

Seasonal variation in the maximum rate of leaf gas exchange of canopy and understory tree species in an Amazonian semi-deciduous forest

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ABSTRACT

Leaf gas exchange, water potential, and specific leaf area of two tropical semi-deciduous tree species, *Brosimum lactescens* S. Moore and *Tovomita schomburgkii* Planch & Triana, were quantified to establish how these properties were affected by seasonal variations in rainfall and leaf canopy position. The study was conducted at a site near Sinop Mato Grosso, Brazil, which is located within the ecotone of savanna and tropical rain forest. Both species exhibited significant declines in leaf water potential (Ψ_L), specific leaf area, area- and mass-based light saturated photosynthesis and dark respiration, and maximum stomatal conductance during the dry-season, suggesting that leaf structural properties and gas exchange are significantly altered by drought that develops during the 4-month dry season. Internal leaf CO₂ concentrations (C_i) were consistently lower during the dry season suggesting that the decline in maximum photosynthesis was due in part to a decline in stomatal conductance. However, seasonal variations in leaf gas exchange were larger for upper-canopy leaves, indicating an important interaction between drought stress and canopy position. The seasonal variation in leaf gas exchange and morphology was presumably due to a combination of drought stress and leaf lifespan. The results of this study suggest that drought has important implications for the leaf physiology and morphology of semi-deciduous Amazonian forest trees.

Key words: Brazil, *Brosimum lactescens*, climate change, ecotone, photosynthetic response, *Tovomita schomburgkii*, tropical transitional forest.

INTRODUCTION

Amazonian semi-deciduous forests are located within the savanna (cerrado)-rainforest ecotone along the southern and eastern borders of the Amazon Basin. Under current climate conditions the annual carbon budget of these forests appears to be in balance (Vourlitis et al. 2001, 2004, 2005; Keller et al. 2004; Priante et al. 2004). However, semi-deciduous forests of the southern Amazon Basin have experienced significant temperature increases over the last 30 years (Malhi and Wright 2005) and are also subjected to periodic warming and

drought during El Niño (Potter et al. 2004). Drought can reduce net primary production (NPP), net ecosystem production (NEP), and evapotranspiration (Nepstad et al. 2002; Priante et al. 2004; Vourlitis et al. 2002, 2008), and cause an increase tree mortality (Condit et al., 1995). Thus, understanding how drought influences rates of C and H₂O exchange is important for understanding current and future rates of NPP, NEP, and evapotranspiration.

Seasonal patterns of C and H₂O exchange are affected by variations in leaf gas exchange, which in turn

are regulated by a trade-off between seasonal patterns in rainfall and light availability. While these variations may be small in amplitude, they can significantly alter the physiological behavior of plants (Hogan et al. 1995; Miranda et al. 2005). In general, rates of photosynthesis increase considerably during the wet-season, even though an increase in cloudiness can limit light availability, because plants are exposed to high levels of soil water content, while declines in water availability during the dry season cause an overall reduction in leaf water potential and maximum photosynthesis (Percy 1987, Miranda et al. 1996, Sun et al. 1996, Miranda et al. 2005). However, the effects of seasonal drought are not likely to be similar for canopy and understory leaves and trees because of differences in physiology and resource allocation, phenology, and/or canopy growth microclimate (Boardman 1977; Cabral et al. 1996). For example, canopy trees are exposed to higher light, warmer temperatures, and lower atmospheric humidity than understory trees (Cabral et al. 1996), which can limit rates of gas exchange (Chaves et al. 1992). Leaves in the upper-canopy may have higher tissue N concentration, which will afford higher rates of maximum photosynthesis but at a higher respiratory cost (Reich and Walters 1994; Meir et al. 2001). Large trees may also have deep roots with access to water that can sustain high rates of gas exchange during the dry season (Nepstad et al. 1994).

Although a good deal of research has addressed how drought and light availability affect rates of photosynthesis in tropical forests, less is known about how these rates are affected by seasonality. This research is especially important in seasonally dry tropical forests, which experience significant temporal variation in rainfall and soil water content. Climate change from deforestation and fossil fuel combustion is anticipated to increase the magnitude and/or duration of seasonal drought (Cramer et al. 2005; Cowling et al., 2005), and semi-deciduous tropical forests are likely to be very sensitive climate change due to their transitional nature (Longman and Jenik 1992; Arris and Eagleson 1994; Vourlitis et al. 2005). Thus, the objective of this study was to evaluate how leaf gas exchange and related traits were influenced by seasonality and canopy position in a semi-deciduous, tropical transitional forest in the southern Amazon Basin. We hypothesize that seasonal variations in gas exchange

will be large and correlated with variations in rainfall; however, the magnitude of the seasonal variation in gas exchange will be a function of canopy position.

MATERIALS AND METHODS

Site and species descriptions: The study was conducted in an intact, mature, upland (*terra firme*) semi-deciduous forest located near Sinop, Mato Grosso, Brazil (11°24.75'S; 55°19.50'W) at an elevation of 423 m above sea level. This region is within the rainforest-savanna transition zone, which in northern Mato Grosso lies between 9 and 14°S latitude (Ackerly et al. 1989). Maximum canopy height is 25–28 m, and a survey of the area indicated that there are 35 families and 80 species of trees with a diameter ≥ 10 cm, including *Protium sagotianum* Marchland, *Brosimum lactescens* (S. Moore) C. C. Berg, *Tovomita schomburgkii* Planch & Triana, and *Qualea paraensis* Ducke. However, three species, *P. sagotianum* (Burseraceae), *B. lactescens* (Moraceae), and *T. schomburgkii* (Clusiaceae), make up about 50% of individuals. Leaf area index (LAI) varies between 6.0 m²m⁻² at the end of the wet season (April) and 2.5 m²m⁻² at the end of the dry season (August) reflecting the semi-deciduous nature of the forest (Vourlitis et al. 2004; Sanches et al. 2008a). The soil is a quartzipsamments with a sandy, porous texture that drains rapidly after rainfall. The mean annual air temperature is approximately 24°C, and average annual rainfall is about 2.0 m (Vourlitis et al. 2002). About half of the annual rainfall is received during the December–February wet season while only about 1% occurs during the June–September dry season (Vourlitis et al. 2002).

Two species located near a 40 m tall tower at the study site were selected for measurement due to their proximity to the tower or because they were short enough to be measured from the forest floor. *Brosimum lactescens* (Moraceae) is a semi-deciduous canopy emergent tree found in Amazonian evergreen and semi-deciduous forests (Ackerly et al. 1989, Lorenzi 2000). At our study site this species is 25–28 m tall with an average (± 1 SD) diameter of 24.6 \pm 11.5 cm. *Tovomita schomburgkii* (Clusiaceae) individuals are 4–17 m tall and are found in Amazonian forests in northeastern and central Brazil (Mariz 1974). At our study site these species account for 30% of all trees ≥ 10 cm diameter.

Gas exchange measurements: Photosynthetic light-response curves were generated using a portable photosynthesis system (model LI-6400, LI-COR, Lincoln, NE., USA). One *B. lactescens* and three *T. schomburgkii* individuals were sampled during each season, because these trees were accessible either from the forest floor or from the tower at varying heights. In order to obtain multiple *in situ* measurements high within the forest canopy the leaves had to be readily accessible from the tower, which is why only one *B. lactescens* individual was sampled.

B. lactescens leaves were measured at canopy heights of 28, 20, and 12 m, while *T. schomburgkii* leaves were measured at 12, 10, and 1 m. Twelve light curves were generated at each of these heights during both the dry (July 2005) and wet (January 2006) seasons. To determine the effect of humidity on leaf gas exchange half of the light curves ($n = 6$) were generated at a relative humidity of 40% and half were generated at a relative humidity of 70%. These humidity levels corresponded to a leaf-air vapor pressure deficit of 2.6 kPa and 1.5 kPa, respectively given the temperature conditions associated with the photosynthesis measurements, and are indicative of the mid-day relative humidity and atmospheric vapor pressure deficit that canopy leaves are exposed to during the dry and wet seasons, respectively (Vourlitis et al. 2004; 2005, 2008). Leaves were exposed to $400 \mu\text{mol mol}^{-1} \text{CO}_2$ and photosynthetic photon flux density (Q) levels of 2000, 1500, 1000, 500, 250, 100, 50 and $0 \mu\text{mol quanta m}^{-2}\text{s}^{-1}$ using the LI-6400 LED light source. Chamber temperature was held at 28°C for all measurements.

Additional measurements: Leaf water potential (Ψ_L) was measured after every light curve using a pressure chamber (model 670, PMS Instrument Company, Albany, OR, USA) on fresh leaves adjacent to those measured for gas exchange. After measurement of Ψ_L digital photos were taken of the leaves and the one-sided area was quantified using digital-image processing software (Sigma Scan Pro, version 5.0, Aspire Software International, Leesburg, VA, USA). Leaves were then dried at 70°C for at least 48 hours to determine dry mass, and the projected specific leaf area (SLA) was calculated as the ratio of one-sided leaf area per unit dry weight.

Data analysis and photosynthesis modeling: Area-based photosynthetic data were fitted to a model that

estimated net CO_2 assimilation (P_{net} ; $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$) as a function of Q :

$$P_{\text{net}} = \frac{(\Phi Q + P_{\text{marea}} - ((\Phi Q + P_{\text{marea}})^2 - 4\theta\Phi Q P_{\text{marea}})^{0.5})}{2\theta} \quad (1)$$

where Φ = the maximum quantum yield ($\mu\text{mol CO}_2 \mu\text{mol Q}^{-1}$), P_{marea} = the maximum area-based rate of net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$), and θ = the dimensionless convexity of the curve (Thornley 1976, Ögren and Evans 1993). Non-linear least squares regression was used to estimate the model coefficients (θ , Φ and P_{marea}). Maximum stomatal conductance (g_{max}), and internal CO_2 concentrations (C_i) were calculated using the portable photosynthesis system using the same levels of CO_2 , irradiance, temperature, and relative humidity discussed above, while area-based dark respiration (R_{darea}) was calculated when $Q = 0 \mu\text{mol quanta m}^{-2}\text{s}^{-1}$. Mass-based maximum photosynthesis (P_{mmass}) and dark respiration (R_{dmass}) rates were calculated by multiplying area-based rates by SLA.

Variations in Ψ_L and SLA across season and canopy height were statistically evaluated using a two-factor analysis of variance. Multivariate analysis of variance (MANOVA) was used to determine whether there were differences in P_{marea} , P_{mmass} , R_{darea} , R_{dmass} , g_{max} , and C_i across season, height, and relative humidity. The response of these variables as a function of season and canopy height did not differ with humidity, so in further analyses data were pooled across humidity. In the event of a significant season x height interaction a one-way analysis of variance was used to determine whether differences existed across height and/or season.

RESULTS

Leaf water potential and specific leaf area: Leaf water potential (Ψ_L) declined during the dry season for *T. schomburgkii* and *B. lactescens*, but understory leaves experienced a smaller seasonal decline in Ψ_L than mid- and upper-canopy leaves (Fig. 1). For example, the Ψ_L of *T. schomburgkii* mid-canopy leaves (12 m) was approximately 0.3 MPa lower during the dry season, while the average decline in Ψ_L for *T. schomburgkii* understory leaves (10 m and 1 m) was only about 0.15 MPa. The Ψ_L of *B. lactescens* upper-canopy (28 m) and mid-canopy (20 m and 12 m) leaves was on average 0.65 MPa lower during the dry season.

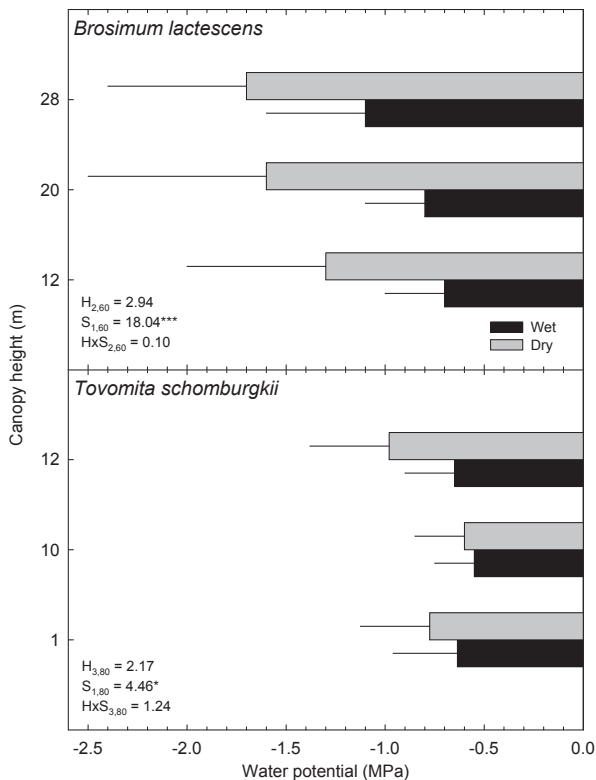


Figure 1. Mean (\pm SD) leaf water potential for *Tovomita schomburgkii* and *Brosimum lactescens* during the wet season (black bars) and the dry season (grey bars). $N = 12$ measurements per canopy height, season, species combination. Also shown are the results (F -statistics and degrees of freedom) from a 2-way ANOVA for differences between season (S), canopy height (H), and the season \times height interaction (H \times S). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

The specific leaf area (SLA) of *T. schomburgkii* differed significantly among seasons and canopy heights; however, *B. lactescens* leaves only exhibited statistically significant differences in SLA on a seasonal basis (Fig. 2). During the dry season, the SLA for *T. schomburgkii* ranged from an average (\pm SD) of $198 \pm 50.1 \text{ cm}^2 \text{ g}^{-1}$ in the forest understory to $73 \pm 25.8 \text{ cm}^2 \text{ g}^{-1}$ in the mid-canopy, while during the wet season, the average SLA of mid-canopy leaves increased by almost 30%. Seasonal variation in SLA notwithstanding, the SLA of *T. schomburgkii* was negatively correlated with height. In contrast, seasonal variations in SLA were significantly positively correlated with leaf water potential for *B. lactescens*. The SLA of both mid-canopy and upper-canopy leaves of *B. lactescens* was approximately $83 \text{ cm}^2 \text{ g}^{-1}$ during the dry season, but during the wet-season, the SLA of upper-canopy leaves remained at $85 \text{ cm}^2 \text{ g}^{-1}$ while mid-canopy leaves

showed an increase of more than 20% to $110 \pm 6.3 \text{ cm}^2 \text{ g}^{-1}$ (Fig. 2).

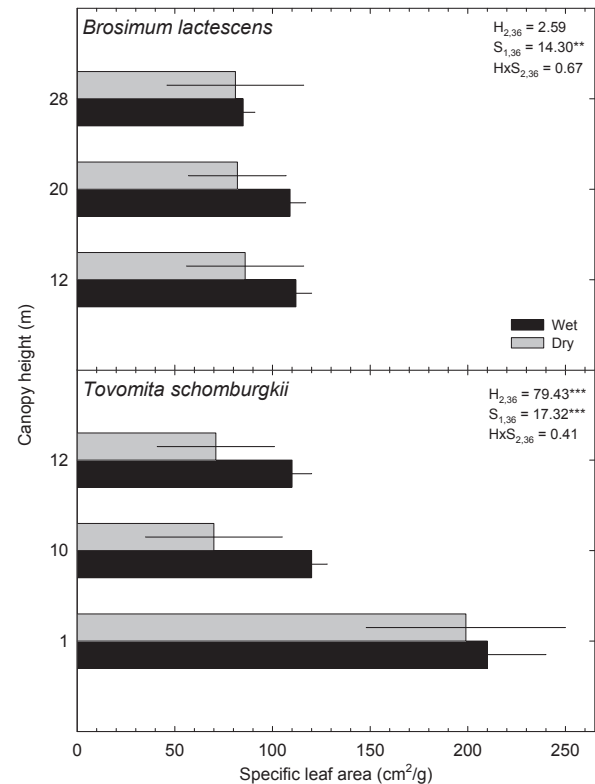


Figure 2. Mean (\pm SD) specific leaf area for *Tovomita schomburgkii* and *Brosimum lactescens* during the wet season (black bars) and the dry season (grey bars). $N = 8$ measurements per canopy height, season, species combination. Also shown are the results (F -statistics and degrees of freedom) from a 2-way ANOVA for differences between season (S), canopy height (H), and the season \times height interaction (H \times S). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Leaf gas exchange: The photosynthetic light-response of both tree species was well described by equation 1, and the coefficient of determination (r^2) values ranging between 0.95-0.97 (Table 1). The effect of humidity on the estimated coefficients was minimal; however, both species exhibited consistent seasonal differences in the quantum yield (Φ), maximum rate of light-saturated photosynthesis (P_{marea}), and the convexity index of the hyperbolic curve (Table 1). Values of the Φ and P_{marea} were on average 2 and 1.7-times higher during the wet-season, while values of the convexity index were about 50% lower in the wet-season indicating a lower propensity of leaf photosynthesis to saturate at higher levels of Q .

Table 1. Model coefficients quantum yield (Φ ; $\mu\text{mol CO}_2 \mu\text{mol Q}^{-1}$), maximum photosynthesis (P_{marea} ; $\mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$), and convexity (θ ; dimensionless) calculated for *Tovomita schomburgkii* and *Brosimum lactescens* trees at 40% and 70% relative humidity using equation 1 (see Methods). Also shown is the coefficient of determination (r^2) and average estimated values for each species x height combination (n = 6 measurements).

40% Relative humidity		Φ		P_{marea}		θ		r^2	
Species	Height	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>T. schomburgkii</i>	1 m	0.028	0.038	2.96	3.72	0.74	0.50	0.97	0.96
	10 m	0.033	0.038	4.31	5.47	0.84	0.70	0.98	0.96
	12 m	0.024	0.046	4.31	7.76	0.72	0.32	0.95	0.97
<i>B. lactescens</i>	12 m	0.028	0.040	4.10	5.32	0.51	0.24	0.97	0.95
	20 m	0.017	0.035	3.14	6.50	0.75	0.61	0.94	0.97
	28 m	0.012	0.043	3.77	7.26	0.67	0.14	0.91	0.95
70% Relative humidity		Φ		P_{marea}		θ		r^2	
Species	Height	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>T. schomburgkii</i>	1 m	0.025	0.036	3.08	4.04	0.84	0.39	0.97	0.96
	10 m	0.032	0.046	4.10	6.29	0.90	0.33	0.96	0.97
	12 m	0.022	0.052	3.98	8.36	0.60	0.29	0.94	0.97
<i>B. lactescens</i>	12 m	0.032	0.052	4.11	5.73	0.56	0.34	0.97	0.96
	20 m	0.022	0.036	3.11	7.07	0.41	0.29	0.93	0.97
	28 m	0.011	0.041	4.49	8.01	0.56	0.32	0.92	0.96

The results of the MANOVA indicated a significant main effect of season and height, and a significant season by height interaction on area- and mass-based light saturated photosynthesis (P_{marea} , P_{mass}), area- and mass-based dark respiration (R_{darea} , R_{dmass}), maximum stomatal conductance (g_{max}), and internal CO_2 concentration (C_i) (Table 2). Both species, regardless of their canopy position, exhibited significantly higher rates of P_{marea} during the wet season, though the smallest increases were seen in understory leaves (Fig. 3). Upper-canopy (20 and 28 m) *B. lactescens* and mid-canopy (12 m) *T. schomburgkii* leaves exhibited the highest rates of P_{marea} , with mean (\pm SD) rates of 7.2 ± 0.84 and $7.9 \pm 0.81 \mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$, respectively. Mid-canopy *T. schomburgkii* leaves experienced a 40-50% increase in P_{marea} during the wet season, while understory leaves exhibited smaller increases of 15-30%. Upper-canopy leaves of *B. lactescens* experienced a 40-55% increase in P_{marea} , while mid-canopy leaves increased by 25-30%. P_{marea} increased with canopy height during both the wet and dry seasons in *T. schomburgkii* leaves, but increases with height were only observed during the wet season for *B. lactescens*. Rates of P_{mass} responded similarly to rates of P_{marea} (data not shown), increasing significantly during the wet season at all canopy heights; however, canopy position did not have as large an effect on rates of P_{mass} .

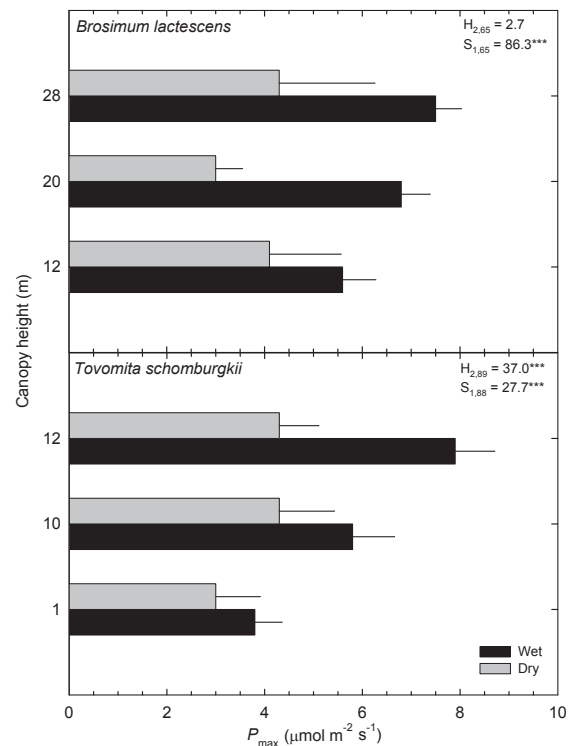


Figure 3. Mean (\pm SD) area-based maximum net photosynthesis (P_{marea}) for *Tovomita schomburgkii* and *Brosimum lactescens* during the wet season (black bars) and the dry season (grey bars). N = 12 measurements per canopy height, season, species combination. Also shown are the results (F -statistics and degrees of freedom) from individual 1-way ANOVAs for differences between season (S) and canopy height (H). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Data were pooled across humidity because the leaf gas exchange response did not differ with humidity. One-way ANOVAs were conducted because MANOVA analyses revealed a significant season x height interaction.

Table 2. Response of area- and mass-based maximum photosynthesis (P_{max} , P_{mass}), area- and mass-based dark respiration (R_{darea} , R_{dmass}), maximum stomatal conductance (g_{max}), and internal CO_2 concentration (C_i) of *Tovomita schomburgkii* and *Brosimum lactescens* to variations in humidity, height, and season. Shown are the results of a Multivariate Analysis of Variance (MANOVA) including the probability of type-I error (p -value), the F -statistic calculated using Wilks' criterion, and the associated effect and error degrees of freedom (effect, error df).

<i>Tovomita schomburgkii</i>	F -statistic	df	p
Humidity	1.20	6,73	0.31
Height	141.48	12,146	< 0.001
Season	91.21	6,73	< 0.001
Humidity x Height	0.77	12,146	0.68
Humidity x Season	1.85	6,73	0.10
Height x Season	11.74	12,146	< 0.001
Humidity x Height x Season	0.77	12,146	0.68
<i>Brosimum lactescens</i>	F -statistic	df	p
Humidity	1.00	6,49	0.44
Height	41.98	12,98	< 0.001
Season	446.24	6,49	< 0.001
Humidity x Height	0.55	12,98	0.88
Humidity x Season	1.02	6,49	0.42
Height x Season	33.47	12,98	< 0.001
Humidity x Height x Season	0.26	12,98	0.99

Average rates of R_{darea} and R_{dmass} were also consistently higher during the wet season for both species. The smallest seasonal variation in R_{darea} was observed in the understory and upper-canopy leaves, which experienced increases of 15-25% in the wet season, whereas mid-canopy leaves displayed seasonal increases of 30-50% (Fig. 4). R_{darea} also tended to increase with height in the forest canopy where leaves were exposed to more sunlight. The R_{dmass} (data not shown) response to canopy height in both species was very similar to the response of P_{mass} , with *B. lactescens* exhibiting very little change with canopy height within season and *T. schomburgkii* exhibiting large differences in the dry season only.

During the dry season, maximum stomatal conductance (g_{max}) was consistently less than $65 \text{ mmol m}^{-2}\text{s}^{-1}$ at all canopy heights; however during the wet season, g_{max} increased considerably in leaves higher in the canopy that are exposed to higher levels of irradiance, reaching levels as high as $175 \text{ mmol m}^{-2}\text{s}^{-1}$ (Fig. 5). Understory leaves also experienced an increase in g_{max} during the wet-season, but it was much smaller than in leaves exposed to more sunlight. Mid-canopy (12 m) *B. lactescens* leaves exhibited an increase of 52-57% while the understory leaves of *T. schomburgkii* had the smallest increase of 18-42%.

Values of C_i were consistently higher in the wet-season than in the dry season (Fig. 5). The largest seasonal differences in C_i were observed in mid- and upper-canopy plants, which exhibited increases of 7-12% in the wet season, while smaller increases were observed in the understory, ranging from 0-5%. The average (\pm SD) ratio of internal CO_2 concentration (C_i) to ambient atmospheric CO_2 (C_a) was 0.64 ± 0.03 during the dry season and 0.71 ± 0.03 during the wet season. The optimal ratio for C_3 plants is 0.70 (Wong et al. 1979), which indicates that photosynthesis may have been limited by available internal CO_2 during the dry season (Miranda et al. 2005).

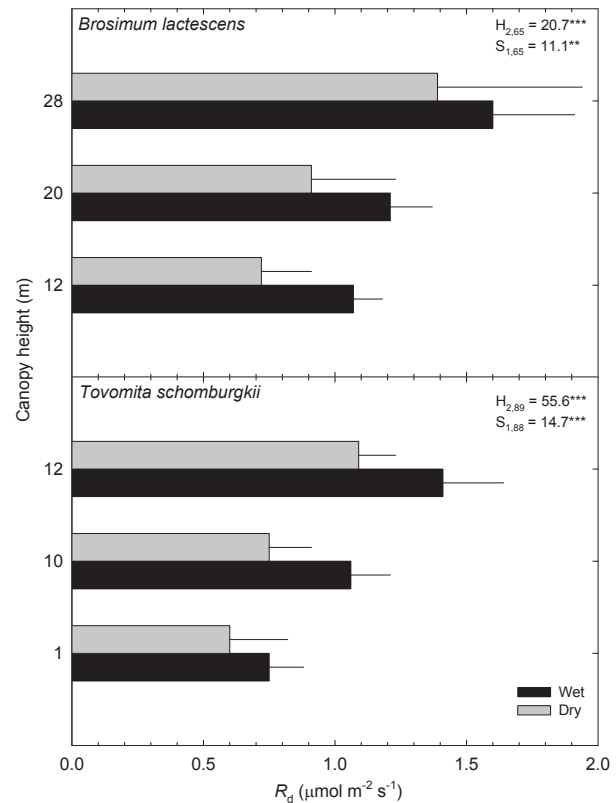


Figure 4. Mean (\pm SD) area-based dark respiration (R_{darea}) for *Tovomita schomburgkii* and *Brosimum lactescens* during the wet season (black bars) and the dry season (grey bars). $N = 12$ measurements per canopy height, season, species combination. Also shown are the results (F -statistics and degrees of freedom) from individual 1-way ANOVAs for differences between season (S) and canopy height (H). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Data were pooled across humidity because the leaf gas exchange response did not differ with humidity. One-way ANOVAs were conducted because MANOVA analyses revealed a significant season x height interaction.

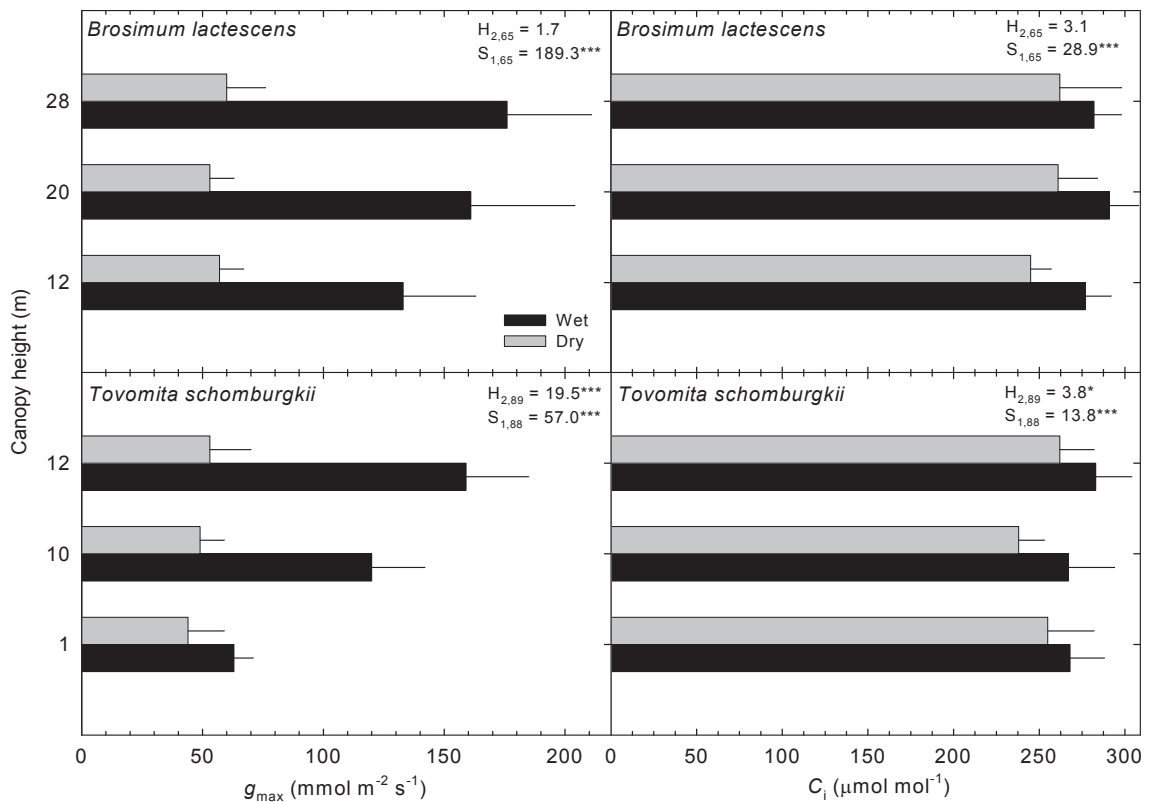


Figure 5. Mean (\pm SD) area-based stomatal conductance (g_{max} ; left-panels) and internal leaf CO_2 concentration (C_i ; right-panels) for *Tovomita schomburgkii* and *Brosimum lactescens* during the wet season (black bars) and the dry season (grey bars). $N = 12$ measurements per canopy height, season, species combination. Also shown are the results (F -statistics and degrees of freedom) from individual 1-way ANOVAs for differences between season (S) and canopy height (H). *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Data were pooled across humidity because the leaf gas exchange response did not differ with humidity. One-way ANOVAs were conducted because MANOVA analyses revealed a significant season \times height interaction.

DISCUSSION

We hypothesized that the leaf gas exchange of *T. schomburgkii* and *B. lactescens* would be significantly lower in response to seasonal drought; however, the decline in gas exchange would be larger for leaves in the upper canopy. Our results support this hypothesis, as all measures of leaf gas exchange were significantly lower during the dry season and the significant season \times height interaction indicates that the sensitivity of seasonal drought was dependent on canopy position (Table 2).

Large seasonal variations in leaf gas exchange were expected given that the majority of the rainfall in this region falls during the wet season, while only 1% falls during the dry season (Vourlitis *et al.* 2002, Keller *et al.* 2004). Since the soils in the study site drain rapidly after rainfall, the forest can experience

significant drought during the dry season (Malhi *et al.* 1998, Williams *et al.* 1998). With drought plants tend to close their stomata due to increasing evaporative demand at the surface of the leaf, which in turn decreases leaf photosynthetic rates (Meinzer *et al.* 1993), and even slight decreases in leaf water potential (Ψ_L) can trigger stomatal closing (Wright *et al.* 1992, Allen and Pearcy 2000). Interestingly, recent data suggests that rates of sap flow for *B. lactescens* and *T. schomburgkii* and whole-forest evapotranspiration may be relatively stable over seasonal cycles (Vourlitis *et al.* 2008), suggesting that plants have access a stable groundwater source (Nepstad *et al.* 1994). The stability in canopy evapotranspiration appears to be driven by seasonal trade-offs in net radiation (lower in the wet season due to cloud cover) and atmospheric evaporative demand (higher in the dry season due to lower atmospheric humidity). The high evaporative demand experienced during

the dry season, coupled with possible limitations in hydraulic conductance, would lead to a decline in Ψ_L and g_{max} (Meinzer et al. 1993; Vourlitis et al. 2008).

Understory leaves of *T. schomburgkii* experienced the smallest seasonal variation in P_{marea} , P_{mmax} , and g_{max} , perhaps because these leaves are exposed to lower levels of sunlight and experience a lower evaporative demand (Whitehead et al. 1981, Tobin et al. 1999). These tree species also exhibited smaller seasonal variations in sap flow than taller trees in the forest canopy (Vourlitis et al. 2008), suggesting more consistent seasonal rates of leaf gas exchange. The internal CO_2 concentrations (C_i) of these understory leaves remained relatively constant between seasons, decreasing by less than 6% during the dry season, indicating relatively small stomatal limitations to CO_2 diffusion. Upper-canopy *B. lactescens* leaves and mid-canopy leaves of both species exhibited substantially larger seasonal variation in P_{marea} , P_{mmax} , and g_{max} than understory *T. schomburgkii* leaves. In all cases, the Ψ_L in the mid- and upper-canopy was significantly higher during the wet season, so it appears that these leaves experienced less water stress during the wet season and were able to increase levels of stomatal conductance (Whitehead et al. 1981; Yordanov et al. 2000). However, the significant increase in photosynthetic rates that was observed in upper-canopy leaves does not appear to be fully explained by the increased diffusion of CO_2 considering that the C_i during the wet season increased by only as much as 12%. Additionally, the increase in photosynthetic rates during the wet season did not coincide with increased leaf nitrogen (data not shown), which is known to affect the rate at which plants can fix CO_2 for use in photosynthesis (Evans 1989).

Large seasonal variation in P_{marea} , P_{mmax} , and g_{max} may have been caused in part by differences in leaf age (Hogan 1988; Reich et al. 1991; Osada et al. 2001). Leaves generally develop and become fully expanded during the wet season when photosynthetic rates, SLA, and stomatal conductance are highest (Miyaji et al. 1997). These leaf traits are negatively correlated with leaf age (Chabot and Hicks 1982; Field and Mooney 1986) and decline throughout the year until the dry season when leaf shedding occurs in response to drought (Reich and Borchert 1984; Sanches et al. 2008b).

Our data suggest that seasonal variations in rainfall distribution and drought significantly alter the leaf gas exchange of tropical understory and canopy tree species.

These data are consistent with other studies in tropical savanna (Franco 1998; Prado et al. 2004), semi-deciduous forest (Hogan et al. 1995; Miranda et al. 2005), and rainforest (de A. Sa et al. 1996; Bonal et al. 2000), and suggest that periodic drought represents a key control on tropical tree productivity. Given the anticipated 3-4°C increase in average annual temperature for the Brazilian tropics (Giorgi et al. 2001), the potential magnitude and/or duration of seasonal drought is likely to increase. Anticipated changes in precipitation are expected to be small, ranging from 0.0-1.0 mm d⁻¹, but many models predict an intensification of the dry season in eastern South America (Malhi et al. 1999; Giorgi et al. 2001). Higher temperatures may lead to increased water stress (Malhi et al. 1999), and species that are more vulnerable to decreases in water potential will have a decreased gas exchange and likelihood of survival. Thus, changes in gas exchange may significantly alter the species composition and productivity.

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REFERENCES

- Ackerly, D.D., W.W. Thomas, C.A.C. Ferreira and J.R. Pirani. 1989. The forest-cerrado transition zone in southern Amazonia: results of the 1985 Projeto Flora Amazônica Expedition to Mato Grosso. *Brittonia* 41:113-128.
- Allen, M.T. and R.W. Pearcy. 2000. Stomatal behavior and photosynthetic performance under dynamic light regimes in a seasonally dry tropical rain forest. *Oecologia* 122:470-478.
- Arris LL & PS Eagleson (1994) A water use model for locating the boreal/deciduous forest ecotone in eastern North America. *Water Res. R.* **30**: 1-9.
- Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28:355-377.
- Bonal, D., T. S. Barigah, A. Granier, and J. M. Guehl (2000) Late-stage canopy tree species with extremely low $\delta^{13}C$ and high stomatal sensitivity to drought in the tropical rain forest of French Guiana. *Plant, Cell and Environment* 23: 445-459.
- Cabral, O. M. R., A. L. C McWilliam and J. M. Roberts (1996) In-canopy microclimate of Amazonian forest and estimates of transpiration. Pages 207-220 in Gash, J. H. C., C. A. Nobre, and R. M. Roberts, and R. I. Victoria (eds.) Amazonian climate and deforestation. J. M. Wiley and Sons, New York.
- Chabot, B.F. and D.J. Hicks. 1982. The ecology of leaf life spans. *Annual Review of Ecological Systems* 13:229-259.

- Chaves MM, ML Osorio, J Osorio & JS Pereira (1992) The photosynthetic response of *Lupinus albus* to high temperature is dependent on irradiance and leaf water status. *Photosynthetica* 27: 521-528.
- Chazdon, R.L. and N. Fetcher. 1984. Light environments of tropical forests. In *Physiological Ecology of Plants in the Wet Tropics*. Eds. E. Medina, H.A. Mooney and C. Vasquez-Yanes. Junk, The Hague. pp 27-36.
- Condit, R., S.P. Hubbell and R.B. Foster. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419-439.
- Cowling, S.A., R.A. Betts, P.M. Cox, V.J. Ettwein, C.D. Jones, M.A. Maslin and S.A. Spall. 2005. Modelling the past and future fate of the Amazonian forest. Pages 191-198 in Mahli, Y and O. L. Phillips (eds), *Tropical Forests and Global Atmospheric Change*, Oxford University Press, Oxford, UK.
- Cramer, W., A. Bondeau, S. Schaphoff, W. Lucht, B. Smith, and S. Sitch. 2005. Twenty-first century atmospheric change and deforestation: Potential impacts on tropical forests. Pages 17-30 in Mahli, Y and O. L. Phillips, editors. *Tropical Forests and Global Atmospheric Change*. Oxford University Press, Oxford, UK.
- de A. Sa., T. D., J. de P. R. da Costa, and J. M. Roberts, Forest and pasture conductances in southern Para, Amazonia, pages 241-264 in Gash, J. H. C., C. A. Nobre, J. M. Roberts & R. L. Victoria (eds), *Amazonian climate and deforestation*. J. M. Wiley and Sons, New York, NY, USA, 1996.
- Evans, J.R. 1989. Partitioning of nitrogen between and within leaves grown under different irradiances. *Australian Journal of Plant Physiology* 16:533-548.
- Field, C. and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function*. Ed. T.J. Givnish. Cambridge University Press, Cambridge. pp 25-55.
- Franco, A. C. 1998. Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen savanna species. *Plant Ecology* 136: 69-76.
- Giorgi, F., B. Hewitson, J. Christensen, M. Hulme, H. von Storch, P. Whetton, R. Jones, L. Mearns, and C. Fu. 2001. Regional climate information-Evaluation and projections. Pages 585-638 in Houghton, J. T., Y. Ding, D. J. Griggs, M. Nogour, P. F. van der Linder, X. Dai, K. Maskell, and C. A. Johnson, editors. *Climate Change 2001: The Scientific Basis*. Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.
- Hogan, K.P. 1988. Photosynthesis in two neotropical palm species. *Functional Ecology* 2:371-377.
- Hogan, K.P., A.P. Smith and M. Samaniego. 1995. Gas exchange in six tropical semi-deciduous forest canopy tree species during the wet and dry seasons. *Biotropica* 27:324-333.
- Keller, M., A. Alencar, G.P. Asner, B. Braswell, M. Bustamante, E. Davidson, T. Feldpausch, E. Fernandez, M. Goulden, P. Kabat, B. Kruijt, F. Luizão, S. Miller, D. Markewitz, A.D. Nobre, C.A. Nobre, N. Priante-Filho, H. Da Rocha, P. Silva Dias, C. Von Randow and G.L. Vourlitis. 2004. Ecological research in the large-scale biosphere-atmosphere experiment in Amazonia: Early results. *Ecological Applications* 14:S3-S16.
- Longman, K.A. and J. Jenik. 1992. Forest-savanna boundaries: General considerations. In *Nature and Dynamics of Forest-Savanna Boundaries*. Eds. P.A. Furley, J. Proctor and J.A. Ratter. Chapman and Hall, Inc., New York. pp 3-20.
- Lorenzi, H. 2000. *Avores Brasileiras*, Vol. 1. Instituto Plantarum de Estudos da Flora, Ltd., São Paulo, Brazil.
- Malhi, Y. and J. Wright. 2005. Late-twentieth-century patterns and trends in the climate of tropical forest regions. In *Tropical Forests and Global Atmospheric Change*. Eds. Y. Malhi and O.L. Phillips. Oxford University Press, Oxford. pp 3-16.
- Malhi, Y., A.D. Nobre, J. Grace, B. Kruijt, M.G.P. Pereira, A. Culf and S. Scott. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research* D24:31593-31612.
- Malhi, Y., D.D. Baldocchi and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment* 22:715-740.
- Mariz, G. 1974. Two new species of *Tovomita* Aublet (Guttiferae) from northeastern Brazil. *Bulletin of the Torrey Botanical Club* 101:367-371.
- Meinzer, F.C., G. Goldstein, N.M. Holbrook, P. Jackson and J. Cavalier. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant, Cell and Environment* 16:429-436.
- Meir, P., J. Grace and A.C. Miranda. 2001. Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature. *Functional Ecology* 15:378-387.
- Miranda, A.C., H.S. Miranda, J. Lloyd, J. Grace, J.A. Mcintyre, P. Meir, P. Riggan, R. Lockwood and J. Brass. 1996. Carbon dioxide fluxes over a cerrado *sensu stricto* in central Brazil. In *Amazonian deforestation and climate* Eds. J.H.C. Gash, C.A. Nobre, J.M. Roberts and R.L. Victoria. J.M. Wiley and Sons, New York. pp 353-361.
- Miranda, E.J., N. Priante, P.C. Priante, J.H. Campelo Jr., G.S. Suli, C.L. Fritzen and G.L. Vourlitis. 2005. Leaf and forest CO₂ exchange of a transitional tropical forest in southern Amazonia. *Journal of Tropical Ecology* 21:451-460.
- Miyaji, K., W.S. Da Silva and P.T. Alvim. 1997. Productivity of leaves of a tropical tree, *Theobroma cacao*, grown under shading, in relation to leaf age and light conditions within the canopy. *New Phytologist* 137:463-472.
- Nepstad DC *et al.* (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon Forest. *Journal of Geophysical Research* 107(D20): 8085, doi: 10.1029/2001JD000360.
- Ögren, E. and J.R. Evans. 1993. Photosynthetic light-response curves I. The influence of CO₂ partial pressure and leaf inversion. *Planta* 189:182-190.
- Osada, N., H. Takeda, A. Furukawa and M. Awang. 2001. Leaf dynamics and maintenance of tree crowns in a Malaysian rain forest stand. *Journal of Ecology* 89:774-782.
- Pearcy, R.W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Functional Ecology* 1:169-178.
- Potter, C, S Klooster, M Steinbach, PN Tan, V Kumar, S Shekhar & CR Carvalho (2004) Understanding global teleconnections of climate to regional model estimates of Amazon ecosystem carbon fluxes. *Glob. Chan. Biol.* 10: 693-703.
- Prado, C. H. B. A., Z. Wenhui, M. H. C. Rojas, and G. M. Souza. 2004. Seasonal leaf gas exchange and water potential in a woody cerrado species community. *Brazilian Journal of Plant Physiology* 16: 7-16.
- Priante-Filho, N., G.L. Vourlitis, M.M.S. Hayashi, J. de S. Nogueira, J.H. Campelo Jr., P.C. Nunes, L.S.E. Sousa, E.G. Couto, W. Hoeger, F. Raiter, J.L. Trienweiler, E.J. Miranda, P.C. Priante, C.L. Fritzen, M. Lacerda, L.C. Pereira, M.S. Biudes, G.S. Suli, S. Shiraiwa, S.R. Do Paulo and M. Silveira. 2004. Comparison of the mass and energy exchange of a pasture and a mature transitional tropical forest of the southern Amazon Basin during a seasonal transition. *Global Change Biology* 10:863-876.
- Reich, P.B. and M.B. Walters. 1994. Photosynthesis-nitrogen relations in Amazonian tree species. *Oecologia* 97:73-81.
- Reich, P.B. and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72:61-74.
- Reich, P.B., C. Uhl, M.B. Walters and D.S. Ellsworth. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* 86:16-24.
- Sanches L, NLR Andrade, JS Nogueira, MS Biudes & GL Vourlitis (2008a) Índice de área foliar em floresta de transição Amazonia cerrado em diferentes métodos de estimativa. *Ciência e Natura* 30: 57 - 69
- Sanches L, CMA Valentini, OB Pinto Júnior, JS Nogueira, GL Vourlitis, CJ Silva, P Bambi, & FA Lobo (2008b) Seasonal and interannual litter dynamics of a tropical semi-deciduous forest of the southern Amazon Basin, Brazil. *J. Geophys. R.-Biogeosciences*, in press.

- Sun, J., J.N. Nishio and T.C. Vogelmann. 1996. High-light effects on CO₂ fixation gradients across leaves. *Plant, Cell and Environment* 19:1261-1271.
- Thornley, J.H.M. 1976. *Mathematical models in plant physiology*. Academic Press, London. pp 92-110.
- Tobin, M.F., O.R. Lopez and T.A. Kursar. 1999. Responses of tropical understory plants to a severe drought: tolerance and avoidance of water stress. *Biotropica* 31:570-578.
- Vourlitis, G.L., N. Priante-Filho, M.M.S. Hayashi, J.S. Nogueira, F.T. Caseiro and J. Holanda Campelo. 2001. Seasonal variations in the net CO₂ exchange of a mature Amazonian transitional tropical forest (cerradão). *Functional Ecology* 15:388-395.
- Vourlitis, G.L., N. Priante-Filho, M.M.S. Hayashi, J.S. Nogueira, F.T. Caseiro and J. Holanda Campelo. 2002. Seasonal variations in the evapotranspiration of a transitional tropical forest of Mato Grosso, Brazil. *Water Resources Research* 38:1-11.
- Vourlitis, G.L., N. Priante-Filho, M.M.S. Hayashi, J.S. Nogueira, F. Raiter, W. Hoegel and J.H. Campelo. 2004. Effects of meteorological variations on the CO₂ exchange of a Brazilian transitional tropical forest. *Ecological Applications* 14:S89-S100.
- Vourlitis, G.L., J.S. Nogueira, N. Priante-Filho, W. Hoeger, F. Raiter, M.S. Biudes, J.C. Arruda, V.B. Capistrano, J.L.B. Faria and F.A. Lobo. 2005. The sensitivity of diel CO₂ and H₂O vapor exchange of a tropical transitional forest to seasonal variation in meteorology and water availability. *Earth Interactions* 9: 9-027.
- Vourlitis, G.L., J.S. Nogueira, F.A. Lobo, K.M. Sendall, J.L.B. Faria, C.A.A. Dias, and N.L.R. Andrade. 2008. Energy balance and canopy conductance of a tropical semi-deciduous forest of the southern Amazon Basin. *Water Resources Research* 44, W03412, doi: 10.1029/2006WR005526.
- Whitehead, D., D.U.U. Okali and F.E. Fasehun. 1981. Stomatal response to environmental variables in two tropical forest species during the dry season in Nigeria. *Journal of Applied Ecology* 18:571-587.
- Williams, M., Y. Malhi, A.D. Nobre, E.B. Rastetter, J. Grace and M.G.P. Pereira. 1998. Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modeling analysis. *Plant, Cell and Environment* 21:953-968.
- Wong, S.C., I.R. Cowan and G.D. Farquar. 1979. Stomatal conductance correlates with photosynthetic capacity. *Nature* 282:424-426.
- Wright, S.J., J.L. Machado, S.S. Mulkey and A.P. Smith. 1992. Drought acclimation among tropical forest shrubs (*Psychotria*, Rubiaceae). *Oecologia* 89:457-463.
- Yordanov, I., V. Velikova and T. Tsonev. 2000. Plant responses to drought, acclimation, and stress tolerance. *Photosynthetica* 38:171-186.