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# Parameterization of Canopy Structure and Leaf-Level Gas Exchange for an Eastern Amazonian Tropical Rain Forest (Tapajós National Forest, Pará, Brazil)

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**ABSTRACT:** Carbon flux of Amazonian primary forest vegetation has been shown to vary both spatially and temporally. Process-based models are adequate tools to understand the basis of such variation and can also provide projections to future scenarios. The parameterization of such process-based

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models requires information from the vegetation in question simply because ecosystem-level gas exchange is a direct result of the tightly coupled interaction between local vegetation and regional climate. In this study, data are presented concerning canopy structure [leaf area index (LAI), and the ratio of leaf dry mass to leaf area (LMA)], leaf chemistry [area-based foliar nitrogen content ( $N_{\text{area}}$ ) and carbon isotope composition ( $\delta^{13}\text{C}$ )], and photosynthetic gas exchange [maximum carbon assimilation rates ( $A_{\text{max}}$ ), stomatal conductance ( $g_s @ A_{\text{max}}$ ), maximum carboxylation capacity ( $V_{\text{cmax}}$ ), and respiration rates ( $R_d$ )] versus relative height from an extensive survey of primary forest vegetation of the Santarém region (eastern Amazon, Santarém, Federal State of Pará, Brazil). Ground-level LAI values ranged between 4.5 and 5.9. Both  $A_{\text{max}}$  and  $V_{\text{cmax}}$  showed large variations within the canopy profile with values ranging between 2.4 and 15.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and between 10.1 and 105.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. Also,  $N_{\text{area}}$  varied between 0.75 to 4.19  $\text{gN m}^{-2}$ , and similar to  $A_{\text{max}}$  and  $V_{\text{cmax}}$ , showed higher values at the top of the canopy. Variations were detected among sites in patterns of vertical distribution of  $N_{\text{area}}$  and LAI, indicating spatial heterogeneity of the forest. Also, no statistically significant evidence of seasonal variations on parameters was observed, indicating that there is limited gas exchange acclimation by the vegetation to wet or dry seasons.

**KEYWORDS:** Carbon; Photosynthesis; Rain forest

## 1. Introduction

The Amazon rain forest has been recognized as a major component of the global energy budget and the cycling of carbon, nutrients, and water (Dickinson 1989; Lean and Warrilow 1989; Shukla et al. 1990; Malhi and Grace 2000; Cramer et al. 2004). An emerging consensus points to the Amazonian rain forest as a dynamic ecosystem changing in response to today's global changes (Phillips et al. 2004). Because of the global significance of this biome, it is important to answer questions such as: Is the Amazon region currently behaving as a source or a sink for atmospheric carbon? And furthermore, how will such behavior change in the future?

To build up the necessary knowledge needed to answer such questions, several studies evaluated measurements and models of carbon fluxes and stocks for a variety of primary forest sites in Amazonia. In summary, such studies involved measurements of carbon dioxide fluxes (Wofsy et al. 1988; Fan et al. 1990; Grace et al. 1995; Malhi et al. 1998; Kuck et al. 2000; Andreae et al. 2002; Araújo et al. 2002; Carswell et al. 2002; Saleska et al. 2003; Chambers et al. 2004; Garcia-Montiel et al. 2004; Goulden et al. 2004; Miller et al. 2004), biomass monitoring (Phillips et al. 1998; Nepstad et al. 2002; Rice et al. 2004;), and modeling of primary productivity (Sellers et al. 1989; Lloyd et al. 1995; McKane et al. 1995; da Rocha et al. 1996; Potter et al. 1998; Raich et al. 1991; Tian et al. 1998; Williams et al. 1998; Asner et al. 2000; Botta and Foley 2002; Chou et al. 2002; Zhan et al. 2003; Santos and Costa 2004). While some studies identified rain forest Amazonian ecosystems as sinks for atmospheric carbon (Grace et al. 1995; Malhi et al. 1998; Phillips et al. 1998; Andreae et al. 2002; Araújo et al. 2002; Carswell et al. 2002), other studies indicate an equilibrium situation or even that these

ecosystems are a source of CO<sub>2</sub> to the atmosphere (Chou et al. 2002; Saleska et al. 2003; Goulden et al. 2004; Miller et al. 2004; Rice et al. 2004). Such findings point to a large spatial and temporal variability in carbon fluxes, which probably depend more on biology than on micrometeorology (Keller et al. 2004).

The carbon balance of a site depends essentially on rates of two opposing processes: photosynthesis and respiration. Because carbon-balance estimates for Amazonian tropical forest were done with different methods, at different periods, and for different regions, simple comparison of net primary productivity (NPP) provides limited understanding on processes governing regional carbon exchange. For example, net ecosystem exchange (NEE) measurements alone cannot clarify whether or not spatial and temporal variations in carbon fluxes are due to changes in photosynthetic assimilation, respiration, or both (Valentini et al. 2000; Ehleringer et al. 2002). To fulfill such a gap, process-based carbon assimilation models are used to scale up fluxes and provide new understanding necessary to improve carbon budgets (Canadell et al. 2000). Furthermore, predictive power is attained by applying mechanistic interpretations of how vegetation controls fluxes, allowing realistic projection of future and past carbon balance (Collatz et al. 1991; Baldocchi and Harley 1995; Baldocchi et al. 1996; de Pury and Farquhar 1997; Sellers et al. 1997).

To help explain the observed spatial and temporal variations of carbon fluxes in Amazonia, a more complete understanding of canopy-scale carbon assimilation is necessary. While respiratory processes are relatively straightforward and dependent on temperature (metabolism rate) and water availability (microbial activity), photosynthetic carbon assimilation is much more complex and depends on assimilation capacity, canopy structure, and microclimate. Models of leaf-level gas exchange are commonly based on both the biochemical understanding of photosynthetic carbon assimilation (Farquhar et al. 1980), and the environmental and physiological effects on stomatal conductance (Jarvis 1976; Ball et al. 1987). At a given temperature and irradiance, carbon assimilation rates result from the dynamics between carboxylation capacity ( $V_{cmax}$ ) and the CO<sub>2</sub> concentration at the site of carboxylation. Area-based leaf nitrogen content ( $N_{area}$ ) is a fairly easily accessed parameter and scales with  $V_{cmax}$  because a high proportion of the nitrogen present on a leaf is allocated into carbon fixation enzymes (Evans et al. 1989). Furthermore, according to the theory of optimal nutrient allocation (Field and Mooney 1986), this resource is distributed throughout the canopy in proportion to light availability. Finally, the distribution of light within the canopy profile is a result of the leaf distribution. A series of factors (e.g., water, nutrients, energy availability, biological interactions, and local climate) play a role on the establishment of such profiles. Such intimate adjustment of resource allocation, canopy structure, and assimilation rates results from the interaction of the local ecosystem diversity with local climate, making obvious the necessity of parameterization of process-based carbon assimilation models with local data.

The changes observed within the canopy profiles comprise a second class of biological parameters that are essential to scaling leaf-level fluxes to the canopy level, namely, canopy structure (Baldocchi et al. 1996; Weiss et al. 2004). Among the most relevant issues on scaling fluxes up is the adequate representation of canopy light levels and assimilation capacities. Strategies for the representation of the canopy vary ranging from single layer models (big leaf; e.g., Lloyd et al. 1995),

sun and shade models (Zhan et al. 2003), and multilayer models (e.g., Williams et al. 1998). The increased complexity of models might improve accuracy of canopy-level carbon assimilation calculations, although it calls for more extensive parameterization.

In this work, we report on studies of canopy structure and leaf properties of the vegetation from the Tapajós National Forest (Flona-Tapajós, Santarém, Federal State of Pará, Brazil), a site representative of eastern Amazon terra firme evergreen primary rain forest ecosystem. For that, we used well-established relationships among canopy structure, leaf chemistry, and gas exchange parameters. The present study is nested into the wide-ranging efforts of the Large-Scale Biosphere–Atmosphere Experiment in the Amazon (LBA), which seeks a better understanding of the interactions between Amazonian ecosystems and the atmosphere. In a sense, the present work provides the tools for computations of gross primary productivity (GPP) and for the evaluation of the biological control exerted by local vegetation over carbon and water fluxes. In an extension of this study we plan to use these data to test the ability to scale leaf-level fluxes to the whole canopy.

## 2. Methods and materials

### 2.1. Study site

Primary vegetation from eastern Amazonian lowland tropical rain forest was the focus of this study. Data for characterization of canopy parameters were collected within the Flona-Tapajós, a National Forest reserve of the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA, further information available online at <http://www.ibama.gov.br/projetotapajos/>). This reserve was established in 1974 between the Tapajós River and the road BR-364 (Cuiabá-Santarém) in the state of Pará, Brazil. Four walk-up towers, which individually composed the four study sites used in this study, granted access to the canopy. The first site contained a 40-m tower and is named here Flona-1. It was located 67 km south of Santarém (2.856 7°S, 54.958 9°W) and corresponds to the LBA mature forest site “Tapajós National Forest km 67” of Keller et al. (Keller et al. 2004). The second and third sites (2.898 33°S, 54.955 83°W), 30 m apart from each other, and named Flona-2.1 and Flona-2.2, were located approximately 10 km from the Flona-1 site, in the control plot of the rain exclusion experiment conducted by the Instituto de Pesquisas Amazônicas (IPAM) and the Woods Hole Research Institute (Nepstad et al. 2002). The towers at this site reached the top of the canopy at a height of about 25 m. Finally, a fourth site named Flona-3 was located 16 km south of Flona-1 site, and corresponds to the LBA mature forest site “Tapajós National Forest km 83” of Keller et al. (Keller et al. 2004). This site underwent selective logging starting February 2001, after our sampling activities, and possessed a tower that reached the canopy at about 30 m.

Information about climate and vegetation for these sites are presented by Ometto et al. (Ometto et al. 2002), Nepstad et al. (Nepstad et al. 2002), da Rocha et al. (da Rocha et al. 2004), and Vieira et al. (Vieira et al. 2004). Briefly, the mean annual precipitation in the Santarém sites is 2207 mm, with a 5-month dry season when precipitation is less than 100 mm (July through November). Air temperature above the canopy varies little throughout the year, with maximum daily temperatures

ranging between 24° and 32°C and minimum daily temperatures ranging between 20° and 25°C. Soil water content at a depth of 10 cm typically stays above 0.3 cm<sup>3</sup> cm<sup>-3</sup> (Goulden et al. 2004). Clay-rich soils (Santarém oxisol) were predominant at this site on plateaus, while soils with increased sand content (Santarém ultisols) occur on slopes and topographic lows (Silver et al. 2000; Telles et al. 2003). In a floristic survey, Vieira et al. (Vieira et al. 2004) reported 460 trees (diameter at breast height > 10 cm) per hectare belonging to 133 species.

## 2.2. Canopy structure

The accumulation of LAI through the forest canopy profile was determined in June 2003 for the towers on sites Flona-1, Flona-2.1, and Flona-2.2. LAI estimates were derived from differences between simultaneous readings from two LAI-2000 sensors (Li-Cor). One of the sensors was placed fixed at the top of the canopy while the other was carried through the canopy. Measurements of LAI within the canopy profile were taken from the towers every 1.5 m (sites Flona-2.1 and Flona-2.2) or every 2 m (site Flona-1). Because of the nature of tower architecture, measurements were alternately taken from the northwest and southeast. LAI-2000 assumes a random distribution of leaves and cannot distinguish leaf area from nonleaf area (stems and branches); therefore, it measures plant area index (Weiss et al. 2004).

Leaves from all branches within reach from towers were sampled for LMA determinations, totaling 754 samples (Flona-1: 458 leaves from 27 species; Flona-2.1: 97 leaves from 21 species; Flona-2.2: 103 leaves from 25 species; Flona-3: 96 leaves from 14 species). Leaf samples were collected during nine field campaigns as follows: November 1999; March, July, and October 2000; February and September 2001; September 2002; and June–December 2003. For LMA determinations, contours of individual leaves were traced on paper sheets immediately after leaf clipping. Paper sheets with leaf drawings were scanned in the laboratory and the area of individual leaf images was determined with National Institute of Health (NIH)-Image software version 1.6 (available online at <http://rsb.info.nih.gov/nih-image/Default.html>). The actual leaves collected were taken to the laboratory for weight determination after being dried at 65°C in convection ovens until constant weight.

## 2.3. Foliage chemistry

Dried subsamples (1–2 mg) of each leaf collected for LMA determinations were used for  $\delta^{13}\text{C}$  and  $N_{\text{area}}$  determinations by continuous-flow isotope ratio mass spectrometry (IRMS Delta Plus Finnigan Mat) coupled with an elemental analyzer (Carlo Erba). Analyses were performed at the Laboratório de Ecologia Isotópica, Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, Piracicaba, Brazil. Carbon isotope ratios are expressed in delta notation relative to PeeDee Belemnite (PDB) standard as

$$\delta^{13}\text{C} = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000,$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are ratios of  $^{13}\text{C}$  to  $^{12}\text{C}$ . The precision of the isotopic measurements was 0.2‰.



Foliar total nitrogen contents were obtained with the elemental analyzer in a mass basis (gN per gram of leaf sample) and multiplied by the correspondent LMA in order to express it on an area basis (gN m<sup>-2</sup>).

## 2.4. Leaf-level gas exchange

Photosynthetic assimilation rates at saturating light ( $A_{\max}$ ), stomatal conductance to water vapor at  $A_{\max}$  ( $g_s@A_{\max}$ ), maximum rates of carboxylation ( $V_{c\max}$ ), and daytime leaf respiration rates under full darkness ( $R_d$ ) were measured on 27 plant individuals belonging to 22 species, concomitant to leaf collection for chemical analyses. Gas exchange measurements were taken with a photosynthetic gas exchange system with a red–blue light source and an external CO<sub>2</sub> source (model LI-6400, Li-Cor). We limited gas exchange measurements to morning hours (0800 to 1300 LT), to avoid afternoon stomatal closure. On all occasions, leaf area used was equal to 6 cm<sup>2</sup>. For  $A_{\max}$  and  $g_s@A_{\max}$  determinations (430 in total), conditions inside the chamber were controlled to maintain leaf temperature at 30°C, relative humidity around 80%, CO<sub>2</sub> concentrations at the sample cell at 360 mmol mol<sup>-1</sup>, and saturating levels of photosynthetic active photon flux density (PPFD; 800 μmol m<sup>-2</sup> s<sup>-1</sup> for understory plants and 1800 μmol m<sup>-2</sup> s<sup>-1</sup> for mid- and top-canopy species). The biochemical photosynthesis model used in Simple Biosphere Model (SiB2) (Sellers et al. 1996) and widely used in other land surface models (Bonan 2002) was used to obtain  $V_{c\max}$  values from both light and CO<sub>2</sub> response curves. This model is based on the approach of Farquhar et al. (Farquhar et al. 1980), modified by Collatz et al. (Collatz et al. 1991). The dependence of carbon assimilation on photosynthetic photon flux density (light response curves, 98 in total) was obtained by 10 stepwise increments in light level, while holding leaf temperature, relative humidity, and ambient CO<sub>2</sub> constant. For the determination of the dependence of carbon assimilation on intercellular CO<sub>2</sub> concentration ( $A-c_i$  curves, 77 in total) under saturating light, 10 ambient CO<sub>2</sub> levels were used, while holding constant leaf temperature and relative humidity. The response curves (98 A-PPFD curves and 77  $A-c_i$  curves) were measured in six species of each of the following plant functional groups top-canopy lianas, top-canopy trees, mid-canopy trees, and understory trees. Measuring time of each response curve spanned between 60 and 90 min.

## 2.5. Data analyses

Each data point presented in this study represents species averages ( $n = 1, \dots, 9$ ) for a specific height in the canopy, from individual sampling campaigns. A summary of sample sizes and number of individual plants and plant species used are presented in Table 1. Additional information about this dataset is available online at <http://lba.cptec.inpe.br/beija-flor/>.

To standardize across sites, height was presented as relative to maximum height. Accordingly, 100% relative height corresponds to 1 m above the uppermost measurement taken from a particular tower (Flona-1 = 41 m, Flona-2.1 and Flona-2.2 = 26 m, Flona-3 = 31 m). For all figures involving canopy profile, relative height was plotted on the y axes for visual clarity. For statistical analyses, however, relative height was considered the independent variable. Linear regressions were used to describe relationships among parameters evaluated. To assess effects of

**Table 1. Summary of parameters evaluated, sampling efforts, and plant species representation.**

Variable	<i>N</i>	Individuals	Plant species
LMA	122	56	47
$N_{\text{area}}$	122	56	47
$\delta^{13}\text{C}$	191	73	59
$A_{\text{max}}$	80	27	22
$g_s@A_{\text{max}}$	80	27	22
$V_{\text{cmax}}$	66	23	18
$R_d$	68	26	22

season or site, analysis of covariance was used to establish comparisons among the slopes derived from linear regressions.

### 3. Results

#### 3.1. Canopy structure

There was a significant relationship between cumulative LAI and canopy height (Figure 1 and Table 3). LAI profiles from Flona-2.2 and Flona-1 had statistically different slopes ( $F = 13.13$ ,  $P = 0.001$ ,  $n = 36$ ), although no difference was detected between Flona-2.1 and Flona-1 ( $F = 2.86$ ,  $P = 0.101$ ,  $n = 33$ ) or between Flona-2.1 and Flona-2.2 ( $F = 1.0$ ,  $P = 0.327$ ,  $n = 29$ ). The increase in LAI with increasing canopy depth occurred significantly faster at the Flona-2.2 site. Total cumulative LAI values at ground level, calculated from the regressions, ranged from 4.5 to 5.9. Because of the significant different patterns observed among the sites, data from each site were plotted individually on Figure 1.

In contrast to LAI patterns, no effect of site ( $F = 0.308$ ,  $P = 0.820$ ,  $n = 122$ ) was detected for the distribution of LMA within the canopy profile (Table 2). Furthermore, no effect of season was detected ( $F = 0.001$ ,  $P = 0.978$ ,  $n = 122$ ). Accordingly, LMA data from all sites were pooled (Figure 2). As a general trend, LMA significantly increased with relative canopy height (Figure 2) and 55% of the variance of LMA could be explained solely by height (Table 3). At the lowest strata, LMA varied from 48 to 90 g m<sup>-2</sup>, and increased at the top of the canopy, ranging from about 90 to almost 200 g m<sup>-2</sup>. We observed a greater variation in LMA values both at the top of the canopy and at the understory than in the middle of the canopy.

#### 3.2. Leaf chemistry

We found significant differences in the slopes of linear regressions between  $N_{\text{area}}$  and relative canopy height (Table 2). Accordingly, two sets of data are presented in Figure 3, one encompassing data from sites Flona-1 and Flona-3, and another pooling data from sites Flona-2.1 and Flona-2.2. No other combination of site comparisons produced significant differences (Table 2). A comparison between these two groups of pooled data again showed a significant difference in slopes ( $F = 10.2$ ,  $P = 0.002$ ,  $n = 122$ ). Clearly,  $N_{\text{area}}$  concentrations were higher at the intermediate canopy strata at Flona-1 and Flona-3 in comparison with Flona-2.1

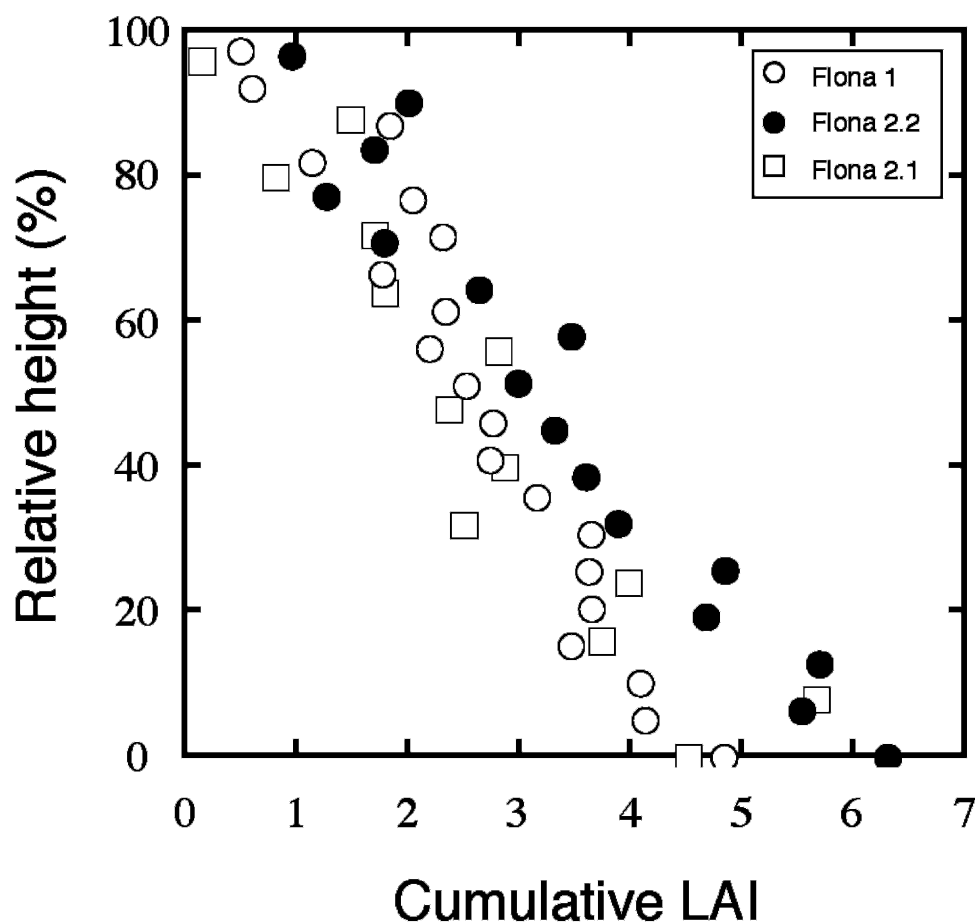


Figure 1. The distribution of leaf area index (LAI as cumulative projected leaf area per ground area) within the canopy profile from three sites on Flona-Tapajós National Forest primary forest vegetation, as in Jun 2003.

and Flona-2.2. At the top of the canopy,  $N_{\text{area}}$  values were similar between the two sets of data (Figure 3). The  $N_{\text{area}}$  concentration varied from approximately 0.8 to 2.0  $\text{gN m}^{-2}$  at ground level increasing to approximately 2.0 to 4.0  $\text{gN m}^{-2}$  at the top of the canopy.

Table 2. Intersite similarities evaluated by statistical comparison (*P* values) of slopes resulting from linear regression between parameter (LAI, LMA,  $N_{\text{area}}$ , and  $\delta^{13}\text{C}$ ) and relative height considering the effect of site for primary forest vegetation from Flona-Tapajós, Brazil. Alpha = 0.05.

Comparison	LAI	$N_{\text{leaf}}$	LMA	$\delta^{13}\text{C}$
Flona-2.1 Flona-2.2	0.327	0.995	0.601	0.136
Flona-2.1 Flona-1	0.101	0.011	0.537	0.062
Flona-2.1 Flona-3	—	0.007	0.988	0.395
Flona-2.2 Flona-1	0.001	0.021	0.914	0.595
Flona-2.2 Flona-3	—	0.002	0.618	0.447
Flona-1 Flona-3	—	0.220	0.462	0.501



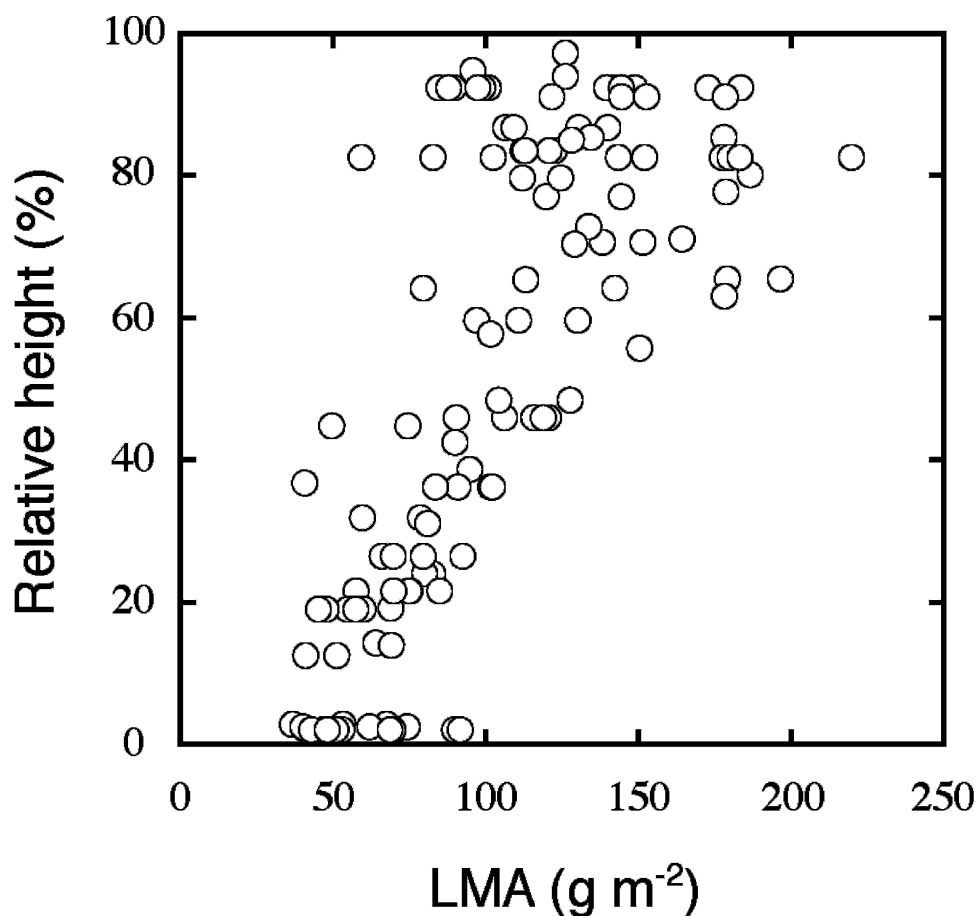


Figure 2. The distribution of LMA within the canopy profile from four sites on Flona-Tapajós National Forest primary forest vegetation. A regression line fitted to data pulled together from four different sites and without season distinction describes the function:  $LMA = 53.3 + 0.95 \times \text{Relative Height}$  ( $r^2 = 0.55$ ,  $P < 0.0001$ ,  $n = 122$ ).

Table 3. Linear regressions between relative height (%) and both canopy structure and leaf chemistry parameters, derived from data collected at four FLONA-Tapajós primary forest sites without distinction of season of the year. Dependent variable = Intercept + Slope  $\times$  (Relative Height).

Dependent variable	Site	Intercept	Slope	Regression coefficient	<i>n</i>	<i>P</i> value
LAI	Flona-2.2	5.93	-0.052	0.94	16	< 0.0001
	Flona-2.1	4.85	-0.046	0.87	13	< 0.0001
	Flona-1	4.47	-0.037	0.93	20	< 0.0001
$N_{\text{area}}$	Flona-2.1 & 2.2	0.79	0.025	0.62	30	< 0.0001
	Flona-1 & 3	1.40	0.014	0.46	92	< 0.0001
LMA	all sites	53.3	0.95	0.55	122	< 0.0001
$\delta^{13}\text{C}$	all sites	-34.9	0.07	0.71	192	< 0.0001

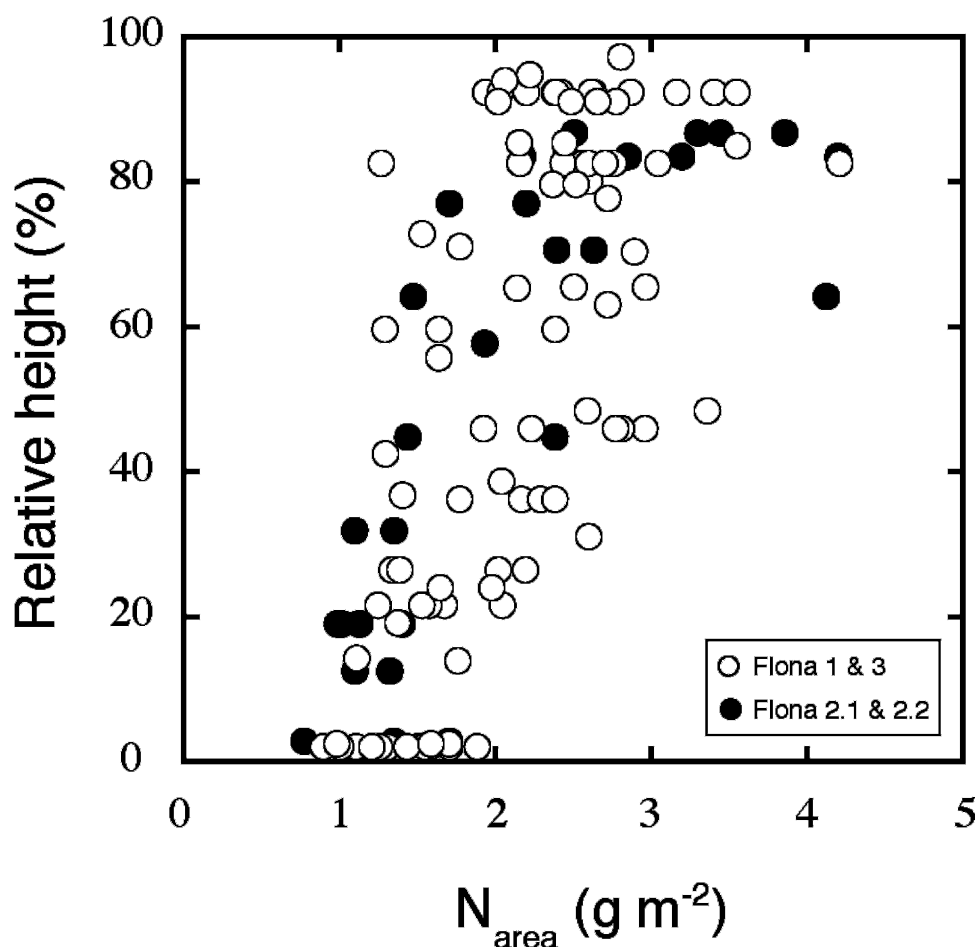


Figure 3. The distribution of area-based foliar nitrogen concentration ( $N_{\text{area}}$ ) within the canopy profile from four sites on Flona-Tapajós National Forest primary forest vegetation. Because of significant differences in slopes, data are separated into two datasets corresponding to grouping of different sites. Linear regression information for individual datasets is presented on Table 3.

We could not detect any seasonal ( $F = 0.256$ ,  $P = 0.614$ ,  $n = 192$ ) or spatial differences (Table 2) in the slopes of linear regressions between leaf  $\delta^{13}\text{C}$  and relative canopy height. Therefore, all data available were pooled together for the calculation of the linear regression (Figure 4). Approximately 70% of the variance in the foliar  $\delta^{13}\text{C}$  values was explained by the canopy height (Table 4). At the ground level, values varied from approximately  $-37\text{‰}$  to  $-33\text{‰}$ , increasing at the top of the canopy to approximately  $-31\text{‰}$  to  $-26\text{‰}$ , a difference of around  $6\text{‰}$  (Figure 4).

### 3.3. Leaf-level gas exchange

No effect of season was detected by analyses of covariance on the slopes of the linear regressions between  $A_{\text{max}}$  and  $g_s @ A_{\text{max}}$  ( $F = 0.616$ ,  $P = 0.435$ ,  $n = 80$ )

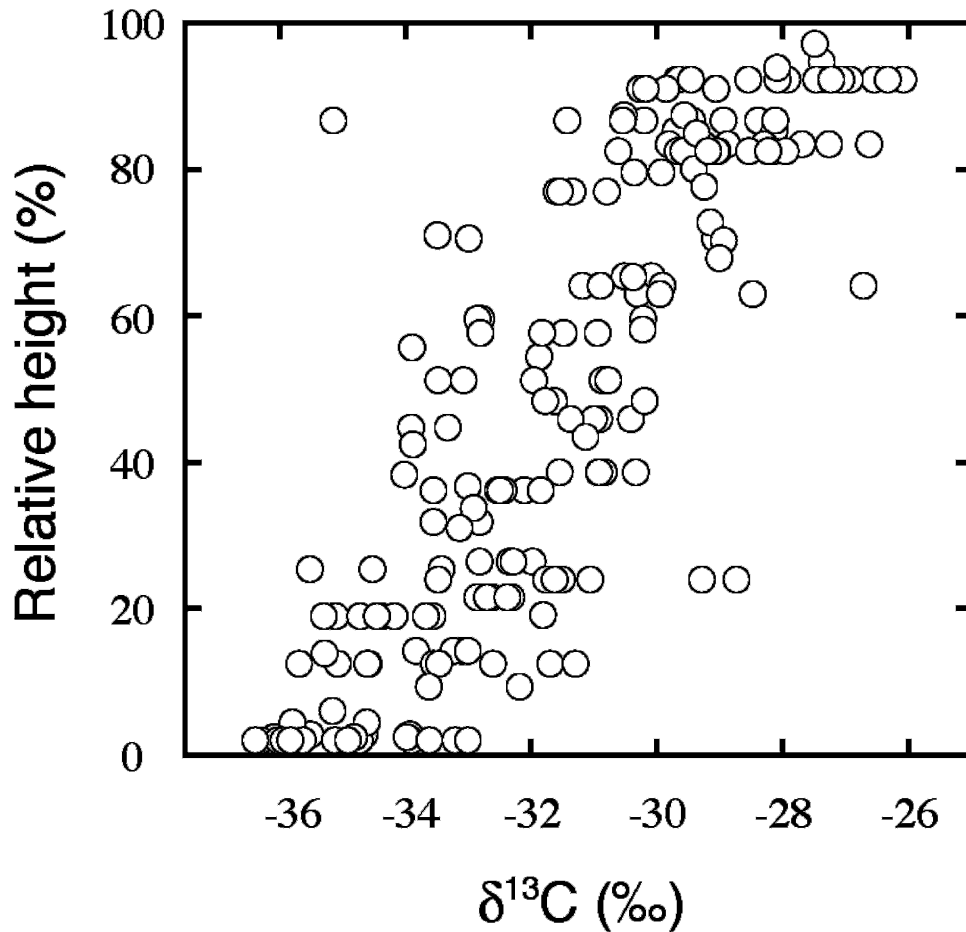


Figure 4. The distribution of foliar carbon isotope composition ( $\delta^{13}\text{C}$ ) within the canopy profile for the primary forest vegetation at the Flona-Tapajós National Forest. A regression line for data pulled together from four different sites, without season distinction describes the function:  $\delta^{13}\text{C} = -34.9 + 0.07 \times \text{Relative Height}$  ( $r^2 = 0.71$ ,  $P < 0.0001$ ,  $n = 192$ ).

Table 4. Linear regressions among photosynthetic gas exchange parameters and leaf chemistry derived from data collected at four FLONA-Tapajós primary forest sites without distinction of season of the year. Dependent variable = Intercept + Slope  $\times$  (Independent Variable).

Dependent variable	Independent variable	Intercept	Slope	Regression coefficient	<i>n</i>	<i>P</i> value
$A_{\text{max}}$	$g_s @ A_{\text{max}}$	1.97	46.9	0.62	80	< 0.0001
$A_{\text{max}}$	$V_{\text{cmax}}$	1.71	0.14	0.74	66	< 0.0001
$A_{\text{max}}$	$N_{\text{area}}$	1.18	2.97	0.40	73	< 0.0001
$V_{\text{cmax}}$	$N_{\text{area}}$	-7.02	23.0	0.51	62	< 0.0001
$R_d$	$V_{\text{cmax}}$	0.12	0.013	0.23	62	< 0.0001
$R_d$	$N_{\text{area}}$	-0.11	0.37	0.23	64	< 0.0001

or between  $A_{\max}$  and  $V_{c\max}$  ( $F = 0.0002$ ,  $P = 0.989$ ,  $n = 66$ ). Accordingly, no distinction of season was made (Figures 5 and 6). Although we had not enough data from each site to test for differences in slopes among them, we included data from all sites in these analyses to increase species representation. Here,  $A_{\max}$  had a significant positive increase with both  $g_s@A_{\max}$  and  $V_{c\max}$  (Table 4). Approximately 62% of the variation of  $A_{\max}$  was explained by  $g_s@A_{\max}$ , and 74% by  $V_{c\max}$  (Table 4). Measured  $A_{\max}$  and  $g_s@A_{\max}$  ranged from 2.4 to 15.8  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , and from 0.02 to 0.33  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , respectively (Figure 5). Calculated  $V_{c\max}$  ranged from 10.1 to 105.7  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Figure 6).

No seasonal variation in slopes of the linear regressions was detected by analysis of covariance for  $N_{\text{area}}$  versus  $A_{\max}$  ( $F = 2.351$ ,  $P = 0.130$ ,  $n = 73$ ; Figure 7a);  $N_{\text{area}}$  versus  $V_{c\max}$  ( $F = 0.147$ ,  $P = 0.703$ ,  $n = 62$ ; Figure 7b); and  $N_{\text{area}}$

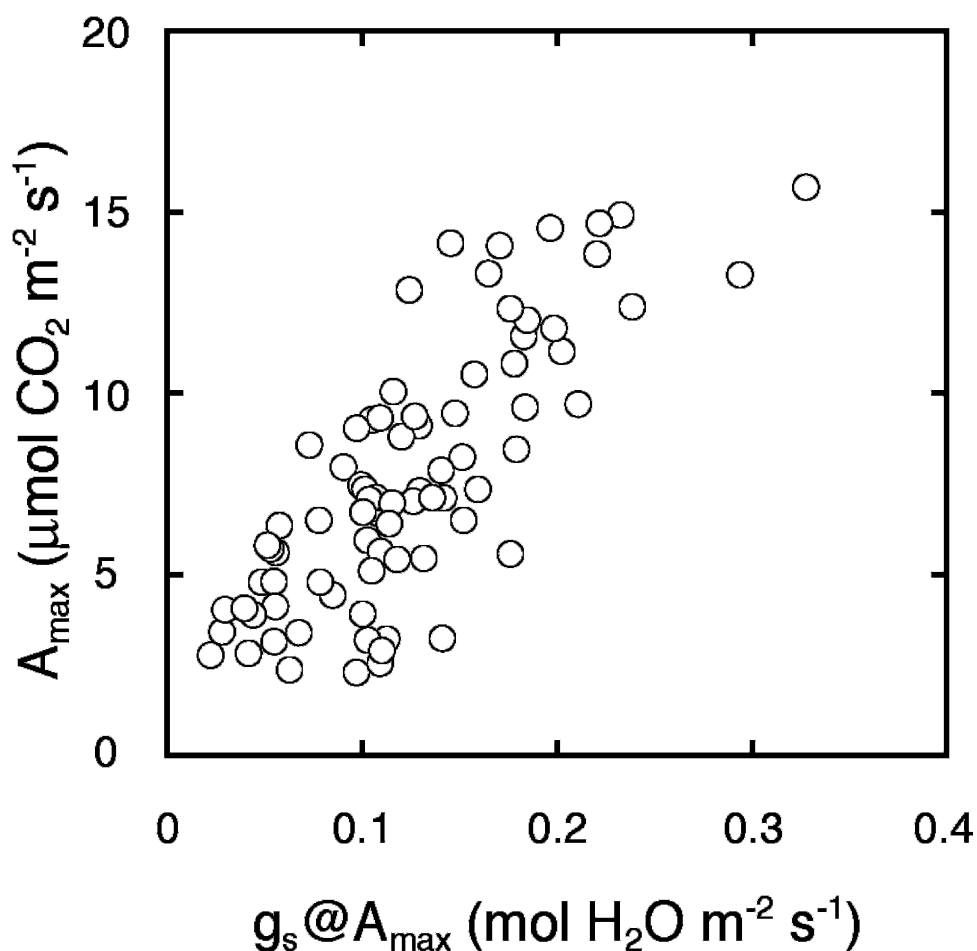


Figure 5. Relationship between stomatal conductance to water vapor ( $g_s@A_{\max}$ ) and carbon assimilation rate at saturating light ( $A_{\max}$ ) for primary forest vegetation within the Flona-Tapajós National Forest. A regression line fitted to the dataset describes the function:  $A_{\max} = 1.97 + 46.9 \times g_s@A_{\max}$  ( $r^2 = 0.62$ ,  $P < 0.0001$ ,  $n = 80$ ).

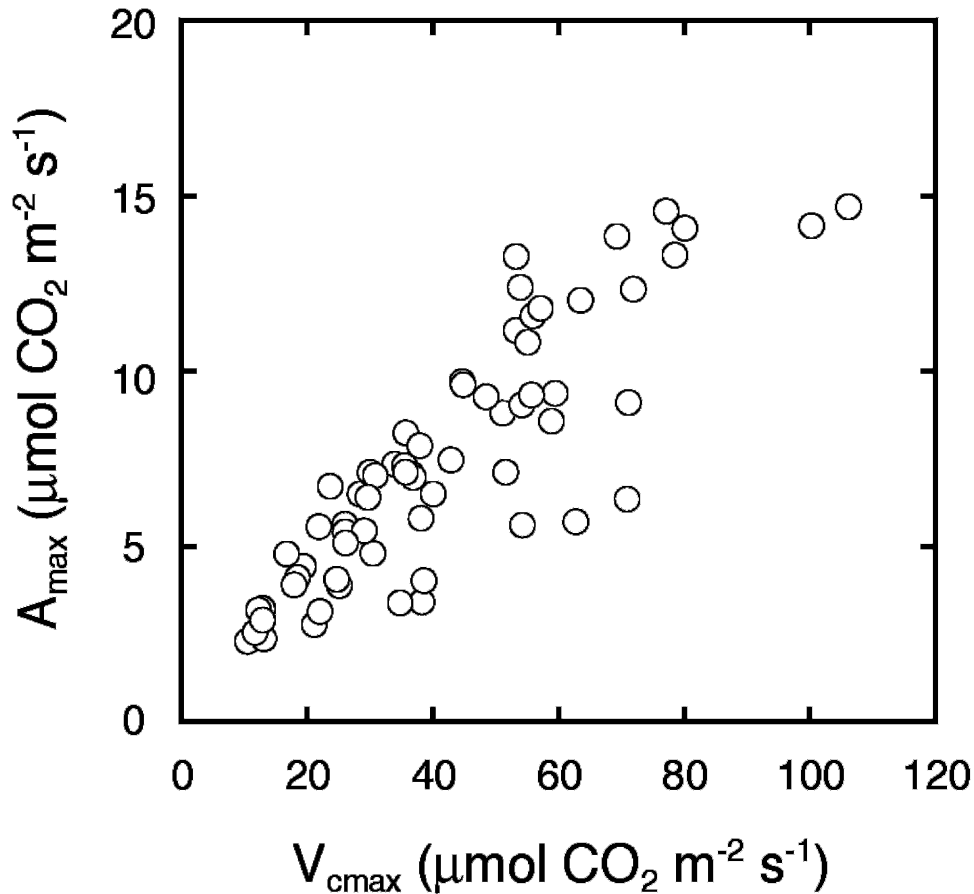


Figure 6. Relationship between maximum carboxylation capacity ( $V_{cmax}$ ) and carbon assimilation rate at saturating light ( $A_{max}$ ) for primary forest vegetation within the Flona-Tapajós National Forest. A regression line fitted to the dataset describes the function:  $A_{max} = 1.71 + 0.14 \times V_{cmax}$  ( $r^2 = 0.74$ ,  $P < 0.0001$ ,  $n = 66$ ).

versus  $R_d$  ( $F = 0.638$ ,  $P = 0.428$ ,  $n = 64$ ; Figure 7c). Again, we had insufficient data to test for site effect, but we included data from all sites to increase species representation. Data without distinction between site and season were grouped together for linear regression analyses (Figure 7 and Table 4). Here,  $N_{area}$  was positively related with  $A_{max}$ ,  $V_{cmax}$ , and  $R_d$ . The variation in  $A_{max}$  and  $V_{cmax}$  was reasonable explained by  $N_{area}$  concentration ( $r^2 = 0.40$  and  $0.51$ , respectively); however, the variance of  $R_d$  was poorly explained by either  $N_{area}$  ( $r^2 = 0.23$ ) or  $V_{cmax}$  ( $r^2 = 0.23$ ; Table 4).

#### 4. Discussion

Considering the high species diversity, coupled with the heterogeneity in vegetation formations and climate found within the Amazon basin, the actual ecophysi-

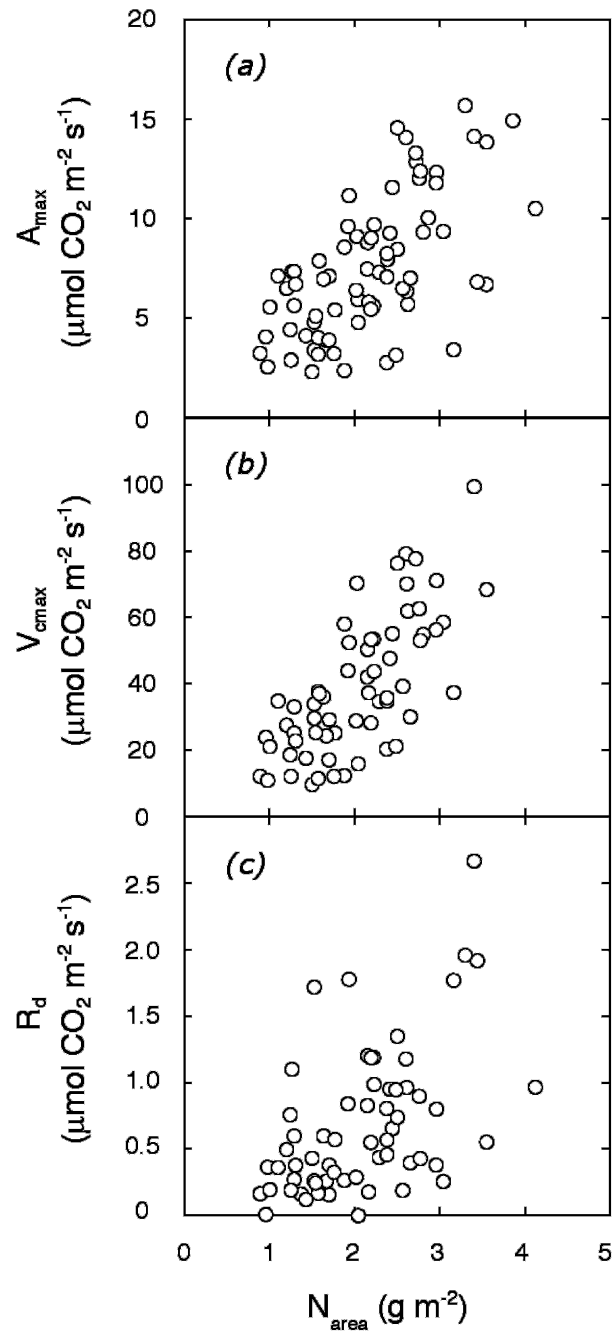


Figure 7. Relationship between area-based foliar nitrogen concentration ( $N_{\text{area}}$ ) and carbon assimilation rate at (a) saturating light ( $A_{\text{max}}$ ), (b) maximum carboxylation capacity ( $V_{\text{cmax}}$ ), and (c) daytime leaf respiration rates at dark ( $R_d$ ) for primary forest vegetation within the Flona-Tapajós National Forest. Regression lines fitted to the dataset describe the following functions:  $A_{\text{max}} = 1.18 + 2.97 \times N_{\text{area}}$  ( $r^2 = 0.40$ ,  $P < 0.0001$ ,  $n = 73$ ),  $V_{\text{cmax}} = -7.02 + 23.0 \times N_{\text{area}}$  ( $r^2 = 0.51$ ,  $P < 0.0001$ ,  $n = 62$ ), and  $R_d = -0.11 + 0.37 \times N_{\text{area}}$  ( $r^2 = 0.23$ ,  $P < 0.0001$ ,  $n = 64$ ).



ological characterization of Amazonia vegetation is extremely limited. The requirement of information derived from local vegetation stems from the recognition that distinct ecosystems exhibit differences in the vegetation influence over fluxes, and also that variation can exist on the nature of relationships among drivers and parameters (Bonan 2002). Furthermore, the relationships among parameters and canopy profiles presented in this work allow the parameterization of different kinds of canopy assimilation models (e.g., big leaf or multilayer).

#### 4.1. Canopy structure

Several studies highlighted the importance of describing canopy structure through LAI in carbon balance models (Wang and Jarvis 1990; Cowling and Field 2003; Weiss et al. 2004). Canopy structure causes environmental factors such as light levels, wind, and relative humidity to vary within the canopy profile, mainly due to the sheltering by the increasing LAI with increasing depth inside the canopy (Running and Coughlan 1988; Shuttleworth 1989; Roberts et al. 1990). Besides its relevance, reports of LAI profiles are scarce on the literature (Parker 1995). Although Wirth et al. (Wirth et al. 2001) reported an uneven leaf distribution on the canopy profile of a Panamanian tropical rain forest site, where 50% of leaves were found within the top 5 m of the canopy, Shuttleworth (Shuttleworth 1989) argued that foliage at tropical forests is more evenly distributed with canopy height, when compared to temperate forests. In our case, a strong linear relationship was found between cumulative LAI distribution and relative canopy height at FLONA-Tapajós sites (Figure 1; Table 3), indicating that leaves were evenly distributed in the canopy profile with about 35% being located within the top 10 m of the canopy.

Another component of canopy structure used in models is the variation in leaf anatomy with the canopy profile, frequently expressed as LMA. Details of a leaf anatomy are established during leaf expansion and are dependent on light levels, water stress, nutrient availability, leaf life span, and antiherbivore defense mechanisms (Coley 1983; Reich et al. 1994; Evans and Poorter 2001; Wright et al. 2002). Although LMA can be used to convert area-based into mass-based parameters (Baldocchi and Harley 1995), Reich et al. (Reich et al. 1998) argues that LMA by itself influences the slope of the relationship between  $A_{\max}$  and  $N_{\text{area}}$ . If that is a general rule, then the variety of factors influencing LMA will also be reflected in  $A_{\max}$ , further increasing the variability of physiological control over carbon fluxes. On a study concerning a forest with LAI at ground level of about 5.5, but with a short dry season (Manaus, Brazil), Carswell et al. (Carswell et al. 2000) observed a slope between LMA and relative height ( $\text{LMA} = 65.7 + 0.61 \times \text{relative height}$ ) similar to ours (Table 3), although the range of values observed were smaller. Our data revealed a considerable scatter of LMA values on the understory, similar to a pattern found for a French Guiana primary tropical rain forest (Rijkers et al. 2000). Such pattern indicates that factors that influence the increase of LMA with canopy height (e.g., water stress, higher light levels) might be different for understory plants (e.g., defense against herbivory).

#### 4.2. Leaf chemistry

The  $N_{\text{area}}$  values obtained from this study at the Flona-Tapajós sites (Figure 3) fall within the observed range (0.8 to 4.5 gN m<sup>-2</sup>) for Amazonia primary vegetation

(Reich et al. 1991; Reich et al. 1994; Lloyd et al. 1995; Williams et al. 1998; Carswell et al. 2000; Meir and Grace 2002). We observed significant differences in the distribution of  $N_{\text{area}}$  within the canopy profile among some of the sites evaluated in this study (Figure 3);  $N_{\text{area}}$  values increased with canopy height faster at the sites Flona-2.1 and Flona-2.2, when compared to the LBA sites (Flona-1 and Flona-3). Apparently, midcanopy vegetation from LBA sites had higher  $N_{\text{area}}$  values than sites Flona-2.1 and Flona-2.2 (Figure 3). Such differences were partially associated with the relative contribution of legume trees to the  $N_{\text{area}}$  within the canopy profiles. Legume trees from tropical rain forest commonly have higher nitrogen concentration in their leaves (Vitousek et al. 2002; Martinelli et al. 2000) when compared to other plants. The high  $N_{\text{area}}$  values found at the middle of the canopy for the Flona-1 correspond to samples taken from the legume tree *Sclerolobium paraense* Huber, while high values of at the top of the canopy of the Flona-2.1 site correspond to samples obtained from another legume tree (*Tachigali myrmecophila* Ducke). Because the dominance by plant families varies across the Amazon basin (Vieira et al. 2004), the total amount and distribution of  $N_{\text{area}}$  within the canopy profile can vary, even without variation in soil nitrogen availability.

The characteristic negative values of foliar  $\delta^{13}\text{C}$  arrives from fractionation steps during photosynthetic carbon fixation, when atmospheric  $\text{CO}_2$  molecules containing  $^{12}\text{C}$  atoms are assimilated in preference to molecules containing  $^{13}\text{C}$  atoms (Farquhar et al. 1989). The balance between demand (assimilation rates) and supply (stomatal conductance) of  $\text{CO}_2$  determines the extent of such discrimination (Farquhar et al. 1989). Although refixation of biogenic  $\text{CO}_2$  potentially complicates interpretation of leaf  $\delta^{13}\text{C}$  values, this influence is expected only to be significant in the understory of forests with closed canopies (1 to 5 m from the ground for tropical forests; Sternberg et al. 1989; Buchmann et al. 2002; Ometto et al. 2002). The combination of high PPFD and high assimilation capacity found at the top of the canopy results in low  $c_i$  values and, consequentially, higher  $\delta^{13}\text{C}$ . In contrast, the more negative values of leaf  $\delta^{13}\text{C}$  found with increasing canopy depth are associated with decreasing ratio of assimilation capacity to stomatal conductance and lower light levels (Flanagan et al. 1997), and modest influence of refixation of respired  $\text{CO}_2$  (Ometto et al. 2002). Bonal et al. (Bonal et al. 2000) reported a large variation of  $\delta^{13}\text{C}$  values of sunlit leaves (ranging from  $-27.5\text{‰}$  to  $-34.7\text{‰}$ ) occurring at three tropical forest sites from French Guiana. A similar range was reported by Martinelli et al. (Martinelli et al. 1998) for a primary forest site from Ecological Reserve of Samuel (Rondônia State, Brazil), although that analysis involved leaves collected from several heights within the canopy profile. Our top canopy  $\delta^{13}\text{C}$  leaf values were more negative compared to what was reported by Martinelli et al. (Martinelli et al. 1998) and Kruijt (Kruijt 1996) (Reserva Jarú, Rondônia State, Brazil), but agreed with  $\delta^{13}\text{C}$  leaf values also from French Guiana presented by Buchmann et al. (Buchmann et al. 1997). Ometto et al. (Ometto et al. 2002) compared the distribution of leaf  $\delta^{13}\text{C}$  values with canopy height for three Amazonian sites and concluded that the forest at Reserva Jarú had a different slope compared to those obtained from Santarém and Manaus. The Reserva Jarú site had the longest dry season when compared to Manaus and Santarém sites. The relationship established between leaf  $\delta^{13}\text{C}$  values and relative canopy height for this study (Table 3) compared well with data from Buchmann et al. (Buchmann et al. 1997;  $\delta^{13}\text{C} = -34.78 + 0.06 \times \text{relative height}$ ) and Martinelli

et al. (Martinelli et al. 1998;  $\delta^{13}\text{C} = -33.3 + 0.03 \times \text{relative height}$ ). As with our study, Buchmann et al. (Buchmann et al. 1997) did not detect any effect of season on foliage  $\delta^{13}\text{C}$  values.

### 4.3. Leaf-level gas exchange

By actively regulating  $g_s$ , plants are able to adjust the supply of  $\text{CO}_2$  in order to match photosynthetic demand while minimizing water loss by transpiration (Wong et al. 1979; Collatz et al. 1991; Jones 1998; Farquhar et al. 1989). On the onset of water stress, stomata closes and  $g_s$  is reduced, therefore limiting photosynthetic carbon assimilation. Concerning the slopes of the linear regression between  $A_{\text{max}}$  and  $g_s @ A_{\text{max}}$ , no statistical differences were detected between wet and dry season dataset, indicating that drought has little or no influence over the  $A_{\text{max}}$  versus  $g_s @ A_{\text{max}}$  relationship. Compared to the data reported in this study, McWilliam et al. (McWilliam et al. 1996) observed higher  $g_s$  values for a tropical rain forest site with a longer dry season (Reserva Jarú), although associated with considerably lower  $A$  values, describing a noticeably lower slope for the  $A$  versus  $g_s$  regression. On the other hand, values of  $A$  and  $g_s$  presented by Carswell et al. (Carswell et al. 2000) were somewhat lower than the ones presented in this study and no relationship between  $A$  and  $g_s$  was established. Although most of the variation in  $g_s$  can be explained by  $A$ , factors such as vapor pressure deficit, low soil water content, and  $\text{CO}_2$  concentrations might change this relationship (Ball et al. 1987; Aphalo and Jarvis 1993).

Since  $V_{\text{cmax}}$  scales to the amount of activated RUBISCO enzyme present on a given leaf, a tight relationship is observed between  $V_{\text{cmax}}$  and  $A_{\text{max}}$  (Farquhar et al. 1980; Evans 1989). da Rocha et al. (da Rocha et al. 1996) utilized an optimized value of  $V_{\text{cmax}}$  equal to  $81.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , very similar to our top-canopy values (Figure 6), while other models used somewhat lower values (SSiB model: Zhan et al. 2003;  $V_{\text{cmax}} = 60 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ; Simple Tropical Ecosystem model (SITE): Santos and Costa 2004;  $V_{\text{cmax}} = 75 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ; Lloyd et al. 1995;  $V_{\text{cmax}} = 68 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Carswell et al. (Carswell et al. 2000) reported even lower top-canopy values ( $V_{\text{cmax}} = 43 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for an Amazon primary forest site close to Manaus, Brazil. Besides the possible temporal and spatial variability of  $V_{\text{cmax}}$  values, our ability to compare such results is further limited by the different strategies used to derive  $V_{\text{cmax}}$  values.

### 4.4. Leaf nitrogen and gas exchange

It is generally accepted that foliar nitrogen concentration is the most important factor determining leaf-level carbon fluxes, given that no severe water stress is present (Field and Mooney 1986). The  $N_{\text{area}}$  is proportional to assimilation capacity because a large fraction of the total leaf nitrogen is used on the photosynthetic machinery (Evans 1989; Friend 1991). Furthermore, the metabolism involved in protein turnover establishes the relationship between foliar nitrogen levels and respiration rates. A more thorough understanding is still needed on the influence of LMA over both  $N_{\text{area}}$  and  $A_{\text{max}}$  parameters (Reich et al. 1994; Meir et al. 2001). For example, Reich et al. (Reich et al. 1994) found for the particular case of undisturbed terra firme forest, that relationship between leaf nitrogen and photo-

synthetic carbon assimilation were tighter when parameters were expressed on an area basis, while tight correlations are more frequently found when parameters are expressed on a mass basis (Schulze et al. 1994). The regression found between  $N_{\text{area}}$  and  $V_{\text{cmax}}$  for our dataset was stronger than the one found between  $N_{\text{area}}$  and  $A_{\text{max}}$  (Table 4), probably because  $A_{\text{max}}$  is also a function of other factors (Ball et al. 1997; Aphalo and Jarvis 1993). Compared to this study, Carswell et al. (Carswell et al. 2000) reported a lower slope from the regression between  $N_{\text{area}}$  and  $V_{\text{cmax}}$  for the Manaus primary forest, indicating that although leaves from that forest had nitrogen contents similar to those found for the Santarém sites, the photosynthetic carbon assimilation capacity was lower. Wilson et al. (Wilson et al. 2000) demonstrated that, at least for a deciduous forest, temporal variations in  $V_{\text{cmax}}$  could occur without simultaneous changes in  $N_{\text{area}}$ . This could be a reason for the lower values of  $V_{\text{cmax}}$  observed by Carswell et al. (Carswell et al. 2000) since that analysis was based on measurements taken from November 1996, just before the start of the wet season.

The linear regression obtained between  $N_{\text{area}}$  and  $R_d$  was weak, although statistically significant (Table 4). Meir et al. (Meir et al. 2001), studying the primary forest vegetation from Reserva Jarú, also presented a weak coefficient of linear regression between these parameters ( $r^2 = 0.29$ ). That dataset produced a lower slope, with  $R_d$  values rarely being over  $1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , although respiration values were scaled to a lower temperature (25°C).

## 5. Conclusions

Since the nature of relationships between parameters and drivers can change among ecosystems, the understanding of such changes is of fundamental importance for the correct parameterization of a process-based model. The lack of effects of season observed for the relationships presented in this work indicates little or no acclimation of gas exchange plant physiological parameters occurs over the dry (or wet) season. Therefore, observed seasonal variations in NEE may be better explained by variations in climatic conditions or ecosystem-level respiration, rather than variations in photosynthetic carbon assimilation. Differences among sites concerning  $N_{\text{area}}$  indicate that species composition, especially legume trees, can influence nitrogen distribution within the canopy profile, and partially explain differences in drivers–parameters interactions among distinct primary forest ecosystems. Finally, the finding that leaves are distributed evenly within the canopy profile provides a simplification in modeling light distribution within the canopy profile for the Flona-Tapajós primary forest vegetation.

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