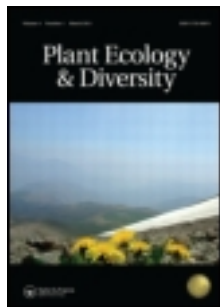


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## Seasonal patterns of leaf-level photosynthetic gas exchange in an eastern Amazonian rain forest

Tomas F. Domingues<sup>a\*</sup>, Luiz A. Martinelli<sup>b</sup> and James R. Ehleringer<sup>c</sup>

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**Background:** Global changes are challenging the equilibrium in the Amazon. Understanding how that biome responds to seasonality in water availability is essential to build scenarios of ecosystem functioning in the near future.

**Aims:** Our aim was to test for seasonal variations in leaf traits related to primary productivity.

**Methods:** Chemical composition, mass to area ratio and photosynthetic response curves to light and CO<sub>2</sub> and of stomatal conductance ( $g_s$ ) to leaf-to-air water pressure deficit ( $v$ ) were determined from leaves of Amazonian trees and lianas.

**Results:** Weak responses of  $g_s$  to  $v$  suggested limited stomatal control over transpiration. Dry season stomatal limitation of photosynthesis was not a common feature as only one individual studied (out of 14) exhibited concomitant decreases in light saturated photosynthetic rate ( $A_{Sat}$ ) and  $g_s$  (measured during  $A_{Sat}$ ) associated with the dry season. Furthermore, 75% of the individuals evaluated did not show decreased photosynthetic capacity ( $V_{cmax}$ ) during the dry season, suggesting limited seasonal leaf acclimation. Grouped analyses indicated that most parameters evaluated remained constant across seasons. The exceptions were leaf nitrogen and its isotopic signature, and the integrated stomatal sensitivity to light, CO<sub>2</sub> and  $v$ .

**Conclusions:** These findings reinforce the notion that the dry season in eastern Amazonia is not associated with significant limitations in leaf-level photosynthesis.

**Keywords:** A-ci; response curve; drought; ecophysiological traits; functional diversity; global change; primary productivity; photosynthesis parameters; stomatal sensitivity

### Introduction

Tropical rain forest vegetation displays a set of particular characteristics that reflect evolution under conditions of year-round abundant water and propitious temperatures, although with variable degrees of seasonality of climatic parameters. Pervasive changes in land cover, atmospheric chemistry and climatic patterns, all influenced by human activities (IPCC 2007), are challenging the dynamic equilibrium of tropical forests. As a consequence, it has been suggested that about 80% of the Amazon forest will by 2100 be susceptible to rapid vegetation shifts (Asner et al. 2010) while undergoing processes where ecosystem functioning is disrupted, resulting in weakened forest resilience (Davidson et al. 2012), further aggravating possible vegetation shifts. Inter-annual variations in patterns of water availability are among the strongest forces that influence primary productivity and species mortality at the Amazon region (Meir and Woodward 2010). Reduction in precipitation within the Amazon basin has long been predicted as a consequence of landscape conversion from old-growth forests with high evapotranspiration to low-biomass land covers such as crops, pastures and natural reforestation with much reduced evapotranspiration (Salati and Vose 1984; IPCC 2007). Furthermore, increased atmospheric CO<sub>2</sub> potentially decreases leaf stomatal conductance and subsequent transpiration, exacerbating the reduction in rainwater recycling (Lloyd and Farquhar 2008). Finally, the apparent

increased frequency and intensity of droughts has raised attention to widespread tree mortality, species composition shifts, and large emissions of CO<sub>2</sub> to the atmosphere (Phillips et al. 2009; Lewis et al. 2011). Knowledge on how plants modulate the carbon and water cycles in response to changes in water availability (Baldocchi et al. 1996) is crucial for the production of reliable future scenarios for the Amazon Basin-scale carbon cycle, and its influence over global climate. Unfortunately, no clear picture has so far emerged from studies regarding primary productivity in the Amazon Basin. At the ecosystem scale, several studies have suggested that the decreased water availability associated with the dry season indeed reduces ecosystem productivity for the Amazon region (Jipp et al. 1998; Malhi et al. 1998; Tian et al. 1998; Williams et al. 1998; Asner et al. 2000; Araújo et al. 2002; Ometto et al. 2002; Asner et al. 2004; Phillips et al. 2009). Contrastingly, other studies have indicated that a typical dry season may not be strong enough to impose physiological stress (Nepstad et al. 1994; Grace et al. 1995; Lloyd et al. 1995; Potter et al. 1998; Carswell et al. 2002; Saleska et al. 2003; Goulden et al. 2004). Furthermore, enhanced primary productivity has also been suggested to result from higher irradiation levels associated with reduced cloud cover during the dry season (Potter et al. 1998; Saleska et al. 2007), although cloudy conditions have been related to increased diffuse radiation better illuminating the canopy interior (Mercado et al. 2009).

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The fact that such disparate conclusions have been reached derives in part from our limited ability in partitioning fluxes into photosynthesis and respiration. For example, increased productivity during the dry season could result from stimulated photosynthesis due to decreased cloud cover and consequent increased radiation input. A plausible alternative explanation could be that a decrease in respiratory carbon losses under water deficit conditions would result in an increased net primary productivity. The identification of seasonal patterns in leaf-level photosynthesis should be an important aid for the interpretation of ecosystem-scale carbon and water fluxes, although a clear scarcity of information prevails at this level (Kitajima et al. 1997). In this study, leaf-level photosynthetic gas exchange and related leaf properties were measured during multiple wet and dry seasons in a primary forest in eastern Amazonia. We hypothesised that photosynthesis parameters would be lower during the dry season while the sensitivity of stomata to a combination of environmental (evaporative demand and  $\text{CO}_2$  concentration) and physiological (assimilation rate) parameters should be higher.

### Material and methods

Measurements and leaf collections were made in an eastern Amazonian lowland tropical rain forest between November

1999 and December 2003. The site was situated within the FLONA–Tapajós, a managed National Forest Reserve, administered by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA). The area is located 67 km south of the town of Santarém, in the State of Pará, Brazil. Leaves of trees and lianas were accessed from four towers, two of them being ca. 25 m in height ( $2^\circ 53' 54''$  S,  $54^\circ 57' 21''$  W), one tower ca. 40 m tall ( $2^\circ 51' 22''$  S,  $54^\circ 57' 29''$  W) and one tower ca. 30 m tall ( $3^\circ 01' 05''$  S,  $54^\circ 58' 08''$  W). Annual precipitation averaged  $2097 \text{ mm year}^{-1}$  between 1999 and 2003 (dataset available at <http://lba.cptec.inpe.br/beija-flor/>). The region usually experiences a 5-month dry season (July through November) when precipitation averages less than  $100 \text{ mm month}^{-1}$  (Keller et al. 2004) (Figure 1). Concerning the years 2000 and 2001, daily evapotranspiration averaged  $3.6 \text{ mm d}^{-1}$  during the wet season and  $4 \text{ mm d}^{-1}$  during the dry season, while soil water content at a depth of 10 cm remained above  $0.3 \text{ cm}^3 \text{ cm}^{-3}$  (da Rocha et al. 2004).

A total of 40 individual plants belonging to 38 species were studied. Within these, 22 individuals, which were accessible from the towers, were chosen for photosynthetic gas exchange measurements. In order to sample representatively the forest ecosystem, plant species evaluated were chosen from the following functional groups: full sun-lit top-canopy trees, full sun-lit top-canopy lianas, middle

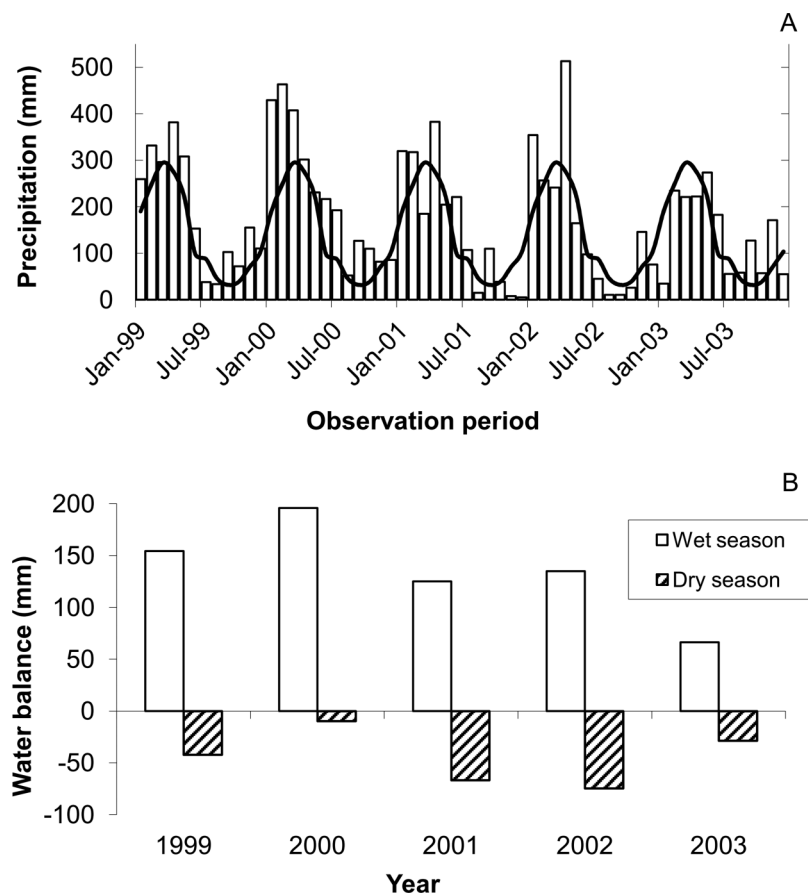


Figure 1. (A) Precipitation pattern at FLONA-Tapajós, Pa, Brazil. Bars indicate monthly accumulated precipitation from Casa-da-Onça station ( $2.90^\circ$  S,  $54.96^\circ$  W) (data kindly provided by Dan Nepstad) and line represents historical averages (1978–1998) from the INMET station (# 254005 – Barragen;  $2.82^\circ$  S,  $54.30^\circ$  W). (B) Water balance for the period studied as the difference between observed precipitation and potential evapotranspiration.

canopy trees and understorey trees (Domingues et al. 2007). Plant voucher materials of species associated with the 40 m tower were sent to the herbarium IAN-EMBRAPA (Belém, Br) for taxonomic identification and subsequent incorporation into its collection. Species identification for the remainder of the species was obtained from existing inventories (Keller et al. 2001; Miller et al. 2004).

Pre-dawn ( $\Psi_{\text{leaf-dawn}}$ ) and mid-day ( $\Psi_{\text{leaf-midday}}$ ) leaf water potentials were measured from a smaller subset of species with a Scholander pressure chamber (SoilMoisture 3005-1422, Goleta, CA, USA), in order to assess the water

1500, 1800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .  $A-c_i$  response curves started with  $\text{CO}_2$  concentrations close to ambient (36 Pa) and followed a specific sequence of steps: 36, 25, 15, 10, 5, 36, 60, 120, 200 Pa. Finally,  $g_s-\nu$  response curves measurements started with the highest relative humidity value possible, ca. 80–90%, and involved on average seven steps where relative humidity was decreased by increasing flow rates and/or diverging the incoming air stream into a desiccant reservoir.

A non-rectangular hyperbola model (Thornley 1976) solved for its negative root was used to describe the  $A$ -PPFD response curves (Equation (1)).

$$A = \frac{\Phi \times \text{PPFD} + A_{\text{Sat}} - \sqrt{\{(\Phi \times \text{PPFD} + A_{\text{Sat}})^2 - 4 \times \Theta \times \Phi \times \text{PPFD} \times A_{\text{Sat}}\}}}{2 \times \Theta} - R_d \quad (1)$$

status of the species. Eight trees within reach of the 40 m tower were evaluated on six occasions, from the wet season of 2000 to the dry season of 2002. Leaves collected for water potential determinations were stored inside plastic bags in a cooler containing ice, and analyses were made within 2 h of sampling. These leaves were not used for photosynthesis determinations.

Gas exchange response curves were determined during nine field campaigns: November 1999; March, July, and October 2000; February and September 2001; September 2002; and June and December 2003. Measurements were made with an infra-red gas analyser, coupled to a leaf chamber equipped with a red–blue light source and an external  $\text{CO}_2$  source (model LI-6400, Li-Cor, Nebraska, USA). For determination of instantaneous assimilation rates, the environment inside the leaf chamber was controlled to maintain leaf temperature at 30 °C, relative humidity ca. 80%,  $\text{CO}_2$  partial pressure at the sample cell at 36 Pa, and saturating levels of photosynthetic active photon flux density (PPFD) (800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for understorey plants and 1800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for other species). All measurements were carried out on fully expanded leaves with no signs of senescence or immaturity, and largely limited to morning hours (8:00 to 13:00 h local time). In addition to this standard procedure, the determination of photosynthetic response curves were made by varying PPFD ( $A$ -PPFD response curves), or intercellular partial pressure of  $\text{CO}_2$  ( $c_i$ ) ( $A-c_i$  response curves). Also, responses of  $g_s$  to variations of the leaf-to-air mole fraction water deficit ( $\nu$ ) ( $g_s-\nu$  response curves) were obtained. Concerning the  $g_s-\nu$  response curves, 68% of the measurements were taken under flow rates ranging between 500 and 750  $\mu\text{mol s}^{-1}$ , 30% within 99–500  $\mu\text{mol s}^{-1}$  and 2% below 99  $\mu\text{mol s}^{-1}$  (total of measurements = 936). The measurement time of each response curve spanned between 60 and 90 min, with the exception of some of the  $g_s-\nu$  response curves, which spanned ca. 180 min ensuring full stomatal response.

For most of the  $A$ -PPFD response curves, the light step sequence was 1800, 1500, 1000, 750, 500, 250, 100, 50, 25, and 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The light sequence adopted for understorey trees started with light levels close to ambient (100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and observed the following sequence: 100, 50, 25, 10, 0, 100, 250, 500, 750, 1000,

The model parameters were curvature ( $\Theta$ , dimensionless), light saturated assimilation rate ( $A_{\text{Sat}}$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ), dark respiration rate (carbon dioxide released under zero light) ( $R_d$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ), and quantum yield ( $\Phi$ ,  $\text{mol CO}_2 \text{mol quanta}^{-1}$ ). The independent variable is the PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and the output is the net carbon dioxide assimilation rate ( $A$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ). The model was fitted to data by the non-linear least square method. Other information obtained from the  $A$ -PPFD response curves was the inflexion point of the curve (PPFD<sub>i</sub>,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), the light level corresponding to the ratio  $A_{\text{Sat}}/\Phi$ .

Maximum carboxylation capacity at 25 °C ( $V_{\text{cmax}}$ ) was obtained from  $A-c_i$  response curves using the Farquhar biochemical photosynthesis model (Farquhar et al. 1980), as described in Domingues et al. (2010).

The response of  $g_s$  to variations in  $\nu$  was evaluated through fitting a logarithmic function (Oren et al. 1999):

$$g_s = \text{intercept} + \text{slope} \times \ln(\nu) \quad (2)$$

When  $\nu$  equals one,  $g_s$  become the intercept ( $g_s$  at 1 kPa  $\nu$ ). The slope of the regression can be considered as a stomatal sensitivity index in response to  $\nu$ . Furthermore, integrated stomatal sensitivity to light,  $\text{CO}_2$  and  $\nu$  was also evaluated using the model proposed by Medlyn et al. (2011):

$$g_s = g_0 + 1.6 \left( 1 + \frac{g_1}{\sqrt{\nu}} \right) \times \frac{A}{c_a} \quad (3)$$

where  $g_s$  is the stomatal conductivity ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  $g_0$  is the intercept,  $g_1$  is the slope and  $c_a$  is the ambient  $\text{CO}_2$  concentration. The cost in water units incurred during carbon gain is represented by  $g_1$ . For analyses with this model, we excluded measurements made with PPFD lower than 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and  $\text{CO}_2$  lower than 5 Pa. As for light response curves, the model was fitted to data by the non-linear least square method, generating estimates for  $g_0$  and  $g_1$ .

Leaf mass to leaf area ratio ( $M_A$ ,  $\text{g m}^{-2}$ ) was obtained by dividing fresh leaf area by its dry weight. Leaf area was obtained by tracing fresh leaves onto paper and

posterior measurement of digitalised images. Leaf weight was obtained after drying the leaves at 65 °C for 48 h. Leaf  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and mass-based nitrogen concentration ( $N_{\text{Mass}}$ ) were determined by continuous-flow isotope ratio mass spectrometry (IRMS Delta Plus Finnigan, San Jose, CA, USA) coupled with an elemental analyser (Carlo Erba, Milan, Italy) at the Laboratório de Ecologia Isotópica, CENA-USP, Piracicaba, Brazil. Area-based nitrogen concentration ( $N_{\text{Area}}$ ) was obtained as the product of  $N_{\text{DW}}$  by  $M_{\text{A}}$ .

In order to detect the influence of season on parameter means of individual trees,  $t$ -tests were applied. To detect trends of seasonality over parameters at the community level, Wilcoxon signed rank tests were applied. To test if slopes of  $g_s$ - $\nu$  response curves were significantly different from zero, analysis of variance (ANOVA) were used. Analyses of covariance were carried out to test for differences between bi-variate regressions obtained for wet and dry season. JMP 5.1 (SAS Institute Inc., Cary, NC, USA) was used for all statistical analyses.

## Results

### Seasonality of water availability

During this study (1999–2003), precipitation amounts were similar to historical patterns for the region (Figure 1(a)), averaging 2097 mm year<sup>-1</sup>. The historical precipitation dataset indicated that on average 21% of the annual precipitation fell during the dry season period (July to November). Water deficit developed in all years of the study (potential evapotranspiration exceeding precipitation) during the dry season, but to variable degrees (Figure 1(b)). The years of 1999 and 2000 were particularly wet (mean annual precipitation equal to 2470 mm) when compared with the 2001–2003 period (mean annual precipitation equal to 1848 mm). The pattern observed for precipitation was reflected in the temporal variations in leaf water potential (Figure 2). Furthermore, when compared with previous years, the 2002 dry season showed lower precipitation (August to October). Regarding data pooled from all species, marginally significant ( $P < 0.1$ ) differences between wet and dry seasons were detected for  $\Psi_{\text{leaf-dawn}}$  data ( $P = 0.09$ ) while no significant difference was observed for  $\Psi_{\text{leaf-midday}}$  ( $P = 0.14$ ) (one-tailed unequal variance  $t$ -tests), suggesting that water availability was slightly lower during the dry season. The lowest water potential values observed were obtained during the 2002 dry season when the top-canopy liana *Tetrapterys* sp. displayed the lowest values for both  $\Psi_{\text{leaf-dawn}}$  (−1.6 MPa) and  $\Psi_{\text{leaf-midday}}$  (−3.3 MPa).

### Leaf traits and photosynthesis

Foliage showed a relatively large range of  $\delta^{13}\text{C}$  values, from −27.2‰ (*Tetrapterys* sp., an upper canopy liana) to −35.8‰ (*Duguetia cadaverica* Huber, an understorey tree) (Table 1). Foliage  $\delta^{15}\text{N}$  values also

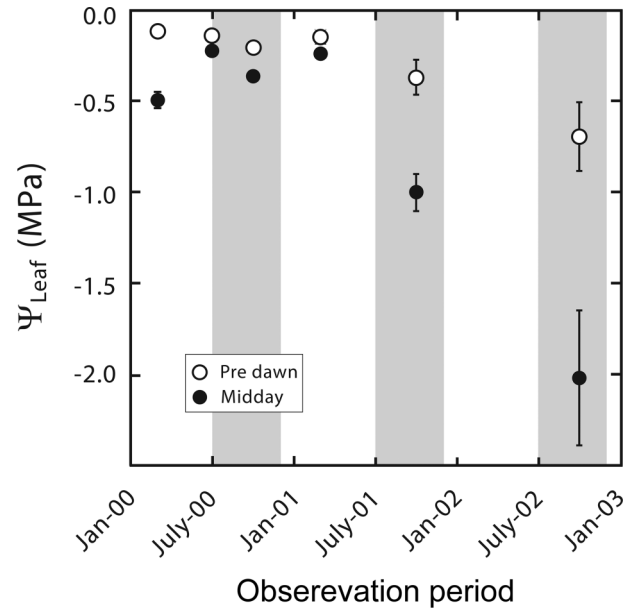


Figure 2. Averages ( $\pm$  SE) of pre-dawn and mid-day leaf water potential for primary forest species from Santarém, Brazil. Grey band denotes dry season periods.

varied considerably, ranging from a maximum average of 10.4‰ (*Prionostemma aff. aspera* (Lam.) Miers, an upper canopy liana) to a minimum average of 3.0‰ (*Pouteria venosa* (Mart.) Baehni, a mid-canopy tree from the Sapotaceae family). The lowest  $N_{\text{Area}}$  value was observed for the understorey tree *Miconia acinodendron* Sweet (1.02 g m<sup>-2</sup>), while the highest value (4.07 g m<sup>-2</sup>) was found for *Tachigali myrmecophila* Duck., a top-canopy legume tree. On a mass basis,  $N_{\text{Mass}}$ , the top-canopy trees *Manilkara huberi* Standl. and *Protium puncticulatum* Macbride averaged the lowest nitrogen concentration (14.0 mg g<sup>-1</sup>), while the understorey tree *Rinorea neglecta* Sandwith showed the highest concentration (36.8 mg g<sup>-1</sup>). The top-canopy liana *Abuta rufescens* Aubl. had leaves with the highest observed  $M_{\text{A}}$  value (180.4 g m<sup>-2</sup>), while the understorey tree *Virola elongata* Warb. showed the lowest value (40.1 g m<sup>-2</sup>).

Tight positive correlations were observed between  $A_{\text{Sat}}$  and  $g_s$  at  $A_{\text{Sat}}$ ,  $A_{\text{Sat}}$  and  $N_{\text{Area}}$ ,  $A_{\text{Sat}}$  and  $V_{\text{cmax}}$ , and between  $N_{\text{Area}}$  and  $V_{\text{cmax}}$  (Figure 3). Analyses of covariance indicated that slopes of the regressions obtained from wet season dataset were not statistically distinct from slopes obtained from data collected during dry season periods, indicating no influence of season over relationships (Figure 3).

Parameters from the  $A$ -PPFD response curves ( $A_{\text{Sat}}$ ,  $R_d$ ,  $\Phi$ , PPFD<sub>i</sub>) showed large variations among the 22 individual trees evaluated (Table 2), largely associated with position within the canopy profile.  $A_{\text{Sat}}$  averages ranged from 2.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the understorey tree *Rinorea neglecta* to 15.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the top-canopy tree *Cordia bicolor* A. DC., comprising an almost six-fold variation. Following a tendency of higher  $A_{\text{Sat}}$  values at the top

Table 1. Mean values of carbon and nitrogen isotope composition, leaf nitrogen contents, and leaf mass per area ratio (mean  $\pm$  SE) for species occurring at the primary forest ecosystems at Santarém, PA, Brazil. Number inside brackets indicates sample size, with the exception of the Height column, where numbers inside brackets indicate relative position from the forest floor within the profile. Plant species were grouped into the following functional groups (FG): Li, lianas at the top of the canopy; Up, trees at the top of the canopy; Mid, trees at the middle of the canopy; Un, trees in the understorey.

Species	FG	Height (m)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$N_{\text{Area}}$ (g m $^{-2}$ )	$M_{\text{A}}$ (g m $^{-2}$ )
<i>Abuta rufescens</i>	Li	33 (86%)	$-28.5 \pm 0.2$ (15)	$8.1 \pm 0.1$ (15)	$2.93 \pm 0.19$ (14)	$180 \pm 7$ (14)
<i>Arrabidaea prancei</i>	Li	26 (85%)	$-28.5 \pm 0.7$ (11)	$5.6 \pm 0.2$ (11)	$3.07 \pm 0.28$ (10)	$125 \pm 11$ (10)
<i>Combretum</i> sp.	Li	34 (83%)	$-29.7 \pm 0.1$ (5)	$7.2 \pm 0.2$ (5)	$1.25 \pm 0.03$ (5)	$58 \pm 2$ (5)
<i>Memora tanaecii</i> <i>carpa</i>	Li	26 (85%)	$-28.1 \pm 0.3$ (12)	$8.2 \pm 0.3$ (12)	$2.45 \pm 0.15$ (8)	$110 \pm 6$ (9)
<i>Prionostemma aff. aspera</i>	Li	38 (93%)	$-29.3 \pm 0.2$ (22)	$10.4 \pm 0.3$ (22)	$2.8 \pm 0.13$ (19)	$155 \pm 5$ (20)
<i>Tetrapteryx</i> sp.	Li	38 (93%)	$-27.2 \pm 0.1$ (37)	$7.4 \pm 0.2$ (37)	$2.37 \pm 0.09$ (34)	$109 \pm 5$ (36)
<i>Copaifera duckei</i>	Up	36 (89%)	$-28.4 \pm 0.2$ (45)	$7.6 \pm 0.1$ (45)	$2.52 \pm 0.10$ (40)	$101 \pm 4$ (40)
<i>Cordia bicolor</i>	Up	27 (86%)	$-30.0 \pm 0.2$ (10)	$5.5 \pm 0.2$ (10)	$3.25 \pm 0.05$ (10)	$131 \pm 5$ (10)
<i>Goupia glabra</i>	Up	26 (85%)	$-28.9 \pm 0.6$ (4)	$4.4 \pm 0.5$ (4)	$2.15 \pm 0.18$ (3)	$120 \pm 10$ (3)
<i>Lecythis lurida</i>	Up	31 (88%)	$-30.2 \pm 0.1$ (9)	$8.2 \pm 0.2$ (9)	$2.59 \pm 0.06$ (9)	$137 \pm 6$ (9)
<i>Licania michelli</i>	Up	22 (72%)	$-31.8 \pm 0.5$ (5)	$5.5 \pm 0.4$ (5)	$1.85 \pm 0.16$ (3)	$127 \pm 10$ (3)
<i>Manilkara huberi</i>	Up	30 (72%)	$-30.0 \pm 0.1$ (35)	$6.8 \pm 0.1$ (35)	$2.55 \pm 0.07$ (33)	$178 \pm 3$ (33)
<i>Micropholis</i> sp.	Up	32 (91%)	$-29.5 \pm 0.2$ (16)	$7.3 \pm 0.1$ (16)	$2.33 \pm 0.07$ (16)	$143 \pm 5$ (16)
<i>Tachigali myrmecophila</i>	Up	27 (86%)	$-30.0 \pm 0.6$ (11)	$7.2 \pm 0.3$ (11)	$4.07 \pm 0.19$ (6)	$111 \pm 9$ (6)
<i>Anomalocalyx uleanus</i>	Mid	21 (60%)	$-30.3 \pm 0.1$ (8)	$6.8 \pm 0.1$ (8)	$2.35 \pm 0.05$ (8)	$128 \pm 4$ (8)
<i>Chimarrhis turbinata</i>	Mid	11 (28%)	$-30.5 \pm 0.4$ (7)	$8.0 \pm 0.2$ (7)	$1.96 \pm 0.02$ (2)	$82 \pm 3$ (2)
<i>Coussarea racemosa</i>	Mid	6 (19%)	$-34.2 \pm 0.3$ (8)	$4.7 \pm 0.2$ (8)	$1.05 \pm 0.05$ (6)	$56 \pm 1$ (6)
<i>Faramaea platyneura</i>	Mid	9 (22%)	$-32.6 \pm 0.1$ (40)	$5.9 \pm 0.1$ (40)	$1.64 \pm 0.06$ (34)	$74 \pm 2$ (35)
<i>Iryanthera sagotiana</i>	Mid	18 (58%)	$-31.4 \pm 0.3$ (4)	$5.2 \pm 0.2$ (4)	$1.91 \pm 0.32$ (3)	$101 \pm 11$ (3)
<i>Lechythis</i> sp.	Mid	14 (35%)	$-32.2 \pm 0.1$ (36)	$7.1 \pm 0.1$ (36)	$2.11 \pm 0.05$ (31)	$92 \pm 2$ (31)
<i>Licaria brasiliensis</i> ind. 1	Mid	23 (73%)	$-32.7 \pm 0.4$ (4)	$4.5 \pm 0.1$ (4)	$2.61 \pm 0.02$ (2)	$137 \pm 2$ (3)
<i>Licaria brasiliensis</i> ind. 2	Mid	14 (45%)	$-33.8 \pm 0.2$ (5)	$6.0 \pm 0.1$ (5)	$1.42 \pm 0.05$ (3)	$74 \pm 4$ (3)
<i>Manilkara huberi</i>	Mid	24 (58%)	$-33.0 \pm 1.0$ (4)	$6.4 \pm 0.3$ (4)	$1.62 \pm 0.12$ (3)	$149 \pm 4$ (3)
<i>Mouriri brachyanthera</i>	Mid	9 (23%)	$-32.1 \pm 0.1$ (4)	$7.3 \pm 0.8$ (4)	$1.32 \pm 0.06$ (3)	$65 \pm 1$ (3)
<i>Perebea mollis</i>	Mid	22 (72%)	$-30.3 \pm 0.8$ (5)	$6.3 \pm 0.3$ (5)	$2.38 \pm 0.13$ (2)	$150 \pm 23$ (3)
<i>Poecilanthus effusa</i>	Mid	4 (13%)	$-32.0 \pm 0.6$ (4)	$5.7 \pm 0.3$ (4)	$1.30 \pm 0.17$ (3)	$50 \pm 4$ (3)
<i>Pouteria macrophylla</i> ind. 1	Mid	16 (40%)	$-32.2 \pm 0.5$ (9)	$8.2 \pm 0.4$ (9)	$2.91 \pm 0.45$ (4)	$97 \pm 7$ (4)
<i>Pouteria macrophylla</i> ind. 2	Mid	10 (31%)	$-33.6 \pm 0.1$ (4)	$5.5 \pm 0.7$ (4)	$1.33 \pm 0.23$ (3)	$78 \pm 11$ (3)
<i>Pouteria venosa</i>	Mid	6 (19%)	$-33.9 \pm 0.2$ (4)	$3.0 \pm 0.2$ (4)	$1.38 \pm 0.08$ (3)	$44 \pm 1$ (3)
<i>Protium puncticulatum</i>	Mid	19 (53%)	$-33.4 \pm 0.1$ (15)	$6.0 \pm 0.1$ (15)	$1.37 \pm 0.04$ (15)	$98 \pm 2$ (15)
<i>Protium</i> sp.	Mid	8 (19%)	$-33.0 \pm 0.3$ (11)	$6.5 \pm 0.4$ (11)	$1.23 \pm 0.13$ (6)	$66 \pm 4$ (6)
<i>Protium spruceanum</i>	Mid	20 (65%)	$-31.2 \pm 0.1$ (4)	$5.2 \pm 0.2$ (4)	$1.46 \pm 0.05$ (3)	$79 \pm 2$ (3)
<i>Sclerolobium paraense</i>	Mid	19 (46%)	$-31.0 \pm 0.1$ (35)	$6.5 \pm 0.1$ (35)	$2.41 \pm 0.09$ (29)	$109 \pm 3$ (29)
<i>Tachigali myrmecophila</i>	Mid	19 (61%)	$-31.1 \pm 0.4$ (6)	$6.4 \pm 0.1$ (6)	$4.04 \pm 0.13$ (3)	$131 \pm 9$ (3)
<i>Amphirrhox surinamensis</i>	Un	2 (7%)	$-33.6 \pm 0.6$ (5)	$5.4 \pm 0.2$ (5)	$1.69 \pm 0.13$ (3)	$67 \pm 3$ (3)
<i>Duguetia cadaverica</i>	Un	3 (8%)	$-35.8 \pm 0.2$ (13)	$6.3 \pm 0.1$ (13)	$1.71 \pm 0.05$ (13)	$64 \pm 2$ (13)
<i>Miconia acinodendron</i>	Un	1 (3%)	$-34.5 \pm 0.2$ (30)	$4.5 \pm 0.2$ (30)	$1.02 \pm 0.03$ (29)	$47 \pm 1$ (29)
<i>Rinorea neglecta</i>	Un	1 (2%)	$-35.5 \pm 0.1$ (22)	$6.5 \pm 0.1$ (22)	$1.61 \pm 0.05$ (21)	$44 \pm 2$ (21)
<i>Sclerolobium paraense</i>	Un	1 (2%)	$-34.8 \pm 0.2$ (36)	$4.2 \pm 0.3$ (36)	$1.55 \pm 0.05$ (35)	$77 \pm 2$ (35)
<i>Virola elongata</i>	Un	3 (8%)	$-35.0 \pm 0.2$ (4)	$4.8 \pm 0.3$ (4)	$1.08 \pm 0.10$ (3)	$40 \pm 3$ (3)

of the canopy and low values at the understorey, highest respiration rate average occurred in leaves of the top-canopy tree *Tachigali myrmecophila* ( $2.87 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), while lowest average was found for the understorey tree *Duguetia cadaverica* ( $0.25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ).

Similar to the *A*-PPFD response curve parameters, individual plants showed large variations in  $V_{\text{cmax}}$  values (Table 3), which was also dependent on canopy position. The highest  $V_{\text{cmax}}$  average observed was found for the top-canopy tree *Manilkara huberi* ( $75.0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ), which had showed the lowest value of  $N_{\text{DW}}$  among top-canopy trees (Table 1). In agreement to *A*-PPFD results, the lowest  $V_{\text{cmax}}$  average ( $10.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was obtained from an understorey tree (*Rinorea neglecta*).

#### Patterns of stomatal conductance

Most plants evaluated in this study showed limited effects of  $\nu$  over  $g_s$  (Table 3). The top-canopy liana *Combretum* sp. showed the lowest  $g_s$  at 1 kPa  $\nu$  ( $0.083 \text{ mol m}^{-2} \text{ s}^{-1}$ ), while the slope of the logarithmic regression for the  $g_s$ - $\nu$  response curves was equal to  $-0.032 \text{ mol m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$ . On the other hand, the top-canopy tree *Tachigali myrmecophila* presented the highest  $g_s$  at 1 kPa  $\nu$  ( $0.370 \text{ mol m}^{-2} \text{ s}^{-1}$ ), associated with the most negative slope ( $-0.201 \text{ mol m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$ ). In general,  $g_s$  at 1 kPa  $\nu$  values obtained from the  $g_s$ - $\nu$  response curves were slightly higher than observed averages of  $g_s$  at  $A_{\text{Sat}}$  (Table 3). There was a significant negative relationship between slopes and intercepts of the  $g_s$ - $\nu$  relationships

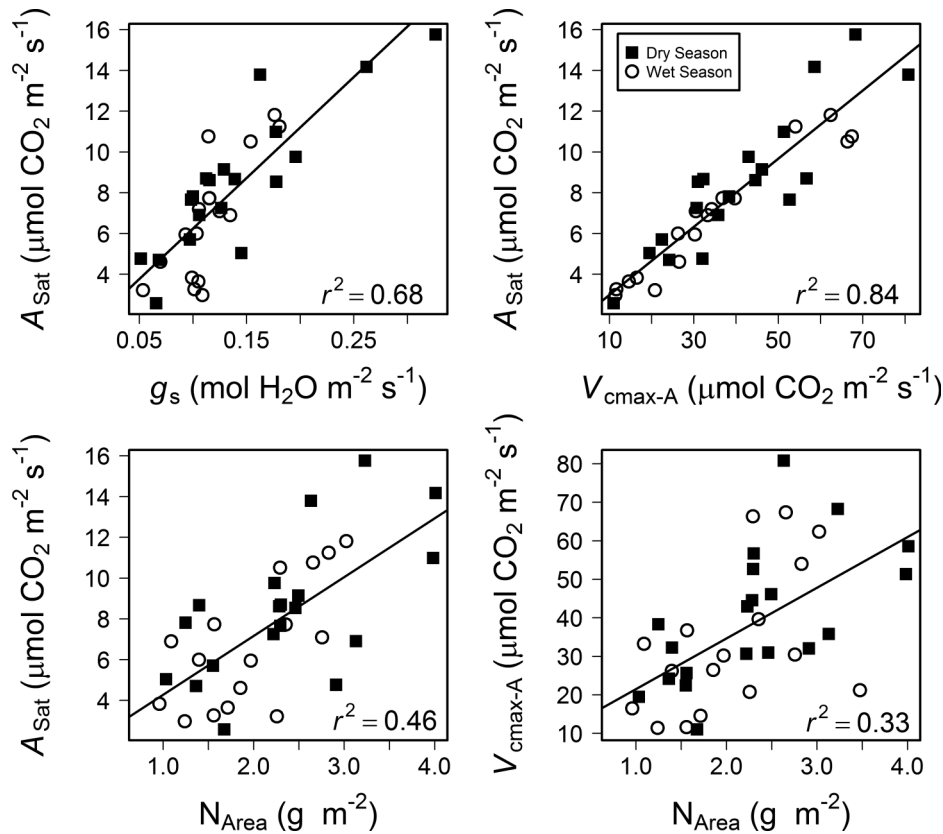


Figure 3. The relationships between averages of carbon assimilation rates at saturating light ( $A_{\text{Sat}}$ ) and corresponding stomatal conductance ( $g_s$ ), photosynthetic capacity ( $V_{\text{cmax}}$ ) and foliar nitrogen concentration ( $N_{\text{Area}}$ ), obtained from plant species occurring at primary rain forest ecosystem near Santarém, Brazil.

Table 2. Species averages (mean  $\pm$  standard deviation) for several species occurring in the primary forest at Santarém PA, Brazil. of measured assimilation rates under saturating light ( $A_{\text{Sat}}$ ) and modelled assimilation rates ( $A_{\text{Sat-model}}$ ), daytime respiration rates under zero light ( $R_d$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), quantum yield ( $\Phi$ ,  $\mu\text{mol CO}_2 \text{ mol Quanta}^{-1}$ ), and light at the inflexion point (PPFD<sub>i</sub>,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) derived from fitting a non-rectangular hyperbola model to  $A$ -PPFD response curves. Number inside brackets indicates sample size. Plant functional groups (FG) as in Table 1.

Species	FG	$A_{\text{Sat}}$	$A_{\text{Sat-model}}$	$R_d$	$\Phi$	PPFD <sub>i</sub>
<i>Abuta rufescens</i>	Li	8.6 $\pm$ 2.9 (5)	7.5 $\pm$ 4.2 (3)	0.67 $\pm$ 0.46 (3)	0.047 $\pm$ 0.013 (3)	152 $\pm$ 51 (3)
<i>Arrabidaea prancei</i>	Li	6.9 $\pm$ 2.9 (4)	11.1 (1)	1.42 (1)	0.081 (1)	137 (1)
<i>Combretum</i> sp.	Li	7.8 $\pm$ 2.1 (6)	11.1 $\pm$ 2.6 (2)	0.99 $\pm$ 0.15 (2)	0.051 (1)	134 $\pm$ 67 (2)
<i>Memora tanaecii</i>	Li	8.5 $\pm$ 0.4 (3)	11.3 (1)	1.95 (1)	0.098 (1)	115 (1)
<i>Prionostemma aff. aspera</i>	Li	5.8 $\pm$ 2.3 (30)	6 $\pm$ 3.7 (4)	0.99 $\pm$ 0.44 (4)	0.067 $\pm$ 0.028 (3)	70 $\pm$ 20 (4)
<i>Tetrapteryx</i> sp.	Li	8.6 $\pm$ 3.5 (44)	11.6 $\pm$ 7.4 (8)	1.34 $\pm$ 0.68 (8)	0.068 $\pm$ 0.033 (7)	176 $\pm$ 103 (8)
<i>Copaifera duckei</i>	Up	9.6 $\pm$ 3.1 (47)	12.5 $\pm$ 4.2 (8)	0.94 $\pm$ 0.34 (8)	0.055 $\pm$ 0.01 (8)	229 $\pm$ 69 (8)
<i>Cordia bicolor</i>	Up	15.8 $\pm$ 3.7 (7)	23.9 (1)	1.77 (1)	0.061 (1)	388 (1)
<i>Lecythis lurida</i>	Up	7.1 $\pm$ 1.4 (6)	0 $\pm$ 0 (0)	0 $\pm$ 0 (0)	0 $\pm$ 0 (0)	0 $\pm$ 0 (0)
<i>Manilkara huberi</i>	Up	12.8 $\pm$ 3.3 (33)	15.7 $\pm$ 3.8 (7)	1.02 $\pm$ 0.36 (7)	0.064 $\pm$ 0.006 (7)	248 $\pm$ 68 (7)
<i>Micropholis</i> sp.	Up	6.2 $\pm$ 3.5 (15)	15.6 $\pm$ 8 (2)	0.93 (1)	0.068 $\pm$ 0 (2)	228 $\pm$ 117 (2)
<i>Tachigali myrmecophila</i>	Up	14.1 $\pm$ 3.5 (7)	15.6 $\pm$ 1.6 (3)	2.42 $\pm$ 0.68 (3)	0.07 $\pm$ 0.012 (3)	226 $\pm$ 42 (3)
<i>Anomalocalyx uleanus</i>	Mid	7.7 $\pm$ 3.5 (8)	8.6 $\pm$ 4.8 (3)	0.54 $\pm$ 0.12 (2)	0.05 $\pm$ 0.014 (3)	201 $\pm$ 171 (3)
<i>Faramea platyneura</i>	Mid	4.7 $\pm$ 1.4 (32)	5.4 $\pm$ 1.3 (9)	0.36 $\pm$ 0.2 (8)	0.066 $\pm$ 0.012 (9)	86 $\pm$ 34 (9)
<i>Lechythis</i> sp.	Mid	6.8 $\pm$ 1.5 (31)	8.1 $\pm$ 1.4 (8)	0.44 $\pm$ 0.12 (8)	0.071 $\pm$ 0.011 (8)	115 $\pm$ 21 (8)
<i>Protium puncticulatum</i>	Mid	6.5 $\pm$ 1.3 (16)	8.3 $\pm$ 1.9 (4)	0.52 $\pm$ 0.16 (4)	0.059 $\pm$ 0.005 (4)	140 $\pm$ 22 (4)
<i>Sclerobium paraense</i>	Mid	10.6 $\pm$ 1.6 (26)	12.5 $\pm$ 1.3 (7)	0.79 $\pm$ 0.41 (6)	0.063 $\pm$ 0.005 (7)	198 $\pm$ 25 (7)
<i>Tachigali myrmecophila</i>	Mid	10.8 $\pm$ 2.8 (5)	14 $\pm$ 2.2 (2)	0.9 $\pm$ 0.05 (2)	0.058 $\pm$ 0.004 (2)	242 $\pm$ 21 (2)
<i>Duguetia cadaverica</i>	Un	3.7 $\pm$ 1 (13)	4 $\pm$ 0.3 (2)	0.35 (1)	0.041 $\pm$ 0.022 (2)	117 $\pm$ 72 (2)
<i>Miconia acinodendron</i>	Un	4.7 $\pm$ 2 (30)	6.2 $\pm$ 2.5 (7)	0.45 $\pm$ 0.19 (6)	0.066 $\pm$ 0.017 (7)	93 $\pm$ 25 (7)
<i>Rinorea neglecta</i>	Un	2.7 $\pm$ 0.7 (24)	3.6 $\pm$ 0.5 (6)	0.31 $\pm$ 0.27 (6)	0.066 $\pm$ 0.015 (6)	56 $\pm$ 13 (6)
<i>Sclerobium paraense</i>	Un	6.6 $\pm$ 2 (33)	7.7 $\pm$ 2.1 (10)	0.38 $\pm$ 0.17 (10)	0.071 $\pm$ 0.012 (10)	109 $\pm$ 25 (10)

Table 3. Maximum carboxylation rate ( $V_{\text{cmax}}$ ) (mean  $\pm$  SEM) for several species occurring in the primary forest at Santarém PA, Brazil. Results are derived from fitting  $A$ - $c_i$  response curves to the Farquhar et al (1982) biogeochemical assimilation model by non-linear least squares. Also shown are species averages of slope and intercept from fitting  $g_s$ - $\nu$  response curves to the model:  $g_s = \text{intercept} + \text{slope} \times \ln(\nu)$ . Plant functional groups (FG) as in Table 1.

Species	FG	$V_{\text{cmax}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$g_s$ at $A_{\text{Sat}}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	Slope $g_s$ - $\nu$	$g_s$ at 1 kPa ( $\text{mol m}^{-2} \text{s}^{-1}$ )
<i>Abuta rufescens</i>	Li	41.1 $\pm$ 6.1 (5)	0.118 $\pm$ 0.030 (5)	-0.046 $\pm$ 0.006 (2)	0.147 $\pm$ 0.006
<i>Arrabidaea prancei</i>	Li	35.8 $\pm$ 5.9 (2)	0.106 $\pm$ 0.039 (4)	-0.048 (1)	0.108
<i>Combretum</i> sp.	Li	38.3 $\pm$ 0.1 (2)	0.100 $\pm$ 0.019 (6)	-0.032 (1)	0.083
<i>Memora tanaeciicarpa</i>	Li	31.0 (1)	0.178 $\pm$ 0.006 (3)	-0.071 (1)	0.169
<i>Prionostemma aff. aspera</i>	Li	29.7 $\pm$ 4.4 (10)	0.077 $\pm$ 0.010 (30)	-0.040 $\pm$ 0.018 (6)	0.103 $\pm$ 0.031
<i>Tetrapterys</i> sp.	Li	55.2 $\pm$ 5.2 (15)	0.102 $\pm$ 0.010 (44)	-0.074 $\pm$ 0.016 (10)	0.173 $\pm$ 0.024
<i>Copaifera duckei</i>	Up	56.3 $\pm$ 3.1 (17)	0.135 $\pm$ 0.010 (47)	-0.077 $\pm$ 0.009 (10)	0.187 $\pm$ 0.022
<i>Cordia bicolor</i>	Up	68.3 $\pm$ 13.4 (4)	0.326 $\pm$ 0.076 (7)	n. s. (1)	
<i>Lecythis lurida</i>	Up	30.5 $\pm$ 3.0 (2)	0.125 $\pm$ 0.019 (6)	-0.094 (1)	0.226
<i>Manilkara huberi</i>	Up	75.0 $\pm$ 4.3 (14)	0.167 $\pm$ 0.008 (32)	-0.060 $\pm$ 0.009 (11)	0.197 $\pm$ 0.024
<i>Micropholis</i> sp.	Up	28.9 $\pm$ 5.9 (5)	0.067 $\pm$ 0.012 (10)	-0.050 $\pm$ 0.009 (4)	0.147 $\pm$ 0.019
<i>Tachigali myrmecophila</i>	Up	54.9 $\pm$ 3.0 (5)	0.266 $\pm$ 0.030 (7)	-0.201 (1)	0.370
<i>Anomalocalyx uleanus</i>	Mid	39.7 $\pm$ 8.2 (4)	0.115 $\pm$ 0.023 (8)	-0.087 (1)	0.179
<i>Faramea platyneura</i>	Mid	25.5 $\pm$ 1.9 (15)	0.070 $\pm$ 0.008 (32)	-0.089 $\pm$ 0.061 (6)	0.099 $\pm$ 0.013
<i>Lechythis</i> sp.	Mid	31.0 $\pm$ 1.5 (16)	0.120 $\pm$ 0.007 (31)	-0.056 $\pm$ 0.016 (8)	0.159 $\pm$ 0.032
<i>Protium puncticulatum</i>	Mid	28.2 $\pm$ 1.4 (6)	0.114 $\pm$ 0.009 (15)	-0.065 $\pm$ 0.020 (3)	0.185 $\pm$ 0.042
<i>Sclerolobium paraense</i>	Mid	47.1 $\pm$ 2.0 (13)	0.200 $\pm$ 0.011 (26)	-0.113 $\pm$ 0.029 (5)	0.333 $\pm$ 0.026
<i>Tachigali myrmecophila</i>	Mid	51.3 $\pm$ 5.5 (4)	0.164 $\pm$ 0.024 (5)	-0.082 (1)	0.193
<i>Duguetia cadaverica</i>	Un	15.1 $\pm$ 1.3 (5)	0.105 $\pm$ 0.010 (13)	-0.061 $\pm$ 0.001 (2)	0.132 $\pm$ 0.014
<i>Miconia acinodendron</i>	Un	21.1 $\pm$ 2.1 (14)	0.137 $\pm$ 0.013 (30)	-0.176 $\pm$ 0.077 (6)	0.224 $\pm$ 0.028
<i>Rinorea neglecta</i>	Un	10.7 $\pm$ 0.8 (11)	0.082 $\pm$ 0.007 (24)	-0.075 $\pm$ 0.010 (5)	0.172 $\pm$ 0.018
<i>Sclerolobium paraense</i>	Un	30.8 $\pm$ 3.1 (16)	0.107 $\pm$ 0.008 (32)	-0.066 $\pm$ 0.020 (4)	0.232 $\pm$ 0.046

obtained from the species evaluated in this study ( $r^2 = 0.57$ ,  $F = 34.12$ ,  $P < 0.0001$ ), with higher stomatal sensitivities for higher stomatal conductances. For a hypothetical reduction of  $\nu$  values from 0.5 to 2 kPa, top-canopy lianas showed the largest relative reduction in  $g_s$  (43%), according to the logarithmic model.

Individual trees and lianas were tested for differences in gas exchange characteristics between wet and dry seasons

(Table 4). A variety of responses were observed based on a two-tailed  $t$ -test evaluation of carbon assimilation rates. Regarding potential photosynthetic carbon assimilation rates, three seasonal trends were detected: (a)  $A_{\text{Sat}}$  values decreased during the dry season; (b)  $A_{\text{Sat}}$  values increased during the dry season; or (c)  $A_{\text{Sat}}$  values did not change significantly between seasons. Wet-dry season differences did not have a significant influence on  $V_{\text{cmax}}$  for

Table 4. Patterns of gas exchange parameters for several plant species occurring in primary forest at Santarém (Br), in relation to season of the year as detected by  $t$ -test (alpha level = 10%). Symbols + and - indicate if a parameter increased or decreased, respectively, in the dry season when compared to wet season averages. The = symbol indicates no significant change with season and blank cell indicates insufficient data for statistical comparison.

Species	FG	$A_{\text{Sat}}$	$N_{\text{Area}}$	$V_{\text{cmax}}$	$g_s$ at $A_{\text{Sat}}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$M_A$	$N_{\text{Mass}}$	slope $g_s$ - $\nu$
<i>Abuta rufescens</i>	Li		-			=	+	-	-	
<i>Prionostemma aff. aspera</i>	Li	=		=	=	=	+		+	=
<i>Tetrapterys</i> sp.	Li	=	=	=	=	=	+	+	-	=
<i>Copaifera duckei</i>	Up	-	-	-	-	+	+	-	=	=
<i>Manilkara huberi</i>	Up	+	+	=	=	=	=	=	=	=
<i>Micropholis</i> sp.	Up	+	=	+	+	=	=	=	=	=
<i>Faramea platyneura</i>	Mid	=	-	=	=	=	-	-	-	=
<i>Lechythis</i> sp.	Mid	+	+	=	+	=	+	+	=	=
<i>Protium puncticulatum</i>	Mid	+	=	+	+	+	+	=	=	=
<i>Protium</i> sp.	Mid		=			-	-	=	-	=
<i>Sclerolobium paraense</i>	Mid	-	-	-	=	=	=	-	-	=
<i>Miconia acinodendron</i>	Un	=	+	=	=	=	+	+	=	=
<i>Rinorea neglecta</i>	Un	-	=	=	=	+	+	=	=	=
<i>Sclerolobium paraense</i>	Un	-	=	-	=	-	+	+	-	=



most of the species, with 25% species exhibiting significant smaller  $V_{\text{cmax}}$  during the dry season, while another 25% species exhibited significant smaller  $V_{\text{cmax}}$  during the wet season (Table 4). Seasonal changes in  $V_{\text{cmax}}$  were always in concert with changes in  $A_{\text{Sat}}$ , although changes in  $A_{\text{Sat}}$  were not always concomitant to changes in  $N_{\text{Area}}$  and  $V_{\text{cmax}}$  (Table 4). Observed seasonal changes in  $g_s$  at  $A_{\text{Sat}}$  were coincident to changes in  $A_{\text{Sat}}$ . Both *Micropholis* sp. and *Protium puncticulatum* showed higher wet season values of  $A_{\text{Sat}}$  not associated with higher  $N_{\text{Area}}$  values. On the other hand, the understory trees *Rinoria neglecta* and *Sclerolobium paraense* showed a decrease in  $A_{\text{Sat}}$  during the dry season, also not associated with changes in  $N_{\text{Area}}$ .

The leaf-level stomatal sensitivity to  $\nu$  (Equation (2)) of the species evaluated in this study was not distinct between wet and dry seasons (Table 4). Among the 113 measured

$g_s$ - $\nu$  response curves, 18% yielded slopes not significantly different from zero (alpha level of 10%). Insensitivity of  $g_s$  to changes in  $\nu$  tended to occur more frequently in measurements performed during the dry season (20%) when compared with the wet season measurements (15%), indicating that the response of  $g_s$  to changes in  $\nu$  might have been influenced by other factors such as leaf water status. Some of the plant species evaluated in this study did not prevent increases in transpiration ( $E$ ) with rising  $\nu$  (Figure 4 – Increasing  $E$ ). Other species showed the opposite response, exerting strong control over  $E$  by adjustments in  $g_s$  (Figure 4 – Constant  $E$ ).

The stomatal responsiveness to environmental-physiological drivers is summarised in Figure 5. The model described in Equation (3) relates the composite response of stomata to  $A$ ,  $\text{CO}_2$  and  $\nu$ . Our dataset (i.e. data recorded at each step-change in light levels from

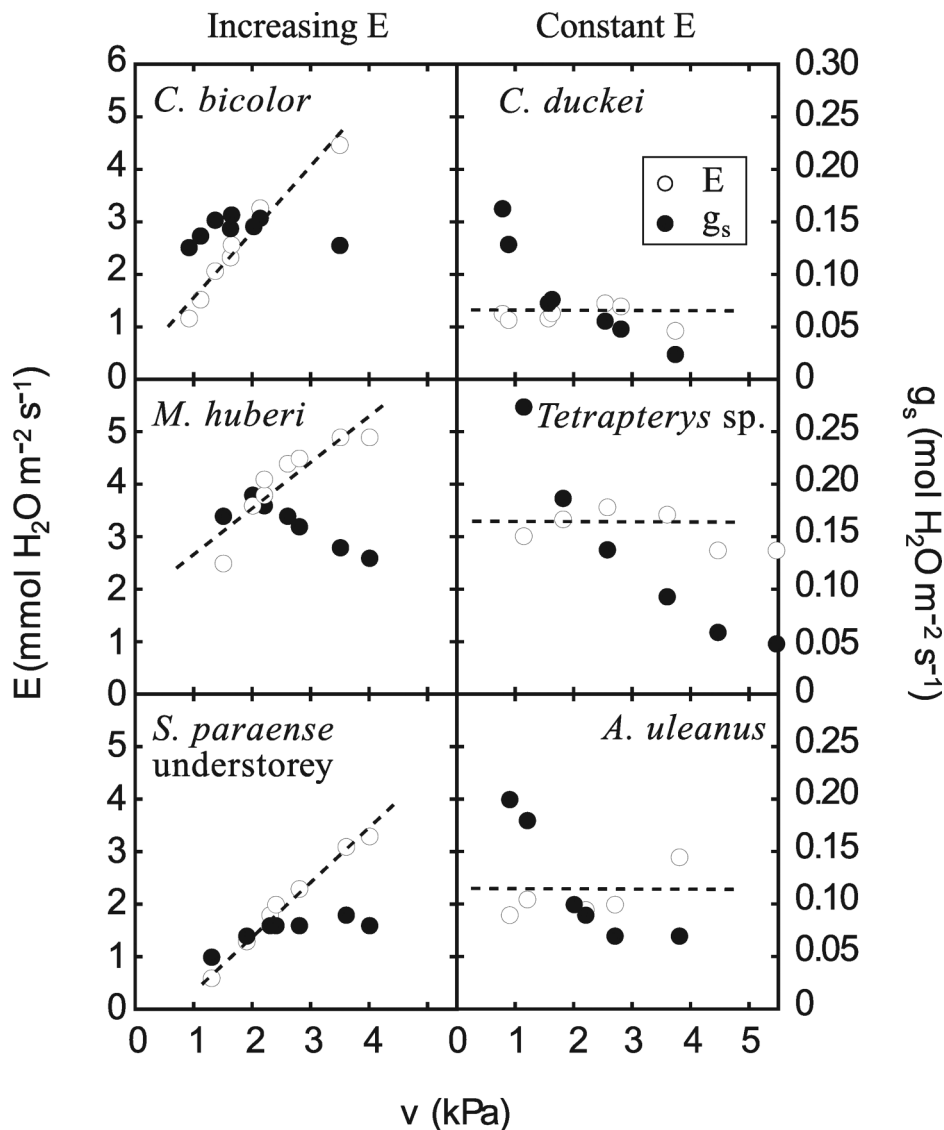


Figure 4. Illustration of the variability in patterns of stomatal conductance ( $g_s$ ) and transpiration ( $E$ ) in response to step changes in leaf-to-air water vapour mole deficit ( $\nu$ ) for species occurring at primary forest. Dashed lines represent linear regression for the ‘Increasing  $E$ ’ column and average  $E$  for the ‘Constant  $E$ ’ column.

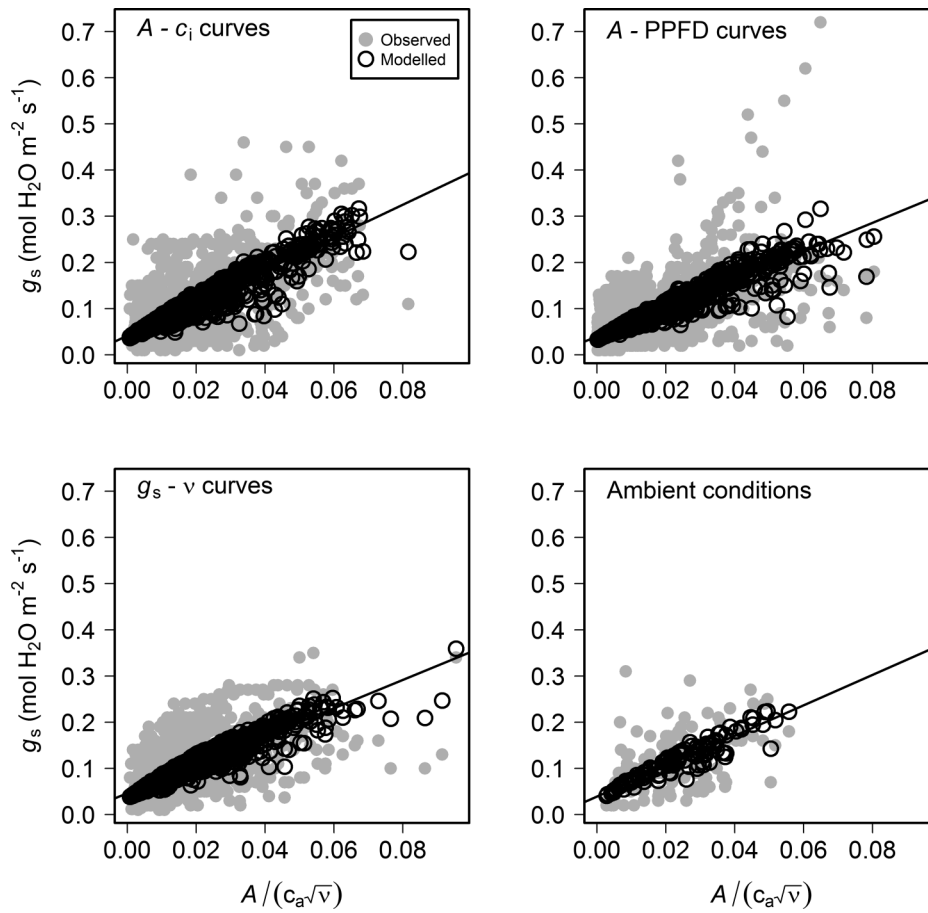


Figure 5. The relationships between environmental drivers from Medlyn's model (Equation (3)), and both observed and modelled stomatal conductance ( $g_s$ ). Environmental drivers were 'CO<sub>2</sub>' derived from  $A$ - $c_i$  response curves, 'Light levels' derived from  $A$ -PPFD response curves, 'Relative humidity' derived from  $g_s$ - $v$  response curves. 'Ambient' data were derived from instantaneous determinations of photosynthetic rates under ambient conditions.

$A$ -PPFD curves, atmospheric CO<sub>2</sub> concentrations from  $A$ - $c_i$  curves, and relative humidity levels from  $g_s$ - $v$  curves, and also taken under ambient conditions) enabled us to test Medlyn's model for individual drivers (CO<sub>2</sub>, light,  $v$  and ambient conditions). The distinct data subsets yielded no significant differences in the ability of the model to predict  $g_s$  (Figure 5). Such result suggests that, when varied individually, drivers of stomatal functioning exert similar influence on  $g_s$ . At the group level (all species pooled together), the integrated responses of  $g_s$  indicated a slightly higher sensitivity ( $g_1$  of Equation (3)) during the dry season period (data not shown). Analyses at the functional group (canopy position) level indicated significant differences in stomatal sensitivity among the groups, although mid-canopy trees and understorey trees were not distinct from each other (Table 5). Furthermore, the Top-Canopy Lianas and Understorey Trees groups showed significant differences with season, showing either an enhanced sensitivity during the dry season or insensitivity during the wet season (Figure 6).

At the individual level, a variety of responses were observed for changes in the averages of parameters between wet and dry season. To evaluate if common patterns

Table 5. Parameters for the stomatal sensitivity model (Equation (3)). The intercept  $g_0$  is the basal stomatal conductance, and the slope ( $g_1$ ) relates to the cost in water units incurred during carbon gain. CI is confidence interval (2.5–97.5%). Derived values of  $g_1$  not connected by the same letter indicate statistically differences among datasets ( $P < 0.05$ ).

Dataset	$g_0$	CI	$g_1$	CI	
All	0.034	0.035–0.032	4.39	4.49–4.29	A
Understorey trees	0.064	0.067–0.061	3.14	3.43–2.86	B
Mid-canopy trees	0.030	0.034–0.027	4.75	4.95–4.55	B
Top-canopy trees	0.013	0.017–0.010	5.24	5.42–5.06	A
Top-canopy lianas	0.007	0.010–0.004	4.76	4.96–4.56	C

existed at the group level, non-parametric Wilcoxon signed ranks were applied for each parameter evaluated in this study (Table 6). At an alpha level of 10%, most parameters showed no significant influence of season, consistent with a lack of physiological adjustments between seasons. Exceptions to this that were detected for measurements involved nitrogen concentration ( $N_{\text{Mass}}$  and  $N_{\text{Area}}$ ), which tended to show higher values during the dry season, and  $\delta^{15}\text{N}$ , which tended to show enriched values during the wet season, indicating an enhanced recycling for this element.

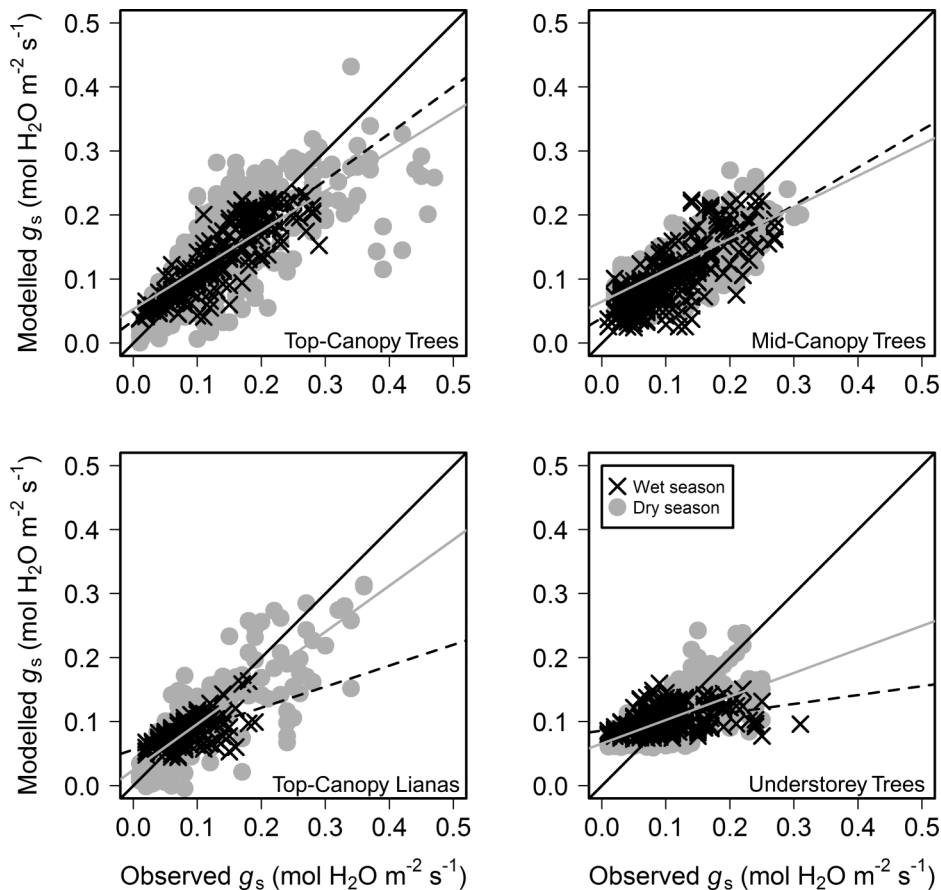


Figure 6. Differences among Amazonian lowland evergreen rain forest functional groups on the dry vs. wet season relationships between observed stomatal conductance ( $g_s$ ) and the modeled  $g_s$  based on Equation (3) (Medlyn et al. 2011). Full line refers to the 1:1 line, grey line to dry season data and dotted line refers to wet season data.

Table 6. The effects of season on ecophysiological parameters for pooled dataset evaluated from Wilcoxon signed rank tests.  $P$  values indicate the probability of the distribution of dry and wet season ranks be centred on the same location. Negative  $z$  indicates that parameter value tended to be higher during the dry season. Positive  $z$  indicates that parameter value tended to be higher during the wet season.

Parameter	$P$	$z$
$\delta^{15}\text{N}$	<b>0.03</b>	–
PPFD <sub>0</sub>	0.23	–
$R_d$	0.23	–
$g_s$ at 1kPa	0.27	–
$\delta^{13}\text{C}$	0.27	–
Curvature	0.34	–
$M_A$	0.39	–
$N_{\text{Mass}}$	<b>0.04</b>	+
$N_{\text{Area}}$	<b>0.09</b>	+
Slope $g_s$ - $v$	0.46	+
PPFD <sub>sat</sub>	0.68	+
$g_s$ at $A_{\text{Sat}}$	0.85	+
$A_{\text{Sat}}$	0.97	+
$V_{\text{cmax}}$	0.97	+

## Discussion

Analyses at either the individual or group levels did not support a clear influence of season over leaf traits related to gas

exchange. Our results suggest the rejection of our initial hypothesis that dry season is related to a decreased primary productivity by lower rates of leaf-level photosynthesis. Therefore, seasonal variations in ecosystem productivity must be explained by other factors, for example ecosystem respiration or changes in total leaf surface area of the canopy.

Stomatal functioning is essential to our understanding of how vegetation responds to seasonal and inter-annual variations in moisture availability. Stomata regulate water and  $\text{CO}_2$  fluxes according to environmental conditions and physiological status (Wong et al. 1979; Farquhar and Sharkey 1982; Oren et al. 1999). Several studies concerning tropical vegetation have demonstrated the stomatal response to atmospheric humidity deficits (Whitehead et al. 1981; Mooney and Chu 1983; Roberts et al. 1990; Meinzer et al. 1993, 1997). Although less often and in agreement with our results, a lack of stomatal response of some tropical species has also been reported in the literature (Fanjul and Barradas 1985; Phillips et al. 2001). The species evaluated in the present study tended to show significant correlations between  $g_s$  and  $v$  (Table 3), although slopes were modest. Furthermore, a considerable number of the  $g_s$ - $v$  response curves (21 out of 113) did not exhibit slopes significantly different from zero. Because of the assumed non-linear nature of the stomatal conductance behaviour, it

is possible that an apparent lack of response results from the relatively low  $g_s$  in our dataset. While the average  $g_s$  at  $A_{\text{Sat}}$  obtained from top-canopy trees ( $0.18 \text{ mol m}^{-2} \text{ s}^{-1}$ ) was similar to the reported global average for tropical rain forest ( $0.20 \text{ mol m}^{-2} \text{ s}^{-1}$ ) (Schulze et al. 1994), some of our top-canopy species (e.g. *Micropholis* sp. and *Prionostemma aff. aspera*) displayed considerably lower averages of both  $A_{\text{Sat}}$  and  $g_s$  at  $A_{\text{Sat}}$  (Table 3). Low  $A_{\text{Sat}}$  and  $g_s$  at  $A_{\text{Sat}}$  is an indication of conservative water use in some species. Williams et al. (1998) suggested that tropical rain forest species maximise daily carbon uptake, extending water use into the afternoon (a period with high evaporative demand) by maintaining low fluxes during the morning period. Despite that, the relative reduction in  $g_s$ , calculated as the difference between  $g_s$  at 0.5 kPa and  $g_s$  at 2 kPa, averaged 48% among the plant functional groups and 45% among all individuals. Similar weak stomatal responses led to the hypothesis that stomatal functioning of tropical vegetation might not conform to the temperate vegetation model, in the sense that stomata might be less sensitive to  $\nu$  since ambient relative humidity is often high (Mooney and Chu 1983). The pattern exhibited on Figure 6 by the Understorey Trees functional group suggests that the environmental drivers incorporated into Equation (3) do not fully represent stomatal functioning for that group. The understorey environment of tropical forests is characteristically shady with moist and still air. Stomatal behaviour of tropical understorey trees is thought to be adapted to such a condition. It is thought that  $g_s$  is often lower than leaf surface boundary layer conductance, resulting in a decoupling between  $E$  and  $\nu$  (Knapp and Smith 1990). Also, there are indications that several understorey species keep stomata opened most of the time, as a strategy to increase carbon uptake during brief sunflecks, therefore reducing limitation by  $\text{CO}_2$  diffusion (Tinoco-Ojanguren and Pearcy 1992). Accordingly, stomatal behaviour of understorey trees might be less responsive to  $\nu$ ,  $\text{CO}_2$  and  $A$ . Furthermore, the application of Medlyn's model (Equation (3)) to our data consistently resulted in underestimated  $g_s$  (Figures 5 and 6), perhaps due to reasons similar to those that arose for the Understorey group. Although low stomatal response to humidity might increase species competitiveness by conferring higher carbon uptake, it might also be extremely disadvantageous during strong drought due to the risk of xylem cavitation and decreased survivorship (Condit et al. 1995; Sperry 2000). Medlyn et al. (2011) indicated a large variation in stomatal sensitivity among broad functional groups/vegetation types ( $g_1$  varying between 6.1 up to 12.1 for broadleaf plants). Our functional groups showed a smaller range (3.14–5.24, Table 5), although significant differences were detected among them. The top-canopy lianas and understorey trees were most sensitive to dry season conditions.

The results of the present study indicate that, within a continuum, two extremes of water-use patterns existed (Figure 4). The first extreme was characterised by plants allowing transpiration ( $E$ ) to vary with  $\nu$ , while  $g_s$  remained constant (Figure 4 – Increasing  $E$ ). The second pattern

consisted of adjustments in  $g_s$  in response to changes in  $\nu$ , resulting in constant  $E$  (Figure 4 – Constant  $E$ ). The 'Increasing  $E$ ' pattern agrees with the hypothesis presented by Mooney and Chu (1983) and has been classified as 'regime B' in Monteith (1995), probably occurring in species that show limited stomatal response to changes in leaf water potential caused by high  $E$  rates (Oren et al. 1999; Phillips et al. 2001). The somewhat common observation of 'Increasing  $E$ ' in the present dataset disagrees with its supposedly rare condition indicated by Monteith (1995), and suggests the need for more comparisons between tropical and temperate vegetation. Finally, it is important to keep in perspective that plants have alternative ways to respond to the increased transpiration demands of the dry season. Besides short-term stomatal regulation, a second long-term mechanism used by tropical vegetation to regulate water status is to reduce evaporative surface by leaf shedding and therefore reducing canopy water flux (Phillips et al. 2001).

Stomatal conductance at saturating light was equivalent or significantly higher during the dry season for all but one of the species that were sampled extensively enough to allow statistical comparisons (Table 4). McWilliam et al. (1996), studying a south-western site in Brazilian Amazonia (Reserva Jarú, Rondônia), found no statistical distinction between wet and dry season  $g_s$ , while Sá et al. (1996) suggested reduced dry season  $g_s$  for both pasture and forest ecosystems for a south-eastern site in Brazilian Amazonia (Marabá, Pará), although with occasional high  $g_s$  values recorded. Several factors might have contributed to the observed pattern. First, dry season rainfall exceeded  $100 \text{ mm month}^{-1}$  on eight occasions during the length of this study (Figure 1(a)), which might have alleviated drought conditions. Second, Nepstad et al. (1994) provided evidence that eastern Amazonian vegetation was able to maintain a green canopy during the dry season by accessing water from deeper soil layers. Third, the occurrence of hydraulic redistribution exhibited by some tropical rain forest species might extend water availability to other plants in the community (Oliveira and Dawson 2005). Finally, canopy thinning during the dry season might help tropical rain forest plants to maintain a more favourable water status during the dry season due to reduced evaporative surface (Asner et al. 2000; Phillips et al. 2001; Goulden et al. 2004).

Although dry season  $\Psi_{\text{leaf-dawn}}$  was significantly lower than wet season  $\Psi_{\text{leaf-dawn}}$ , the small differences observed in this study (Figure 2) and by Nepstad et al. (2007) favour the hypothesis of a relatively small dry season reduction in water availability. Furthermore, most of the species (64%) showed invariant leaf  $\delta^{13}\text{C}$ , indicating a tendency to maintain the balance between  $g_s$  and  $A$  constant through both wet and dry season (assuming a constant rate of leaf production), a pattern also observed by Buchmann et al. (1997) in a study involving a tropical rain forest site in French Guiana. Leaf  $\delta^{13}\text{C}$  values indicate a long-term integration of water use efficiency (Farquhar et al. 1989). The  $\delta^{13}\text{C}$  values obtained for top-canopy plants

in this study showed much less variation when compared with results from Bonal et al. (2000), although that study evaluated a larger set of species and individuals. The average  $\delta^{13}\text{C}$  value of mid-canopy trees in the present study ( $-32.2\text{‰}$ ) was almost identical to the mid-canopy average ( $-32.1\text{‰}$ ) presented by Martinelli et al. (1998) for another tropical rain forest site (Rondônia, Brazil). Studying a French Guiana tropical rain forest site with annual precipitation rate ( $2200\text{ mm year}^{-1}$ ), similar to the Santarém site, Buchmann et al. (1997) found a difference between top-canopy and understory  $\delta^{13}\text{C}$  values similar to the difference observed in the present study ( $5\text{‰}$  and  $5.8\text{‰}$ , respectively). On the other hand, Ometto et al. (2002) observed slightly higher differences between top-canopy and understory  $\delta^{13}\text{C}$  values for two other Amazonian sites (Manaus =  $8\text{‰}$ , Ji-Paraná =  $7\text{‰}$ ). The inter-site comparison of  $\delta^{13}\text{C}$  averages and ranges indicates basin-wide similarities in ecophysiological properties and/or canopy structure of the Amazonian tropical rain forest vegetation, despite differences in annual precipitation rates and length of the dry season. Also, a positive relationship observed between  $\delta^{15}\text{N}$  and relative canopy position ( $\delta^{15}\text{N} = 5.3 + 0.02$  canopy position,  $n = 75$ ,  $r^2 = 0.18$ ,  $P = 0.001$ ) indicates that canopy processes might be involved in leaf  $\delta^{15}\text{N}$  value determination, and could be helpful in canopy structure comparison among different sites.

The concentration of nitrogen present in leaves scales with its assimilation capacity because a large fraction of the nitrogen pool is allocated into carbon-fixing and light-harvesting proteins (Evans 1989). The  $N_{\text{Area}}$  values obtained in this study were similar to values presented by Carswell et al. (2000), but with a slightly higher range compared with Reich et al. (1994) or Lloyd et al. (1995). Leaves tend to become less efficient in performing photosynthesis as they age, although the rate of efficiency loss can vary extensively (Kikuzawa and Lechowicz 2011). As Amazonian lowland rain forest tree leaves tend to reach the end of their lives during the light limited wet season (Myneni et al. 2007; Doughty and Goulden 2008), lower efficiency can be expected for this period, when rates of older leaves being shed seems to increase. Our results did not conform to this notion, as the interdependence of  $A_{\text{Sat}}$ ,  $g_s$ ,  $V_{\text{cmax}}$ , and  $N_{\text{Area}}$  displayed in Figure 3 indicated that relationships among parameters did not change with season.

The community as a whole showed little evidence that season affected leaf-level gas exchange rates (Table 6). Yet, individual plants presented divergences in ecophysiological characteristics in relation to season. Regarding  $A_{\text{Sat}}$ , three seasonal patterns could be observed. Four species showed a significant decrease in  $A_{\text{Sat}}$  values during the dry season, while four other species showed a significant decrease in  $A_{\text{Sat}}$  values during the wet season. Yet another four species showed no significant seasonal change in  $A_{\text{Sat}}$  values (Table 4). Our general hypothesis that photosynthetic carbon assimilation rates were lower during the dry season due to stomatal limitation was thus rejected for most of the species. The understorey trees *R. neglecta* showed seasonal

changes in  $A_{\text{Sat}}$  that were not associated with  $g_s$  or  $V_{\text{cmax}}$ , or associated with  $N_{\text{Area}}$  (a proxy for  $V_{\text{cmax}}$ ) (Table 4). All other observed seasonal changes in  $A_{\text{Sat}}$  were consistently associated with changes in  $g_s$ ,  $V_{\text{cmax}}$  or  $N_{\text{Area}}$ , indicating a relatively strong degree of acclimation with season of photosynthetic functions. Studying a deciduous forest in Oak Ridge (TN, USA), Wilson et al. (2000) demonstrated that seasonal changes in  $V_{\text{cmax}}$  might be a source of variation in  $A$ . In the present case, 58% of the species showed no seasonal variation in  $V_{\text{cmax}}$  values (Table 4), suggesting limited biochemical acclimation of leaves to season. Two species that showed significantly lower dry season  $V_{\text{cmax}}$  displayed synchronous decreases in  $N_{\text{Area}}$ , suggesting nutrient limitation of  $A$ . It has been suggested that periods of low nutrient availability might arise due to limited litter decomposition during the dry season (Wright 1996; Saleska et al. 2003). Furthermore,  $\delta^{15}\text{N}$  and  $N_{\text{Mass}}$  indeed showed significant differences between seasons (Table 6), indicating possible shifts in biogeochemical processes at the ecosystem level. The two species that showed significantly higher dry season  $V_{\text{cmax}}$  also showed higher  $A_{\text{Sat}}$  and  $g_s$  at  $A_{\text{Sat}}$  for that season, indicating that those species might up-regulate its photosynthetic capacity during the dry season, possibly to match increased light availability (Potter et al. 1998).

## Conclusions

Only one species out of 14 displayed concomitant dry season decreases in  $g_s$  at  $A_{\text{Sat}}$  and  $A_{\text{Sat}}$ , indicating that during the study period the dry season was not associated with substantial increase in water stress and consequent limitation in gross primary productivity. As leaf-level productivity did not change with season, other factors must be responsible for observed seasonal variations in ecosystem productivity (e.g. ecosystem respiration rates, or active biomass). The minor seasonal changes in  $N_{\text{Area}}$  and  $V_{\text{cmax}}$  support the adoption of constant values of these parameters into biochemical carbon assimilation models. The limited responses of stomata to step changes in  $\nu$  observed for most of the individuals analysed in this study suggests that a tight control of  $E$  by stomata is not a necessary condition for tropical rain forest species. Furthermore, the consistent underestimations in modelled  $g_s$  obtained by the Equation (3) model suggests that stomatal functioning in tropical environments is also dependent on factors not fully accounted for at the moment. The identification and quantification of such descriptors of functional biodiversity are crucial for increasing the ability of models to project future scenarios of vegetation in response to ongoing changes (Moorcroft 2006).

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