0.58	0.08	0.04	2.85	2.05
<i>Ouratea spectabilis</i>	7.30	7.15	0.26	0.16	4.83	3.95	5.80	3.30	0.23	0.03	4.75	1.50
<i>Piptocarpha rotundifolia</i>	11.50	8.10	0.56	0.18	5.38	3.90	9.66	5.44	0.36	0.25	6.38	5.09
<i>Stryphnodendron barbadetiman</i>	7.42	6.20	0.38	0.40	5.88	6.43	5.95	4.23	0.16	0.13	4.00	3.83
<i>Tibouchina stenocarpa</i>	8.20	7.10	0.60	0.39	5.54	5.40	6.15	1.62	0.20	0.05	3.72	1.97
MEAN VALUES	9.32a	7.77b	0.39a	0.25b	5.04a	4.75a	6.52a	2.89b	0.16a	0.09b	4.02a	3.02b

Gas exchange in young plants

Adult plants of cerrado vegetation have deep root systems (Rawitscher, 1948), but the root systems of young plants germinated from seeds are probably restricted to the upper layer of the soil during the first dry season; in spite of these shallow root systems, young plants must overcome dry periods under field conditions.

The limit of Ψ for complete closure of stomata obtained in young plants of several cerrado species (Table 5) ranged from - 2.7 to - 3.9 MPa and is similar to that found for adult sclerophyllous plants (- 3.0 to -5.0 MPa; Larcher, 1995).

Osmotic potential in potted plants of cerrado and cerrado also changed after induced water stress (Table 6). Osmotic adjustment is an important mechanism of plant survival during periods of stress, because the plant can maintain tissue turgor which, in turn, enables plants to maintain processes such as cell enlargement and stomatal opening in a wide-ranging variation of Ψ .

Table 5. Critical leaf water potentials ($\Psi_A = 0$) for null net photosynthesis in young potted plants of cerrado species during water stress induced by interruption of watering. * determinations by colorimetric method; ** determinations by infrared gas analyzer.

Species	Age (months)	$\Psi_A = 0$ (MPa)	Authors
<i>Anadenanthera falcata</i>	8	- 3.0*	Sato & Moraes (1992)
<i>Bauhinia rufa</i>	3	- 3.5*	Sato & Moraes (1992)
<i>Copaifera langsdorffii</i>	6	- 3.5**	Prado <i>et al.</i> (1994)
<i>Cybistax antisyfilitica</i>	8	- 2.7*	Sato & Moraes (1992)
<i>Serjania caracasana</i>	8	- 3.9*	Sato & Moraes (1992)
<i>Stryphnodendron adstringens</i>	6	- 2.7**	Rocha (1994)

Table 6. Values of osmotic potential (π) and osmotic adjustment (% $\Delta\pi$) in young potted cerrado plants before and after water stress induced by interruption of watering.

Species	Age (month)	π (MPa) before water stress	π (MPa) after water stress	% $\Delta\pi$	Authors
<i>Copaifera langsdorffii</i>	6	- 1.89	- 2.04	8	Prado (1991)
<i>Distictella mansoana</i>	7	- 0.90	- 1.45	61	Rubin Filho & Moraes (1996)
<i>Serjania caracasana</i>	7	- 1.40	- 1.61	15	Rubin Filho & Moraes (1996)
<i>Stryphnodendron adstringens</i>	6	- 1.59	- 1.94	22	Rocha (1994)

Another factor that could affect gas exchange in cerrado plants is low air humidity. This situation can occur in the summer (rainy season) when the temperature is very high at midday, or during winter (dry season) when relative humidity is also very low at midday, as observed by Moraes *et al.* (1989) and Perez & Moraes (1991 a, b).

Prado *et al.* (1995) observed in young potted plants of *Copaifera langsdorffii* that when leaf - air water vapor concentration difference (ΔW) increased during the day, stomatal conductance (g_s), net photosynthetic rate (A) and water use efficiency (WUE) decreased in both control and water stressed plants. Moderate ΔW induced lower values of g_s and A in unwatered than in the control plants. High ΔW in the atmosphere resulted in a strong reduction of g_s (from 0.22 to 0.01 $\text{mol m}^{-2} \text{s}^{-1}$) and A (from 6.5 to 0.7 $\text{mmol m}^{-2} \text{s}^{-1}$) in control plants around midday, with recovery of Ψ (Fig. 6).

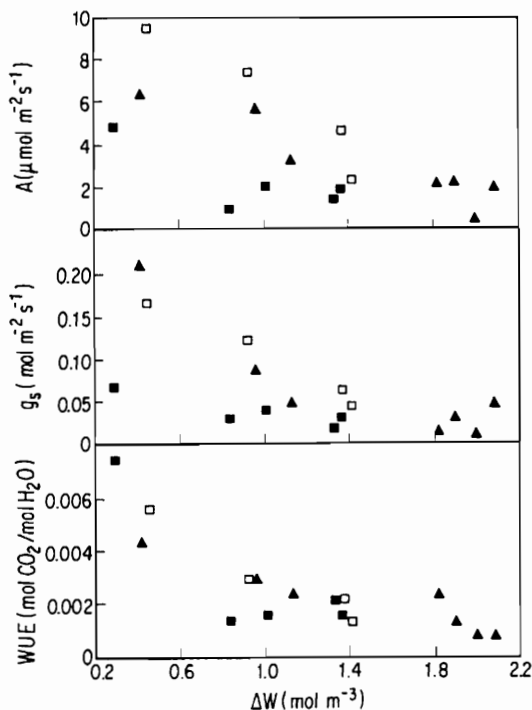


Fig. 6. Net photosynthesis (A), stomatal conductance (g_s) and water use efficiency (WUE) in young potted plants of *Copaifera langsdorffii* (6 month old) as function of leaf-air water vapor concentration difference (ΔW). All values were obtained in daily courses under different water stress conditions: \square = maximum ΔW 1.4 mol m^{-2} without soil water stress (predawn leaf water potential -0.6 MPa); \blacksquare = maximum ΔW 1.4 mol m^{-2} with soil water stress (predawn leaf water potential -1.8 MPa); \blacktriangle = maximum ΔW 2.1 mol m^{-2} without soil water stress (predawn water potential -0.6 MPa). Data from Prado *et al.* (1995).

ΔW is a minor problem for adult plants with deep roots in the cerrado area but young plants have additional soil water stress. Therefore, a sensitive response of g_s to low air humidity could be an adaptive feature that maintains leaf water status during some diurnal hours, enabling assimilation at least in early morning and afternoon.

Final remarks

The brevideciduousness of woody cerrado plants is probably a mechanism to avoid dry periods of winter (June to September). The reduction of the transpiring system of the plant is the most obvious mechanism to avoid drought.

Several reports have shown that stomatal conductance and net photosynthesis values of woody cerrado plants decrease during the dry season under field conditions (Moraes *et al.*, 1989; Perez & Moraes, 1991a; Mattos, 1992; Kanno, 1993; J.A.P.V. Moraes & C.H.B.A. Prado, unpubl. data). Vapor pressure deficit between leaf and atmosphere can also decrease water vapor and CO_2 gas exchange in young woody cerrado species (Prado *et al.*, 1995).

However, mechanisms of drought tolerance were also registered for some woody cerrado species such as osmotic adjustment (Perez & Moraes, 1991) and stomatal closure only at low values of water potential during induced water stress in young plants (Sato & Moraes, 1992; Prado *et al.*, 1994). Young plants were also able to adjust osmotically in response to induced periods of drought (Rocha, 1994; Rubin Filho & Moraes, 1996).

Therefore, cerrado species are able to activate several drought resistance mechanisms keeping pace with drought intensity during the dry season: a) leaf fall, b) decrease of stomatal conductance and c) osmotic adjustment. These mechanisms enable them to maintain autotrophy in the remaining leaves, improving their carbon balance under several stress factors.

Chapin (1991) suggests that all plants respond to environmental stress basically in the same way: through a decline in growth rate and in the rate of acquisition of all resources. Some of these traits are observed in species that have been adapted evolutionarily to low-resource environments and in any plants that have been adjusted physiologically to a low resource supply.

Cerrado species experience large seasonal and daily fluctuations in air temperature and soil and atmospheric moisture. Moreover, these species also need to overcome high aluminium availability, low pH values and poor nutrient supply as edaphic stress factors. This stressful scenario causes decline in growth rate and in the rate of acquisition of all resources as proposed by Chapin (1991) for species that are continuously encountering new combinations of environmental stresses.

References

- ARENS, K. 1958a. Considerações sobre as causas do xeromorfismo foliar. *Boletim da Faculdade de Filosofia Ciências e Letras da USP Botânica*, **15**: 25-56.
- ARENS, K. 1958b. O cerrado como vegetação oligotrófica. *Boletim da Faculdade de Filosofia Ciências e Letras da USP Botânica*, **15**: 57-77.
- BARROS, M.A.D. & L.S. CALDAS. 1980. Acompanhamento de eventos fenológicos apresentados por cinco gêneros nativos do Cerrado. *Brasil Florestal*, **42**: 7-14.
- CHAPIN III, F.S. 1991. Integrated responses of plants to stress. *Bioscience*, **41**(1): 29-35.
- COUTINHO, L.M. 1978. O conceito de Cerrado. *Revista Brasileira de Botânica*, **1**: 17-23.
- CRESSWELL, C.F.; P. FERRAR; J.O. GRUNOW; D. GROSSMAN; M.C. RUTHERFORD & J.J.P. van WYK. 1982. Phytomass, seasonal phenology and photosynthetic studies. pp. 476-497. In: Huntley, B.J. & B.H. Walker (eds.), *Ecology of Tropical Savannas*. Springer Verlag, Berlin.
- FERRAR, P.J. 1980. Environmental control of gas exchange in some savanna woody species. I. Controlled environmental studies of *Terminalia serica* and *Grewia flavescens*. *Oecologia*, **47**: 204-212.
- FERRI, M.G. 1979. Uma década (1968-1977) de trabalho no cerrado. pp. 23-60. In: Goodland, R. & M.G. Ferri (eds.), *Ecologia do cerrado*. EDUSP, São Paulo.
- FIELD, C.; J. MERINO & H.A. MOONEY. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia*, **60**: 384-389.
- FRANCO, A.C. 1983. *Fotossíntese e Resistência Foliar em Didimopanax macrocarpum*. M.Sc. Dissertation. Universidade de Brasília. 79 pp.
- GOODLAND, R.J.A. & M.G. FERRI. 1979. *Ecologia do Cerrado*. Editora Itatiaia, Belo Horizonte, 193 pp.
- GOODLAND, R.J.A. & R. PALLARDY. 1983. The Brazilian Cerrado vegetation: a fertility gradient. *Journal of Ecology*, **61**(1): 219-224.

- HULL, J.C. & H.A. MOONEY. 1990. Effects of nitrogen on photosynthesis and growth rates of four Californian annual grasses. *Acta Oecologica*, **11**(4): 453-468.
- JOHNSON, C.; A.C. FRANCO & L. CALDAS. 1993. Fotossíntese e resistência foliar em espécies do cerrado: metodologia e resultados preliminares. *Revista Brasileira de Botânica*, **6**(2): 91-97.
- KANNO, S.S. 1993. *Curso diário e sazonal das trocas gasosas e potencial hídrico foliar em três espécies lenhosas do cerrado: Anacardium nanum St Hill, Andira humilis Marth. ex Benth, e Eriotheca gracilipes (K. Schum) A. Robins.* M.Sc. Dissertation. Universidade Federal de São Carlos. 100 pp.
- KÖRNER, C.; A. JUDITH; A. SCHEEL & H. BAUER. 1979. Maximum leaf diffusive conductance in vascular plants. *Photosynthetica*, **13**(1): 45-82.
- LARCHER, W. 1995. *Physiological Plant Ecology*. Springer-Verlag, New York, 506 pp.
- LOVELESS, A.R. 1961. A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. *Annals of Botany*, **25**: 168-184.
- LOVELESS, A.R. 1962. Further evidence to support a nutritional interpretation of sclerophylly. *Annals of Botany*, **26**: 551-561.
- MANTOVANI, W. 1983. *Composição e similaridade florística, fenologia e espectro biológico do Cerrado da reserva biológica de Mogi-Guaçu, Estado de São Paulo*. M.Sc. Dissertation. Universidade Estadual de Campinas. 146 pp.
- MATTOS, E.A. 1992. *Trocas gasosas em folhas de tres espécies arbóreas do cerradão da Fazenda Canchin, São Carlos (SP): A disponibilidade hídrica de inverno limita a abertura estomática?* M.Sc. Dissertation. Universidade Federal de São Carlos. 156 pp.
- MEDINA, E.; V. GARCIA & E. CUEVAS. 1990. Sclerophylly and oligotrophic environment. Relationships between leaf structure, mineral nutrient content and drought resistance in tropical rain forest of the upper Rio Negro regions. *Biotropica*, **22**(1): 51-64.
- MOONEY, H.A. 1981. Primary production in Mediterranean climate regions. pp. 249-255. *In: Di-Castri, F., D.W. Goodall, R.L. Specht (eds.), Mediterranean-Type Shrublands*. Elsevier, Amsterdam.

- MOONEY, H.A., C. FIELD; S.L. GULMON & F.A. BAZZAZ. 1981. Photosynthetic capacity in relation to leaf position in desert *versus* old-field annuals. *Oecologia*, **50**: 109-112.
- MOONEY, H.A.; C. FIELD; S.L. GULMON; P. RUNDEL & F.J. KRUGER. 1983. Photosynthetic characteristic of South African sclerophylls. *Oecologia*, **58**: 398-401.
- MOONEY, H.A. & S.L. GULMON. 1982. Constraints on leaf structure and function in reference to herbivory. *Bioscience*, **32**(3): 198-206.
- MORAES, J.A.P.V., S.C.J.G.A. PEREZ & L.F. CARVALHO Jr. 1989. Curso diário e sazonal do potencial da água e da resistência estomática em plantas de um cerradão. *Annals of the Missouri Botanical Garden*, **27**: 13-23.
- NETTO, A.B.P. & J.D. HAY. 1986. Fotossíntese em *Caryocar brasiliense* no cerrado. *Revista Brasileira de Botânica*, **9**: 259-262.
- NIX, H.A. 1983. Climate of tropical savannas. pp. 37-62. In: Bourlière, F. (ed.), *Ecosystems of the World: Tropical Savannas*. Elsevier, Amsterdam.
- PAULILO, M.T. & G.M. FELIPPE. 1992. Crescimento de folhas de árvores de *Qualea grandiflora*. *Revista Brasileira de Botânica*, **15**(2): 85-93.
- PEREZ, S.C.J.G.A. & J.A.P.V. MORAES. 1983. Efeito da geadá sobre as relações hídricas em plantas do cerrado. *Anais do Seminário Regional de Ecologia III*: 277-283. São Carlos, SP.
- PEREZ, S.C.J.G.A. & J.A.P.V. MORAES. 1991a. Curso diário e sazonal do potencial da água e da condutância estomática em espécies de cerradão. *Revista Brasileira de Biologia*, **51**(4): 805-811.
- PEREZ, S.C.J.G.A. & J.A.P.V. MORAES. 1991b. Determinações de potencial hídrico, condutância estomática e potencial osmótico em espécies dos estratos arbóreo, arbustivo e herbáceo de um cerradão. *Revista Brasileira de Fisiologia Vegetal*, **3**(1): 27-37.
- PRADO, C.H.B.A. 1994. *Capacidade Fotossintética de Algumas Espécies Lenhosas do Cerrado sob Condições de Campo*. D.Sc. Thesis. Universidade Federal de São Carlos. 131 pp.
- PRADO, C.H.B.A.; J.A.P.V. MORAES & E.A. MATTOS. 1994. Gas exchange and leaf water status in potted plants of *Copaifera langsdorfii*. 1. Responses to water stress. *Photosynthetica*, **30**(2): 207-213.

- PRADO, C.H.B.A.; J.A.P.V. MORAES & E.A. MATTOS. 1995. Gas exchange and leaf water status in potted plants of *Copaifera langsdorfii*. 2. Probable influence of low air humidity. *Photosynthetica*, **31**(1): 31-36.
- RAWISTCHER, F. 1948. The water economy of the vegetation of the *Campos Cerrados* in southern Brazil. *Journal of Ecology*, **36**: 237-268.
- REICH, P.W. & M.B. WALTERS. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**(3): 365-392.
- RIZZO, J.A.; A.J. CENTENO; J. SANTOS-LOUSA & T.S. FILGUEIRAS. 1971. Levantamento de dados em área de Cerrado e da Floresta Caducifólia Tropical do planalto centro-oeste. pp. 103-110. In: Ferri, M.G. (ed.), *III Simpósio sobre o Cerrado*. Editora Edgard Blücher/EDUSP, São Paulo.
- ROCHA, A.M.S. 1994. Estresse hídrico e trocas do CO₂ gasoso e vapor de água em plantas jovens envasadas de *Stryphnodendron adstringens* (Mart) Coville. M.Sc. Dissertation. Universidade Federal de São Carlos. 112 pp.
- RUBIN FILHO, C.J. & J.A.P.V. MORAES. 1996. Estudos sobre a capacidade de resistência a seca em plantas jovens de espécies de cerrado. *Anais do VIII Seminário Regional de Ecologia* (in press). São Carlos, São Paulo.
- SALISBURY, F.B. & C.W. ROSS. 1992. *Plant Physiology*. Wadsworth, Belmont, 682 pp.
- SAN JOSÉ, J.J. 1977. Potencial hídrico e intercambio gaseoso de *Curatella americana* L. en la temporada seca de la sabana de Trachypogon. *Acta Científica Venezolana*, **23**: 373-379.
- SARMIENTO, G. & M. MONASTERIO. 1983. Life forms and phenology. pp. 79-108. In: Bourliere, F. (ed.), *Ecosystems of the World: Tropical Savannas*. Elsevier, Amsterdam.
- SARMIENTO, G.; G. GOLDSTEIN & F. MEINZER. 1985. Adaptive strategies of woody species in neotropical savannas. *Biological Review*, **60**: 316-355.
- SATO, A. & J.A.P.V. MORAES. 1992. Efeito do estresse hídrico sobre as trocas do CO₂ gasoso em plantas jovens de espécies de cerrado. *Arquivos de Biologia e Tecnologia*, **35**(4): 763-775.
- SOBRADO, M.A. & E. MEDINA. 1980. General morphology, anatomical structure and nutrient content of sclerophyllous leaves of the "Bana" vegetation of Amazonas. *Oecologia*, **45**: 341-345.

WAGNER, J., S.P. MENENDEZ & W. LARCHER. 1993. Bioclima e potenziale di produttività di *Quercus ilex* L. al limite settentrionale del arealle di distribuzione. *Acta Biologica*, **68**: 37-51.

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