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ORIGINAL PAPER

Seasonal gas exchange and water relations in juveniles of two evergreen Neotropical savanna tree species with contrasting regeneration strategies

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Abstract Colonization dynamics of woody species into grasslands in Neotropical savannas are determined by two main factors: plant-available moisture and fire. Considering seasonality of precipitation and high fire frequency in these ecosystems, vegetative reproduction has been suggested as the main regeneration strategy in woody species. This study examined seasonal variations in water relations and photosynthesis in juveniles of two tree species with contrasting regeneration strategies: *Palicourea rigida* (sexual reproduction) and *Casearia sylvestris* (asexual reproduction). The studied species showed similar transpiration rates to deep-rooted adult evergreen tree species during the rainy period, suggesting little water availability limitations on surface soil layers. *P. rigida* juveniles significantly decreased their leaf water potentials from wet to dry seasons. In *C. sylvestris* resprouts, there were no seasonal differences in their predawn water potentials and gas exchange parameters, indicating a water deficit avoidance characteristic derived from their connections to deep-rooted adult counterparts allowing access to moist soil at depth even during the drought period. *P. rigida* rely on strict control of water losses and turgor maintenance through elastic cell walls during the dry season. The iso-hydric behavior of gas exchange and most water relations parameters in *C. sylvestris* enable turgor maintenance during the dry season which also gives the possibility to achieve foliar expansion under water-stressed conditions for shallow-rooted plants. Nevertheless, in absence of water deficits, *P. rigida* had the advantage to be physiologically independent individuals, showing an equal or even superior photosynthetic performance that eventually could be translated into a more favorable whole-plant carbon balance and higher growth rates in wet habitats.

Keywords *Casearia sylvestris* · *Palicourea rigida* · Fire · Water stress · Water use efficiency · Photosynthesis

Introduction

Neotropical seasonal savannas are characterized by a continuous matrix of grasses interrupted by woody species in a large range of densities, from pure grasslands to woodlands. This vegetation complex is found in environments characterized by rainfall seasonality, oligotrophic soils and frequent fires (Sarmiento 1984). Factors and processes that determine the coexistence of grasses and trees, and the spatial and temporal trends of the tree/grass ratio in savanna ecosystems have been analyzed (Scholes and Archer 1997; Sankaran et al. 2004). Overall, tree density seems to be determined by two main factors: plant-available moisture throughout the year and fire (Medina and Silva 1990).

The paradigm that Neotropical savanna trees transpire freely throughout most of the year has been revisited (Goldstein et al. 2008). This pattern of water use accounted by continuous access to water stored deep in the soil was the fundament of the root-niche separation hypothesis to explain the coexistence of two apparent competitors, grasses and trees (Walter 1971). Strong stomatal limitations of maximum daily transpiration rates and total daily transpiration have been evidenced for trees in the Cerrado, a Brazilian seasonal savanna woodland, during both wet and dry seasons (Meinzer et al. 1999). Moreover, despite partial defoliation that occurred in some Cerrado tree

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species (Franco 1998; Goldstein et al. 2008), which helps to maintain a high specific hydraulic conductivity during the dry season, stomatal conductance was lower in the dry season than in the wet season.

The root-niche separation model assumes that water is the limiting factor and hypothesizes that trees have roots on both the topsoil and subsoil, while grasses root only in the topsoil. Under this perspective, seedlings and juveniles of tree species compete for water with grasses, negatively affecting tree seedling establishment.

High fire frequency and prolonged dry seasons are considered the major limitations for sexual reproduction of savanna tree species. Under savanna environmental conditions, vegetative reproduction is considered more successful than sexual reproduction (Rizzini and Heringer 1962; Hoffmann 1998; Setterfield 2002). The costs of vegetative reproduction could be lower, implying lesser restrictions to propagule establishment after a fire (Abrahamson 1980; Lamont 1988; Peterson and Jones 1997).

Although there is little information on seedling establishment in Neotropical savannas, some studies have shown the functionality of sexual reproduction in woody species (Oliveira and Silva 1993; Hoffmann et al. 2004). Successful seedling establishment of savanna trees must synchronize germination at the beginning of the rainy season and a carbon allocation pattern favoring the quick development of deep-root systems in order to reach soil-stored water and overcome the dry season (García-Núñez et al. 2001; Franco 2004). Newly established propagules must cope, on a daily basis, with a combination of high radiation loads, high temperatures and a high evaporative demand. Therefore, a conservative gas exchange pattern and tolerance to water deficit is expected in juveniles of sexually reproducing species, while one may expect a water spender and avoider character in asexual propagules. Water availability measurements at different soil depths in Neotropical savannas (Goldstein et al. 1986; Franco 1998) showed that juveniles with undeveloped root systems could be exposed to pronounced water deficits threatening their survival. In this study we examined seasonal variations in water relations and photosynthesis in juveniles of two tree species with contrasting regeneration strategies: *Palicourea rigida* (sexual reproduction) and *Casearia sylvestris* (asexual reproduction).

Materials and methods

Study site and plant material

The study site is located in a seasonal savanna area at 200 m asl, in the State of Barinas, Venezuela (8°37′N and 70°12′W). It is characterized by a grass cover dominated by C_4 bunch grasses and a tree layer consisting of scattered evergreen trees and semideciduous forest patches (García-Núñez et al. 2001). Annual precipitation is approximately 1,500 mm which is largely confined to the period between April and November and the mean annual temperature is 27°C with little seasonal variation. These savannas are characterized by fires that occur yearly. The soils are oligotrophic and well drained (Goldstein et al. 1986).

We chose two evergreen tree species: *Palicourea rigida* H.B.K. (Rubiaceae) and *Casearia sylvestris* Sw. (Flacourtiaceae), due to their contrasting regeneration strategies (sexual and asexual, respectively). *Palicourea rigida* is a small tree (up to 3 m in height) with simple leaves that are glabrous and rather thick, 10–20-cm long and 6–12-cm wide (Sarmiento et al. 1985). Flowering occurs from January to April; fruits are produced and dispersed until July. Its regeneration strategy is sexual, and seedlings and juveniles are mainly found crowded around adult parent trees (García-Núñez et al. 2001).

Casearia sylvestris is also a small tree (up to 6 m in height) with simple, alternate leaves that are 6–12 cm in length and 1.5–4 cm in width (Sarmiento et al. 1985). During the dry season (December–February) a new cohort of leaves grow, and flowering occurs between February and March. Its regeneration strategy is characterized by the formation of a dense network of interconnected resprouts.

In order to evaluate the distribution of the two selected species, all individuals of *P. rigida* and *C. sylvestris* were counted in two transects of 10 × 100 m (2,000 m^2) and a total of 263 and 469 individuals were found for *P. rigida* (range in size from 0.5 to 210 cm) and *C. sylvestris* (range in size from 0.5 to 170 cm), respectively. In *P. rigida*, 70% of the smaller plants were germinating seedlings and in *C. sylvestris*, 96% of individuals were small resprouts found beneath the grass layer (García-Núñez 2003).

Individuals spread in a 1-ha plot were labeled and used for gas exchange and water potential measurements (newly emerged seedlings and resprouts of *P. rigida* and *C. sylvestris*, respectively; $n = 200$ for each species) at the beginning of the rainy season. These plants were monitored throughout the year and subsequently used for ecophysiological measurements.

For our purpose, the origin of resprouts was verified by excavating around the plants making sure connections were not severed and then covered again with soil.

Field measurements

Gas exchange and water potential measurements were performed, both in the wet and dry season, in juveniles of approximately 7 (wet season measurements) to 10 months (dry season measurements) from their emergence during the early wet season.

Total leaf area of the sampled plants ($n = 30$; 7-month-old plants) were 10.51 ± 2.08 cm^2 and 9.29 ± 1.09 cm^2 for *P. rigida* and *C. sylvestris*, respectively. Mean stem length and rooting depth of *P. rigida* juveniles were 2.07 ± 0.13 cm^2 and 15.36 ± 0.79 cm^2, respectively. For *C. sylvestris*, mean stem length was 6.25 ± 0.55 cm, while rhizomes that connected resprouts were running 4–10 cm deep (García-Núñez 2003). However, it is important to note that connections to adult trees provide access to deeper soil layers. For the study area, Goldstein et al. (1986) found that soil water potential (SWP) declined to about -2.0 MPa at a depth of 10 cm during the dry season while SWP at a depth of 70 cm remained above -0.5 MPa. As a consequence, savanna trees (roots >70 cm in depth) seem to have access to water throughout the year in spite of rainfall seasonality.

The total leaf area of the sampled plants was measured during the dry season before the occurrence of fires (January, February; 10-month-old plants), and were comparable to those sampled in the wet season (October, November; 7-month-old plants) (García-Núñez 2003).

During the study, daily courses of air temperature (T_a), leaf temperature (T_L), relative humidity, photosynthetic photon flux density (PPFD), leaf conductance (Gs), CO_2 assimilation rate (A), transpiration rate (E) and water potential (Ψ_p) were determined from dawn (0600 hours) to dusk (1800 hours) in seven daily courses. Four courses corresponded to the wet season, and three to the dry season. For each daily course, measurements were carried out from dawn to dusk on two fully expanded leaves from five different individuals, in 2-h intervals. For gas exchange measurements the juveniles of *P. rigida* were chosen beneath their adults counterparts at different locations. Plants of *C. sylvestris* utilized for gas exchange measurements were chosen nearby different adult individuals; however, this procedure did not guarantee that they were from different parent plants given that this species forms a dense mat of interconnected resprouts. Since leaves can be damaged or cut during gas exchange measurements for each daily course performed we often had to use different plants. The average leaf areas used for gas exchange measurements ($n = 20$ leaves) were 6.07 ± 0.17 and 5.60 ± 0.23 cm^2 for *P. rigida* and *C. sylvestris*, respectively.

From these different courses, mean daytime values for each of the measured parameters were obtained for each season. Water use efficiency was calculated as the average ratio of maximum assimilation rates and stomatal conductance (intrinsic water use efficiency, IWUE, A/Gs μmol/mol) along the daily course. In addition, a 24-h gas exchange course was used to integrate CO_2 exchange rates in order to obtain the leaf assimilation/respiration ratio (A/R) (McCree et al. 1984). In the case of *P. rigida* juveniles, the 24-h course was performed in potted plants (10-month-old plants sown in polyethylene bags of 0.0182 m^3 in volume; the substrate consisted in a mixture of loamy savanna soil and sand, 50:50), in irrigated daily ($n = 5$ plants) and in water-stressed plants (30 days without irrigation; $n = 5$ plants). For *C. sylvestris* resprouts, the 24-h course was done under field conditions ($n = 5$ plants) during the wet (7-month-old plants) and dry (10-month-old plants) seasons, respectively.

The functionality of the connection and the recovery capacity of young *C. sylvestris* resprouts were assessed performing daily gas exchange and water potential courses on resprouts ($n = 5$ plants) at 0, 1, 2 and 7 weeks after they were disconnected. Disconnections were performed between 0745 hours and 0815 hours using pruning scissors. Control plants ($n = 5$ plants) were measured for each daily course performed in disconnected plants. The resprouts used in this trial were approximately 13–14 months old from emergence. The experiment was performed in the field during the wet season, between June and July, which represented the first peak of the rainy season with a mean monthly precipitation of 275 and 226 mm for June and July, respectively. Relative soil water content (10 cm in depth) measured for this period reached maximum values of 18% which represent a SWP of -0.005 MPa (García-Núñez 2003).

In the field, a portable gas exchange system, operating in the open mode, was used to measure leaf gas exchange (LCA-4, ADC, Hoddesdon, England). Gas exchange rates were determined for leaves sealed in the chamber for less than 30 s, using calculations from the model of von Caemmerer and Farquhar (1981). Leaf temperatures were measured with copper-constantan thermocouples connected to a digital thermometer (HH-23, OMEGA, Stamford, Connecticut) and attached to the lower leaf surface (three different plants, $n = 3$). Air temperatures were measured with copper-constantan thermocouples placed 1 m above the soil surface ($n = 3$) and relative humidity was measured with a digital hygrometer (RH-200°F, OMEGA, Stamford, Connecticut). Leaf and air temperatures and relative humidity were used to calculate vapor pressure differences (VPD) between leaf and air. Water potential measurements of *P. rigida* juveniles and *C. sylvestris* resprouts were done in the entire aboveground portion of the plants (single shoot, Ψ_p, $n = 5$) with a pressure bomb (PMS Instruments Co., Corwallis, Oregon, USA). The measurements were done at predawn (Ψ_{pd}), noon (Ψ_{min}) and dusk during the different daily courses.

CO_2 assimilation-light response curves were determined in the field for each season under full solar irradiation. For *P. rigida*, we performed four curves during the wet season and two for the dry season and for *C. sylvestris*, we performed three and one curves during wet and dry seasons, respectively. The curves shown in Fig. 1 are those with the best fit to the adjusted equation.

Attenuation of PPFD at the leaf surface was achieved by covering the top of the leaf chamber with mesh layers of neutral density. Since the leaf chamber had no temperature control, changes in leaf temperatures were unavoidable and ranged from 28 to 35°C. At each irradiance level, measurements were taken after CO_2 readings stabilized, usually achieved after 3 min.

Light response curves were fitted to a non-rectangular hyperbola function:

$$A = \varnothing I + A_{\max} - \left([\varnothing I + A_{\max}]^2 - 4\Theta \varnothing I A_{\max}\right)^{1/2} / 2\Theta - R_{\mathrm{d}},$$

where A = net CO_2 assimilation rate; $\varnothing$ = apparent quantum yield; I = PPFD; $A_{\max}$ = light-saturated rate of gross CO_2 assimilation; Θ = curvature factor (range between 0 and 1); R_{d} = dark respiration rate (Lambers et al. 1998).

CO_2 assimilation–intercellular CO_2 concentration (A–C_{i}) response curves were carried out seasonally in the field for *C. sylvestris* young resprouts. In *P. rigida* juveniles, measurements were carried out in potted plants (polyethylene bags of 0.0182 m^3 filled with 50:50 sand, savanna soil mixture), under favorable water conditions (daily watering; $n = 3$) and plants subjected to water deficit (30 days without watering; $n = 3$). A–C_{i} curves were also fitted to a non-rectangular hyperbola function. Carboxylation efficiency (CE) was calculated as dA/dC_{i} on the linear portion of the curve. Measurements were done under natural saturating light intensities (PPFD > 800 μmol m^{-2} s^{-1}; average = 1,458.73 ± 17.43 μmol m^{-2} s^{-1}; $n = 647$ measurement points done in both species at the different CO_2 concentrations). At each intercellular CO_2 concentration (range 80–1,500 vpm with variable steps from approximately 20 vpm at lower concentrations to 200 vpm at higher concentrations), measurements were taken after CO_2 readings stabilized, usually achieved after 3–5 min. Above atmosphere values of CO_2 concentrations were attained using a gas cylinder [2,000 vpm]. Relative stomatal limitation for photosynthesis, L_{s}, was calculated as $L_{\mathrm{s}} = 100\ (A_{\mathrm{o}} - A_{\mathrm{n}})/A_{\mathrm{o}}$, where A_{o} is the photosynthetic rate when $C_{\mathrm{i}} = 350$ μmol mol^{-1} and A_{n} is the net photosynthetic rate at $C_{\mathrm{a}} = 350$ μmol mol^{-1} (Farqhuar and Sharkey 1982).

Laboratory measurements

Pressure–volume curves were carried out on the entire aboveground portions of juveniles ($n = 5$) and young sprouts ($n = 5$) for *P. rigida* and *C. sylvestris*, respectively, replicated three times during a single wet and a single dry season. Measurements were performed 24 h after cutting plant material under water and leaving them in a container

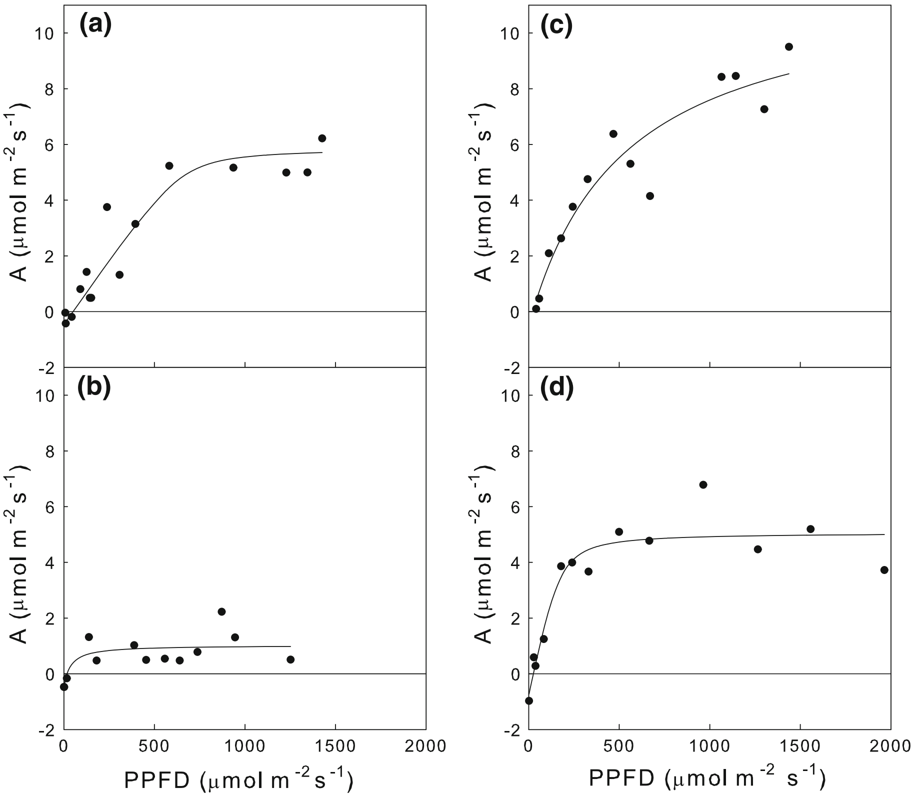

Fig. 1 Response curve for CO_2 assimilation rate (A) in relation to photosynthetic photon flux density (PPFD) for juveniles of *Palicourea rigida* during **a** the wet season ($r^2 = 0.86$) and **b** the dry season ($r^2 = 0.50$); and for young resprouts of *Casearia sylvestris* during **c** the wet season ($r^2 = 0.89$) and **d** the dry season ($r^2 = 0.81$)

to saturate, covered with polyethylene bags in the dark. Osmotic potentials at full turgor (Ψ_π^{100}), at turgor loss (Ψ_π^0) and the modulus of elasticity (ε) were calculated from these curves (Tyree and Hammel 1972).

Nitrogen content was determined seasonally in oven-dried leaf samples by a Kjeldahl procedure (Allen 1989). A composite sample obtained from five fully expanded leaves from three different plants was divided into three replicates which were analyzed and the average values for both seasons are presented in Table 3. Specific leaf area (SLA) was obtained after drying leaves of known area ($n = 30$; 7-month-old plants) at 60°C until reaching a constant weight.

Regression coefficients were considered significant at $P < 0.05$. Statistical significance of other variables was assessed through Mann–Whitney *U* tests at $P < 0.05$.

Results

Seasonal mean values of microclimatic variables, leaf gas exchange and water relations

Marked differences between seasons were found in gas exchange parameters (Table 1) and water potentials (Table 2) for *P. rigida*. For *C. sylvestris*, there were no seasonal differences in carbon assimilation rates in spite of a distinctive decrease in Gs and $\Psi_{\min}$. In relation to microclimatic variables, there were no differences in mean and maximum PPFD values between seasons, while VPD significantly increased from the wet to the dry season.

During the wet season, *P. rigida* juveniles, sheltered by the canopy of adult trees, showed little stomatal restrictions to water vapor losses, reaching relatively high mean Gs and *E* values (279.6 ± 48.7 mmol m^{-2} s^{-1}; 2.7 ± 0.2 mmol m^{-2} s^{-1}, respectively). In the dry season, the surviving juveniles showed a rigorous stomatal control with a significant reduction in Gs and *E* (32.4 ± 5.0 mmol m^{-2} s^{-1}; 1.0 ± 0.1 mmol m^{-2} s^{-1}, respectively). *C. sylvestris* showed high mean Gs values during both seasons while *E* did not show seasonal differences (Table 1).

Predawn leaf water potentials showed a marked reduction from wet to dry season in *P. rigida*, while in *C. sylvestris*, there was no significant seasonal change (Table 2). $\Psi_{\min}$ occurred at midday for both seasons, decreasing considerably as the dry season progressed, reaching −2.3 MPa in *P. rigida* and −2.5 MPa in *C. sylvestris*.

There were no seasonal differences in Ψ_π^{100} and Ψ_π^0 in either species (Table 2). *P. rigida* juveniles presented $\Psi_{\min}$ near zero turgor at midday during the rainy season, while $\Psi_{\min}$ reached values well below Ψ_π^0 in the dry period (Table 2). $\Psi_{\min}$ usually reached values close to Ψ_π^0 during both seasons in *C. sylvestris*, at times of maximum evaporative demand. Seasonally, *P. rigida* showed no differences in RWC°, $\Psi_\pi^{100} - \Psi_\pi^0$ and ε, while in *C. sylvestris* the passive osmotic adjustment capacity ($\Psi_\pi^{100} - \Psi_\pi^0$) increased and the relative water content at zero turgor (RWC°) decreased significantly during the dry period (Table 2).

Photosynthetic responses

In *P. rigida*, maximum assimilation rates (6.2 ± 0.4 µmol m^{-2} s^{-1}) were found mainly in periods of direct illumination during the rainy season, while in the dry season maximum rates decreased significantly (3.0 ± 0.8 µmol m^{-2} s^{-1}) (Table 1). *C. sylvestris* showed mean assimilation rates around 4.0 µmol m^{-2} s^{-1} for both seasons, with maximums of 9.5 ± 0.5 µmol m^{-2} s^{-1} for the rainy and 11.2 ± 1.8 µmol m^{-2} s^{-1} for the dry season. Light response curves, built in the field, showed light saturation above 600 µmol m^{-2} s^{-1} in *P. rigida* (Fig. 1a) in the rainy season, while saturation occurred at low PPFD in

Table 1 Mean CO_2 assimilation rate (*A*), stomatal conductance (Gs), transpiration rate (*E*), intrinsic water use efficiency (IWUE), leaf to air vapor pressure difference (VPD) and photosynthetic photon flux density (PPFD) for all courses carried out during wet ($n = 4$) and dry seasons ($n = 3$)

Species	Season	*A* (µmol m^{-2} s^{-1})	Gs (mmol m^{-2} s^{-1})	*E* (mmol m^{-2} s^{-1})	IWUE (µmol/mol)	VPD (KPa)	PPFD (µmol m^{-2} s^{-1})
P. rigida	Wet	2.05 ± 0.22* (6.2)	279.56 ± 48.74* (1,150)	2.71 ± 0.24* (6.4)	25.50 ± 8.63 (37)	0.92 ± 0.17* (2.6)	386 ± 66 (1,447)
	Dry	0.68 ± 0.13 (3.0)	32.38 ± 4.97 (76)	1.01 ± 0.11 (1.8)	61.77 ± 28.94 (88)	1.50 ± 0.16 (2.4)	553 ± 89 (1,028)
C. sylvestris	Wet	4.06 ± 0.32 (10.0)	301.08 ± 56.72 (1,263)	3.13 ± 0.42 (7.6)	31.84 ± 10.98 (46)	1.12 ± 0.13* (2.0)	535 ± 77 (1,689)
	Dry	4.20 ± 0.51 (11.0)	162.36 ± 27.42 (434)	3.10 ± 0.34 (5.2)	53.48 ± 8.44 (64)	2.36 ± 0.24 (3.9)	509 ± 105 (1,477)

Means ± 1 SE are presented; mean maximums in parenthesis

* Significant differences ($P < 0.05$, Mann–Whitney *U* test) between seasons

Table 2 Seasonal variation in water relation parameters for the two studied species

Species	Season	Ψ_{mean} (MPa)	Ψ_{pd} (MPa)	Ψ_{min} (MPa)	Ψ_{π}^{100} (MPa)	$\Psi\pi°$ (MPa)	RWC° (%)	ε (MPa)
P. rigida	Wet	−1.20 ± 0.13*	−0.63 ± 0.15*	−1.40 ± 0.12*	−1.21 ± 0.06	−1.72 ± 0.07	72.84 ± 1.73	5.33 ± 0.66
	Dry	−2.05 ± 0.20	−1.60 ± 0.19	−2.30 ± 0.19	−1.14 ± 0.14	−1.71 ± 0.09	69.97 ± 5.25	5.50 ± 0.89
C. sylvestris	Wet	−1.03 ± 0.20*	−0.45 ± 0.17	−1.58 ± 0.32*	−1.43 ± 0.13	−1.87 ± 0.14	81.88 ± 2.32*	11.23 ± 1.64
	Dry	−1.66 ± 0.24	−0.77 ± 0.17	−2.51 ± 0.11	−1.56 ± 0.38	−2.33 ± 0.43	71.35 ± 4.50	10.44 ± 1.10

Mean plant water potential (Ψ_{mean}), predawn (Ψ_{pd}) and minimum (Ψ_{min}) water potentials, osmotic potential at saturation (Ψ_{π}^{100}), osmotic potential at the turgor loss point ($\Psi\pi°$), relative water content at the turgor loss point (RWC°) and modulus of elasticity (ε). Mean ± 1 SE are presented

* Significant differences ($P < 0.05$, Mann–Whitney *U* test) between seasons

the dry season (Fig. 1b). *C. sylvestris* did not show light saturation even at PPFD values above 1,200 μmol m^{-2} s^{-1} in the rainy season (Fig. 1c), while in the dry season, light saturation occurred above 500 μmol m^{-2} s^{-1} (Fig. 1d). Both species showed higher *A*/Gs during the dry season (Table 1).

Leaf assimilation/respiration (*A*/*R*) ratios in well watered plants ($\Psi_{\mathrm{pd}} = -0.6 \pm 0.2$ MPa; $\Psi_{\mathrm{pd}} = -0.5 \pm 0.2$. MPa, for *P. rigida* and *C. sylvestris*, respectively) were similar for both species (Table 3).

In *P. rigida*, *A*/*R* was halved in water-stressed plants (potted plants; $\Psi_{\mathrm{pd}} = -1.8 \pm 0.2$ MPa) and also mean dark respiration rates were significantly lower in water-stressed plants (Table 3). *C. sylvestris* resprouts, measured in the field during the dry season ($\Psi_{\mathrm{pd}} = -0.8 \pm 0.2$ MPa), showed no changes in *A*/*R* due to its capacity to maintain similar assimilation and respiration rates as in the rainy season (Table 3). The N content of the leaves was significantly higher in the dry season for both species (Table 3).

Table 3 Photosynthetic, nutritional and morphological characteristics of fully expanded leaves of *Palicourea rigida* and *Casearia sylvestris* juveniles

Parameter/season	*P. rigida*	*C. sylvestris*
Dark respiration (μmol m^{-2} s^{-1})		
Wet season	0.73 ± 0.10*	0.83 ± 0.12
Dry season	0.41 ± 0.18	0.96 ± 0.04
Assimilation/respiration ratio (*A*/*R*)		
Wet season	3.9 ± 0.3*	4.0 ± 0.5
Dry season	1.9 ± 0.1	6.2 ± 0.9
Leaf nitrogen content (mg/g)		
Wet season	13.27	19.97
Dry season	15.97	24.63
Specific leaf area (cm^2/g)		
Wet season	0.018 ± 0.0007	0.014 ± 0.0008
Dry season	–	–

Means ± 1 SE are presented

* Significant differences ($P < 0.05$, Mann–Whitney *U* test) between seasons

A/C_i curves revealed a significant increment in the relative stomatal limitation and decreased carboxilation efficiency with drought in *P. rigida*. In addition, the assimilation rate at saturating C_i (A_{sat}) was lower in water-stressed plants (Table 4). There was no evidence of drought effects on carboxilation efficiency and relative stomatal limitation in *C. sylvestris* resprouts. However, there was a significant decrease in A_{sat} (Table 4), which was accompanied by an increase in the operational C_i ($C_i = 288.8 \pm 3.8$; 327.7 ± 12.9 vpm for the rainy and dry season, respectively).

Functional responses in *C. sylvestris* disconnected resprouts

There was a marked stomatal closure immediately after disconnection in *C. sylvestris* resprouts, with maximum Gs and *E* of 50 and 1.0 mmol m^{-2} s^{-1}, respectively (Fig. 2a, b) and minimum Gs and *E* values at midday. Ψ_{p} of disconnected plants, 1 h after the cut off (1130 hours), was -2.0 ± 0.2 MPa, while control plants maintained higher values (-1.2 ± 0.3 MPa). Consequently, CO_2 assimilation rates underwent a gradual decline from the moment of disconnection (Fig. 2c) with maximum rates of 1.4 μmol m^{-2} s^{-1} to zero or even negative values after midday hours. Leaf gas exchange response measured at 1 and 2 weeks after disconnection was comparable. Both Gs and *E* reached maximum values early in the morning experiencing a sharp decline until the early hours of the afternoon where minimum values were reached. CO_2 assimilation along the day was similar from 1 to 2 weeks from disconnection with maximum values early in the morning hours. An important recovery in all measured gas exchange parameters was evident 7 weeks after disconnection (Fig. 2). However, leaf water potential of disconnected plants remained significantly lower than controls, with dawn values of -0.9 ± 0.3 MPa (-0.18 ± 0.04 MPa in control plants), and Ψ_{min} at midday of -2.0 ± 0.2 MPa (-1.2 ± 0.3 MPa in control plants).

Table 4 Photosynthetic parameters derived from A/C_i curves carried out during wet and dry seasons for juveniles and resprouts of *Palicourea rigida* and *Casearia sylvestris*, respectively ($n = 3$)

Species	Season	Carboxylation efficiency (mol m^{-2} s^{-1})	Relative stomatal limitation (%)	A_{sat}[a] (μmol m^{-2} s^{-1})
P. rigida	Wet	0.0581 ± 0.0041*	17.71 ± 2.02*	15.51 ± 0.61*
	Dry	0.0246 ± 0.0005	28.25 ± 3.76	5.67 ± 1.47
C. sylvestris	Wet	0.0380 ± 0.0003	35.64 ± 0.78	20.17 ± 0.78*
	Dry	0.0444 ± 0.0072	32.80 ± 7.63	8.97 ± 2.61

Mean ± 1 SE are presented

* Significant differences ($P < 0.05$; Mann–Whitney U test) between seasons

[a] Maximum assimilation at saturating C_i

Discussion

Stomatal conductance and transpiration

During the rainy season, both species showed high stomatal conductance and transpiration rates, comparable to those reported for adult individuals of dominant tree species of Neotropical seasonal savannas (Goldstein et al. 1986; Medina and Francisco 1994; Franco 1998; Franco et al. 2005). During the dry period, responses in terms of gas exchange parameters of *P. rigida* juveniles were characterized by severe stomatal control of water vapor losses, tightly coupled to variations in soil water content of surface layers deduced from Ψ_{pd}. Although *C. sylvestris* resprouts showed a distinctive decrease in Gs as the dry season progressed, its transpiration rates were similar to those found in adult individuals throughout the rainy period (Goldstein et al. 1986). Restrictions to water vapor losses in *C. sylvestris* resprouts probably arose from hydraulic limitations derived from its interconnected root systems. For several Cerrado woody species, transpiration does not seem to be limited by soil water per se, but by high atmospheric evaporative demand and hydraulic constraints possibly derived from their deep-rooting habit (Meinzer et al. 1999).

Patterns of gas exchange found in juveniles of the studied species, characterized by similar transpiration rates as the deep-rooted adult evergreen tree species (Goldstein et al. 1986), indicate, first, that there was a modest limitation of water availability in upper soil surface layers during the rainy season. Second, the above-mentioned patterns would suggest that there is little evidence of competition for soil water between tree juveniles and young resprouts with grass species. Competition for soil water in surface layers has been regarded as one of the main restrictions for the establishment of seedlings of savanna trees (Scholes and Archer 1997; Hoffmann et al. 2004). However, studies on seedling establishment in different woody Cerrado species showed that most of the mortality occurred shortly after germination within the wet season and that seasonal drought did not seem to be an important factor (Franco et al. 1996; Nardoto et al. 1998; Kanegae et al. 2000). The success of seedling establishment in *P. rigida* was probably related to the more favorable edaphic conditions around their adult co-specifics or other tree species (García-Núñez et al. 2001). Some studies have documented the beneficial effects of shelters for the successful regeneration of savanna tree species (Belsky et al. 1989; Barnes and Archer 1999). In fact, the micro-environmental conditions registered in shaded *P. rigida* juveniles showed that VPD was 0.2–0.6 kPa lower than that found in individuals located in the open savanna. In addition, water hydraulically lifted to the upper soil layer by deep-rooted trees could be used by neighboring plants including woody and herbaceous species (Moreira et al. 2003).

Water relations

Different studies have shown that several Neotropical savanna trees species are iso-hydric (Goldstein et al. 1986, 2008; Franco 1998; Meinzer et al. 1999), maintaining nearly constant minimum water potentials along the year, despite changes in soil water availability and atmospheric conditions. Strong daytime stomatal control of transpiration, a decrease in total leaf surface area per tree during the dry season and tight coordination between gas and liquid phase conductance have been regarded as the main mechanisms contributing to homeostasis of minimum water potential of Neotropical savanna trees (Bucci et al. 2005). However, seedlings and juveniles may not be able to maintain homeostasis in water potential. The shallowness of root systems in juveniles makes them susceptible to daily and seasonal changes in soil water status. In our study, as expected, *P. rigida* juveniles showed a significant decrease in water potentials from the wet to the dry season. In *C. sylvestris*, there were no seasonal differences in their predawn water potentials which corroborates their dependence on their parent plants for water. Yet, resprouts (this study) did not show homeostasis in Ψ_{min} in spite of tight

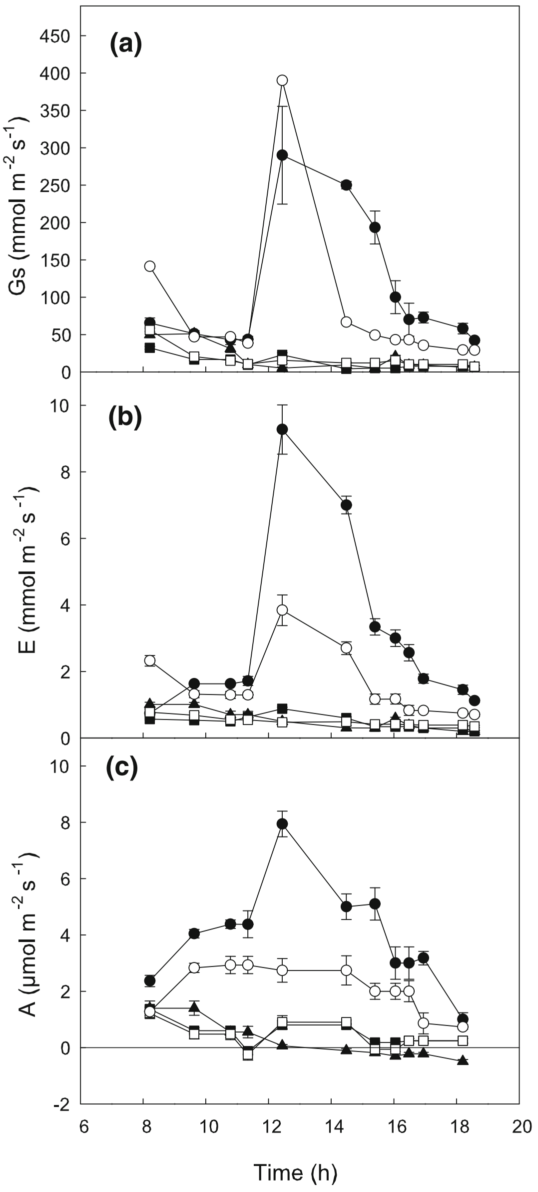

Fig. 2 **a** Stomatal conductance (Gs), **b** transpiration rate (*E*) and **c** CO_2 assimilation rate (*A*), for young resprouts of *Casearia sylvestris* during the experiment where resprouts were disconnected from the adult plants. *Filled circles* control, *filled triangles* same day, *filled squares* 1 week, *open squares* 2 weeks and *open circles* 7 weeks after disconnection. Control curves correspond to the course carried out after 7 weeks of disconnection

stomatal control of transpiration at times of maximum evaporative demands. Similarly, marked seasonal variations in Ψ_{min} have been reported for adult individuals of *C. sylvestris*, attributing this response to a superficial root system (Goldstein et al. 1986). On the contrary, adults of *P. rigida* evidenced slight seasonal changes in Ψ_{min} and homeostasis in stomatal conductance, transpiration and photosynthetic rates, implying a deep-rooting habit (García-Núñez 2003).

Seasonal steadiness of osmotic potentials in *P. rigida* juveniles indicates an avoidance response to water deficit as was described for other adult savanna tree species (Goldstein et al. 1986). In contrast to adult individuals of *C. sylvestris*, reported as water deficit tolerant with seasonal osmotic adjustments (Goldstein et al. 1986), *C. sylvestris* young resprouts also show seasonal steadiness in their osmotic potentials, indicating a water deficit avoidance characteristic derived from the connections to their adult counterparts. This feature permits turgor maintenance during the dry season, which also provides the possibility to achieve foliar expansion under water stress conditions for tree seedlings and herbaceous plants. Ψ_{π}^{100} and Ψ_{π}^{0} for the juveniles of the studied species were within the range of those reported for different woody savanna species (Meinzer et al. 1983; Myers et al. 1997; Le Roux and Bariac 1998; Eamus and Prior 2001; Franco et al. 2005).

The extent of the elasticity modulus (ε) found in *P. rigida* and *C. sylvestris* (ε 5.3–11.2 MPa) was similar to those described for other savanna woody species (Myers et al. 1997; Le Roux and Bariac 1998). Nevertheless, the difference between Ψ_{π}^{100} and Ψ_{π}^{0} found in the studied species was relatively high (0.5–0.8 MPa) and was above the range observed for several savanna tree species (0.1–0.4 MPa; Meinzer et al. 1983; Eamus and Prior 2001).

Photosynthetic responses

The effects of water deficits during the dry season were markedly evidenced in carbon assimilation capacity of *P. rigida* juveniles. Vegetative resprouts respond as their adult counterparts, maintaining similar mean assimilation rates during both seasons. This response in assimilation rates is clearly related to the advantages provided by connections to adult plants in terms of water and nutrient supply during the dry period. Low assimilation rates registered in *P. rigida* in the rainy season were probably associated with low PPFD intercepted and low leaf nitrogen content rather than stomatal limitations. Relative stomatal limitation in irrigated *P. rigida* juveniles was 18%, confirming that during juvenile phases stomatal restrictions were comparatively low in the wet period. Under natural shade conditions in the field, *P. rigida* juveniles showed a 77% reduction in the assimilation rate in relation to exposed individuals during the wet period. The shade effect was also observed through the light response curves (data not shown) with lower light saturation points (300–400 µmol m^{-2} s^{-1}) compared with exposed plants (600 µmol m^{-2} s^{-1}). The relatively high stomatal conductance registered during the wet season permitted a high C_i/C_a ratio, maximizing photosynthetic responses during periods of direct illumination. For juveniles of *Kielmeyera coriacea* and *Bowdichia virgiliodes* in the Brazilian

Cerrado, assimilation rates under natural shade were predicted to be 30–80% lower compared with exposed conditions (Nardoto et al. 1998; Kanegae et al. 2000). These authors conclude that shading produced by the established canopy was one of the major limitations for seedling growth.

Stomatal restrictions to photosynthesis, indicated by a lower C_i/C_a ratio at times of maximum evaporative demands, particularly in the dry season, have been reported for different savanna tree species (Franco 1998; Eamus and Prior 2001). A depression of the photosynthetic rate was observed in the studied species at times of maximum evaporative demands (especially in the midday hours during the dry season). Midday depression of assimilation rates have been reported for different tree species, mainly in those subjected to any combination of high radiation load, high temperature and low atmospheric and soil water content, as it commonly occurs in seasonally dry ecosystems (Prior et al. 1997a, b; Franco and Lüttge 2002). Since the light-response curves were constructed in the field, leaf temperature could become supraoptimal for photosynthesis, partially accounting for the general down regulation of photosynthetic processes shown in the light curves, especially in *P. rigida* juveniles during the dry season. Sarmiento et al. (1985) reported, for two dominant Venezuelan savanna tree species, optimum temperatures for photosynthesis of 25 and 28°C in *Curatella americana* and *Byrsonima crassifolia*, respectively, and a sharp fall above 33°C in both species. Leaf temperatures were tightly coupled to air temperature (1–2°C above air temperature) in our studied species, eventually reaching leaf temperatures close to or above 35°C, mainly during the dry season.

Casearia sylvestris resprouts, in spite of reaching quite negative $\Psi_{\min}$ during the dry season, maintained comparable assimilation rates, leaf *A*/*R*, CE and relative stomatal limitation as in the wet season. Likewise, *P. rigida* juveniles also showed a relatively high tolerance to water deficit maintaining a positive leaf *A*/*R* ratio (1.9) under conditions close to the turgor loss point. The CE found in water-stressed *P. rigida* juveniles was similar to that reported for species of semiarid ecosystems (Tezara et al. 1998). Juveniles of Cerrado woody species showed a strong tolerance to water deficit reaching zero photosynthesis at water potentials between −2.4 and −3.9 MPa (Sassaki et al. 1997; De Moraes and Prado 1998).

High photosynthetic rates in *C. sylvestris* resprouts could be associated with high leaf nitrogen content (Evans 1989). As in the present study, higher nitrogen content during the dry season has been reported for tropical dry forest tree species and may be linked to the synthesis and accumulation of osmotic neutral compounds that do not interfere with enzyme functions (Olivares and Medina 1992).

Intrinsic water use efficiency of the studied species was within the range found for several savanna tree species (Medina and Francisco 1994; Franco 1998; Eamus and Prior 2001), and tends to be higher in the dry season. This trend is similar to that reported for several savanna tree species with different phenologies (evergreen, deciduous or semi-deciduous) (Prado and De Moraes 1997; Prior et al. 1997a, b; Eamus and Prior 2001).

Comparing both reproducing strategies (sexual vs. vegetative), our results show, on the one hand, that besides functional differences derived from intrinsic species characteristics, resprouts were superior in their carbon assimilation capacity under water deficit conditions. The homeostatic behavior of gas exchange and the majority of water relation parameters in the resprouts could be advantageous in terms of growth and survival rates of young plants, particularly during dry spells that commonly occur during the wet season and also to overcome the dry season. Nevertheless, the better photosynthetic performance (higher photosynthetic rates in both seasons) of *C. sylvestris* resprouts could be diluted in terms of growth rates by its vegetative habit, characterized by an intensive interconnected network of resprouts sharing assimilates. On the other hand, in absence of a water deficit, juveniles of *P. rigida* had the advantage to be physiologically independent individuals, showing equal or even superior photosynthetic performance (similar *A*/Gs, lower dark respiration rates, higher CE, and higher SLA) that eventually could be translated in a more favorable whole-plant carbon balance and higher growth rates in wet habitats. Moreover, wide-range seed dispersion mediated by birds (Wütherich et al. 2001) and spatial patterns of seedling establishment sites nourished by adult co-specifics (García-Núñez et al. 2001) could favor sexual reproduction as a tree regeneration strategy.

In general, both species, showed strategies that tend to maximize carbon gain with a high water cost when this resource is not a limiting factor during the rainy season. This trend is mainly marked in *P. rigida* juveniles that showed lower IWUE than adult individuals of deep-rooted tree species (Medina and Francisco 1994).

Our results are in agreement with recent studies in tropical savanna and forests ecosystems (Hoffmann 1998; Dietze and Clark 2008; Busby et al. 2010), which point out that water stress seems to favor resprouting as a tree regeneration strategy and as highlighted by these authors, drier environmental scenarios could imply a shifting in species composition to species with prevalence of vegetative reproduction.

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