Leaf traits and gas exchange in saplings of native tree species in the Central Amazon

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ABSTRACT: Global climate models predict changes on the length of the dry season in the Amazon which may affect tree physiology. The aims of this work were to determine the effect of the rainfall regime and fraction of sky visible (FSV) at the forest understory on leaf traits and gas exchange of ten rainforest tree species in the Central Amazon, Brazil. We also examined the relationship between specific leaf area (SLA), leaf thickness (LT), and leaf nitrogen content on photosynthetic parameters. Data were collected in January (rainy season) and August (dry season) of 2008. A diurnal pattern was observed for light saturated photosynthesis (A_{max}) and stomatal conductance (g_s), and irrespective of species, A_{max} was lower in the dry season. However, no effect of the rainfall regime was observed on g_s nor on the photosynthetic capacity (A_{pot}, measured at saturating $[CO_2]$). A_{pot} and leaf thickness increased with FSV, the converse was true for the FSV-SLA relationship. Also, a positive relationship was observed between A_{pot} per unit leaf area and leaf nitrogen content, and between A_{pot} per unit mass and SLA. Although the rainfall regime only slightly affects soil moisture, photosynthetic traits seem to be responsive to rainfall-related environmental factors, which eventually lead to an effect on A_{max}. Finally, we report that little variation in FSV seems to affect leaf physiology (A_{pot}) and leaf anatomy (leaf thickness).
Key words: diurnal variation, forest understory, photosynthetic capacity, rainfall seasonality

Características foliares e trocas gasosas em arvoretas de espécies nativas da Amazônia Central

RESUMO: Os modelos climáticos globais prevêem mudanças na extensão da época seca na Amazônia, o que pode afetar a fisiologia das árvores. Os objetivos deste trabalho foram determinar o efeito da sazonalidade da precipitação e fração de céu visível (FSV) no sub-bosque da floresta nas características foliares e trocas gasosas de 10 espécies florestais da Amazônia Central. Também examinou-se a relação entre área foliar específica (SLA), espessura da folha (LT) e nitrogênio foliar em parâmetros fotossintéticos. Os resultados foram coletados nos meses de janeiro (época chuvosa) e agosto (época seca) de 2008. Observou-se um padrão de variação diurna na fotossíntese saturada por luz (A_{max}) e na condutância estomática (g_s). Independente da espécie, A_{max} foi menor na época seca. No entanto, não houve efeito da sazonalidade das chuvas em g_s nem na capacidade fotossintética (A_{pot} medida em $[CO_2]$ saturante). A_{pot} e a espessura da folha (LT) aumentaram com FSV, o contrário foi observado para a relação FSV-SLA. Também, observou-se uma relação positiva entre A_{pot} por unidade de área e conteúdo de nitrogênio foliar, e entre A_{pot}, por unidade de massa e SLA. Embora o regime das chuvas apenas levemente influenciou a umidade do solo, características fotossintéticas parecem responderem a fatores relacionados com as chuvas, o que repercute em A_{max}. Finalmente, relata-se que pequenas variações em FSV parecem afetar a fisiologia da folha (A_{pot}) e a anatomia foliar (espessura da folha).
Palavras-chave: capacidade fotossintética, sub-bosque, variação diurna, sazonalidade das chuvas

Introduction

Global climate models predict that in the Amazon the length of the dry season period will be extended as a result of global warming associated to an increase of atmospheric CO_2 concentration (Cox et al., 2004). Indeed, a prolonged dry period may affect plant growth and physiological processes, such as photosynthesis and respiration (Hughes, 2000). Although severe soil moisture depletion during prolonged drought may lead to stomatal closure and a decline in leaf area (Nepstad et al., 1994), there is still controversy on whether draught-in-

duced water deficit limits tree growth in the Central Amazon. During the 2005 drought, for example, Saleska et al. (2007) reported an enhanced vegetation index of the forest based on moderate resolution imaging spectroradiometer (MODIS) satellite data. This is contrary to what should be expected, as changes in precipitation can alter growth rates (Lewis et al., 2004). In a rainfall exclusion experiment, a 60% reduction of incoming throughfall led to a drastic increase (38%) in tree mortality (Nepstad et al., 2007), much higher than commonly recorded in the Central Amazon, about 1.1% per year (Williamson et al., 2000). Although sapling photosyn-

thetic traits of canopy trees have received some attention in tropical forest (e.g. Marenco and Vieira, 2005; Poorter and Oberbauer, 1993), how seasonality of the rainfall regime affects seedling and sapling photosynthetic traits in the Central Amazon still remains to be elucidated.

In addition to soil moisture, light availability is one of the most important factors limiting seedling and sapling growth in the forest understory (Denslow et al., 1990; Valladares and Niinemets, 2008). Through the canopy profile light varies not only in total quantity, but also in quality, as the red/far red (R/Fr) ratio declines towards the forest floor (Smith, 1982). Low irradiance often leads to a decrease in leaf thickness and light saturated photosynthesis (A_{max}), whereas specific leaf area (SLA) commonly increases under low light intensity (Oguchi et al., 2005). Plant growth is the result of a complex of interacting factors intrinsically related to carbon gain via photosynthesis and loss due to respiration. However, over a wide range of plants species and growth conditions there seems to be a positive relationship between plant growth and photosynthetic rates (Kruger and Volin, 2006)

In this study we hypothesized that variation in soil moisture and subtle changes in light availability in the forest understory affect leaf traits and carbon gain in saplings of canopy trees. Thus, the aims of this work were to determine the effect of the seasonal rainfall regime and understory irradiance on leaf traits and gas exchange in ten rainforest tree species. We also examined the effect of specific leaf area (SLA), leaf thickness (LT), and nitrogen content on the photosynthetic capacity.

Material and Methods

The study was conducted 60 km north of Manaus (02°36'21" S; 60°08'11" W), state of Amazonas, Brazil, in an area of native "terra-firme" forest. The region has characteristics of a humid equatorial climate, with a short mild dry season (July-September, with a rainfall of 50-100 mm per month), and a dry-wet transition month (October). The wet season extends from November to May (200-300 mm month^{-1}). Annual precipitation is 2240 mm (Inmet, 2008, mean of 1961 to 1990). The area is covered by a dense forest and the predominant soil type is an Oxisol of low fertility, clay texture and pH of 4.2 to 4.5.

We used saplings (1.5 to 2-m tall) of 10 tree species selected taking into account their shade tolerance, relative abundance of saplings in the forest understory (at least three replications per species), and economic importance (Table 1). The gas exchange parameters were measured with an infrared gas analyzer (Li-6400, Li-Cor, NE, USA) using one or two leaves per plant and three saplings per species on each season. Light saturated photosynthesis (A_{max}) was measured at ambient CO_2 concentration (380 μmol mol^{-1}), light saturation (1000 μmol m^{-2} s^{-1}), and ambient temperature (28 ± 1°C). Potential photosynthesis (A_{pot}, hereafter termed photosynthetic capacity) was also measured at light saturation, but at a [CO_2] of 2000 μmol mol^{-1}, rather than ambient [CO_2]. Gas exchange data were collected after a stabilization period of about 10-15 min (total coefficient of variation < 0.7%). The effect of the time of day on stomatal conductance (g_s) and A_{max} was assessed across species by collecting data between 06h00 and 18h00. Data were collected in January and August 2008 in mature and fully expanded leaves.

Specific leaf area (SLA, the leaf area to leaf mass ratio) was determined in both seasons. As additional information, leaf thickness was determined in the dry season and leaf nitrogen content in the wet season. We measured SLA in a sample of six circles of 240-mm^2- per leaf obtained from a sample of two to eight leaves per plant, depending on leaf size. We only determined nitrogen (Kjeldahl method) in the wet season (first studied season) in order to preserve the foliage for further studies in the same area. Fresh leaf thickness (FLT) and dry leaf thickness (DLT) were measured with digital calipers in 240-mm^2-leaf circles (two per leaf) punched from the widest part of the leaf blade, and between the major veins (accuracy of 10 μm). Leaves used for SLA, leaf nitrogen and leaf thickness measurements were the same or similar in appearance (when more than two leaves were re-

Table 1 – Families and importance of the species.

Species	Family	Importance
Chimarrhis duckeana del Prete	Rubiaceae	Silvicultural system
Ecclinusa guianensis Eyma	Sapotacea	Silvicultural system
Erythroxylum amplum Bth.	Erythroxylaceae	Silvicultural system
Licania oblongifolia Standl.	Chrysobalanaceae	Timber industry
Pouteria guianensis Aubl.	Sapotaceae	Timber industry
Rinorea racemosa (Mart. et Zucc.) O. Ktz.	Violaceae	Silvicultural system
Sorocea guilleminiana Gaudich.	Moraceae	Pharmacological potential
Tetragastris unifoliolata (Engl.) Cuatr.	Burseraceae	Silvicultural system
Virola calophylla (Spruce) Warb.	Myristicaceae	Pharmacological potential
Zygia juruana (Harms) L. Rico	Fabaceae	Silvicultural system

quired for analysis) to those used for gas exchange determinations. Leaf dry mass was obtained after leaf dehydration at 72°C until constant mass. The fraction of sky visible (FSV) beneath the canopy was measured using a canopy analyzer (LAI-2000, Li-Cor, NE, USA), under overcast sky conditions to improve the accuracy of the instrument, and calculated by integrating the gap fraction to yield the fraction of sky not blocked by foliage. For each sapling, six FSV readings, collected at a distance of about 1.5 m from the stem and forming a circle around the plant (the microsite), were recorded at each microsite and a mean value was obtained. The height of the sensor above the ground corresponded to the height of leaves used for the gas exchange measurements (1 to 2 m above the ground). Finally, we used a second LAI-2000 sensor, operating in the remote mode and installed on the top of a 40-m-tall observation tower (located in a nearby area), to log FSV values above the forest canopy.

Irradiance and rainfall data were recorded above the forest canopy at the top of the 40-m tall observation tower. Irradiance at the observation tower (I_{open}) was measured using a quantum sensor (Li-190 SA, Li-Cor, NE, USA). Understory irradiance (I_{und}) was estimated as the product of FSV by I_{open} (i.e. I_{und} = FSV x I_{open}). We are aware that I_{und} is lower than the actual light availability at sapling height, as it does not take into account the background of diffuse light in the forest understory (about 5-8 µmol m^{-2} s^{-1} at midday (Marenco and Vieira, 2005). Temperature and air humidity data were recorded at 30-min-intervals with a sensor (Humitter 50y, Vaisala Oy, Finland) connected to a datalogger (Li-1400, Li-Cor, NE, USA) at a selected site in the understory. In addition, an external quantum sensor (Li-190 SA, Li-Cor, USA) mounted on the Li-6400's irga head was used to log irradiance data at the same time as gas exchange measurements were made. Both in the dry and rainy season, soil moisture was determined gravimetrically: $100(S_w - S_d)/S_w$, where S_w and S_d represent the mass of wet and dry, undisturbed 110-cm^3-soil samples. Soil samples were collected at random in the study area at the depth of 200 mm, both in the wet

(26 samples) and dry season (12 samples). All data, but leaf thickness and N content (determined only in one season), were subjected to analysis of variance (ANOVA) to assess the effect of the rainfall seasonality on the parameters. The Lilliefors test was conducted to assess whether experimental errors were normally distributed. As no transformation was needed, all statistical analyses were carried out on untransformed data. When the effect of rainfall seasonality on the variables was not significant ($p > 0.05$), data were pooled and linear or quadratic regression analyses conducted to examine the effect of FSV and SLA on photosynthetic traits. Tukey post-hoc test was used for mean separation ($p \leq 0.05$).

Results and Discussion

Monthly rainfall was 353 mm in January and 105 mm in August (Table 2), which is in accordance with the historical mean (1961-1990) for the region (Inmet, 2008). In these months, soil moisture ranged between 31% in the dry season to 32% in the wet season, near the soil saturation point of 39% on a wet soil basis (Table 2). Air temperature at the forest floor ranged from 22°C at night to 29°C at noon, and for most of the day the relative humidity was above 90%, with no difference between seasons (Figure 1). Accumulated irradiance at the forest floor was 0.3 and 0.6 mol m^{-2} day^{-1} in the wet and dry seasons, respectively. On the other hand, mean maximum understory irradiance was about 10 and 20 µmol m^{-2} s^{-1} for the wet and dry seasons, respectively, or about 1.5-2% of the irradiance recorded above the forest canopy (Figure 1). I_{und} values reported in this study are a somewhat higher than those observed by others (Kursar and Coley, 1999; Marenco and Vieira, 2005), perhaps because our I_{und} values were recorded about 1-2 m above the ground rather than at the forest floor. Molion (1987) estimated that the irradiance that reaches the forest floor is 1.2% (approximately 14 µmol m^{-2} s^{-1} on a sunny day) of that received above the forest canopy, similar to our I_{und} values observed in the wet season.

Table 2 – Light saturated photosynthesis (A_{max}) (mean ± SE), photosynthetic capacity (A_{pot}), fraction of sky visible (FSV), stomatal conductance (g_s), leaf area index, photosynthetic photon flux density (PFD) above the forest canopy, rainfall and soil moisture observed in January (rainy season) and August (dry season) of 2008.

Parameter	January	August
A_{max} (µmol m^{-2} s^{-1})	3.3 ± 0.3 a	2.5 ± 0.2 b
A_{pot} (µmol m^{-2} s^{-1})	8.04 ± 0.24 a	8.66 ± 0.31 a
FSV (unitless)	0.014 ± 0.001 b	0.020 ± 0.001 a
g_s (mol m^{-2} s^{-1})	0.1 ± 0.01 a	0.1 ± 0.01a
Leaf area index (unitless)	5.1 ± 0.05 a	4.7 ± 0.06 b
PFD (mol m^{-2} day^{-1})	20.83 ± 1.2 b	31.52 ± 1.0 a
[1]Rainfall (mm)	353	105
Soil moisture (%)	32 ± 0.6 % a	31 ± 0.4% a

[1]Value measured in January and August (one data, no SE). Means followed by the same letters within rows do not differ according to Tukey test at 5% probability.

Early in the morning and late in the afternoon stomata did not respond to light stimulus, remaining closed even at saturating irradiance (1000 μmol m^{-2} s^{-1}) for photosynthesis in the leaf chamber (Figure 2). Stomata closed and A_{max} declined as the vapor pressure deficit (VPD) increased (Figure 3). However, as the forest understory became brighter, A_{max} and g_s tended to linearly increase with irradiance (Figure 4), which indicates that in this environment g_s and A_{max} are under the influence of a diurnal cycle, perhaps affected by light and VPD (Figures 3, 4). Our results agree with those reported by Kaiser and Kappen (2000) who observed maximum g_s values between 10h00 and 14h00 and a minimum stomatal aperture at sunset.

Light induces stomatal opening (Shimazaki et al., 2007) and thus stomata may open at irradiances above 2-8 μmol m^{-2} s^{-1} (Habermann, 1973). However, soon after dawn light was ineffective in triggering stomatal opening. Since irradiance, relative humidity and temperature changed during daytime on the forest floor (Figure 1), it is possible that somehow these environmental factors affected stomatal functioning during the day. Although the light environment had an effect on g_s ($p < 0.05$, Figure 4B), the correlation between g_s and irradiance at mea-

suring time was tenuous ($r^2 = 0.05^*$). VPD has an important effect on g_s, but it only explains 24% of variation (Figure 3B). Thus, we cannot rule out the effect of endogenous factors in modulating stomatal functioning, as reported by others, both in herbaceous plants (Gorton et al., 1993; Holmes and Klein, 1986) and forest trees (Doughty et al., 2006).

Although there was no difference in soil moisture between the dry and rainy season, A_{max} was lower in the dry season (Table 2), which suggests that even a slight decline in soil moisture, or perhaps in leaf water potential associated to a higher irradiance in the dry period, may affect some photosynthetic traits of understory saplings, perhaps mesophyll conductance (g_m). Under progressive drought g_m may decline (Flexas et al., 2002). This hypothesis is consistent with the fact that both A_{pot} and g_s were unaffected by rainfall seasonality. As g_s was not influenced by rainfall seasonality (Table 2), differences in A_{max} between seasons may be ascribed to a limitation of carbon uptake imposed by non-stomatal factors. Had the dry season had any detrimental effect on Rubisco
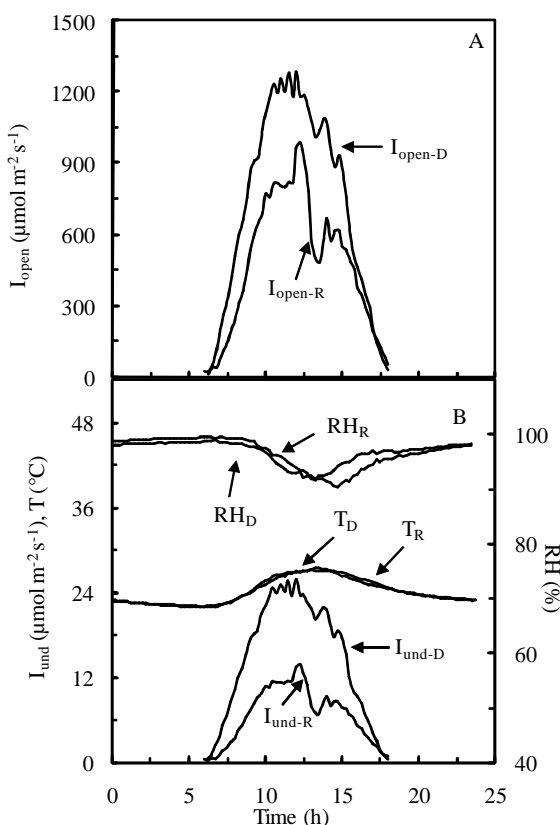

Figure 1 – Diurnal irradiance above the forest canopy (A, I_{open}), and relative humidity (RH), temperature (T) and irradiance at the forest understory (B, I_{und}). Data were collected in January (rainy season, R) and August (dry season, D) of 2008.
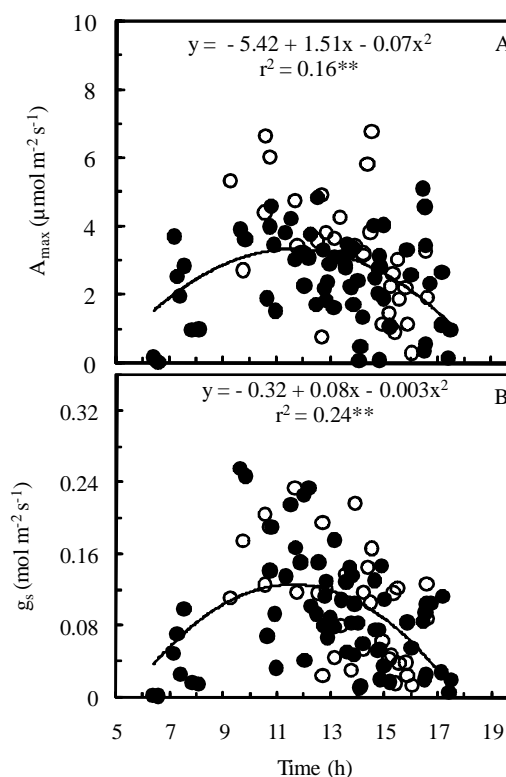

Figure 2 – Diurnal variation in light saturated photosynthesis (A, A_{max}), stomatal conductance (B, g_s) in January (rainy season, open circle, ○) and August (dry season, closed circle, ●) of 2008 in saplings of 10 forest tree species of the Central Amazon. Each symbol represents one leaf (one or two leaves per plant). Measurements were made at a [CO_2] of 380 μmol mol^{-1}, irradiance of 1000 μmol m^{-2} s^{-1} and leaf temperature of 28 ± 1°C. The continuous line shows the trend observed throughout the day. **significant at $p < 0.01$.
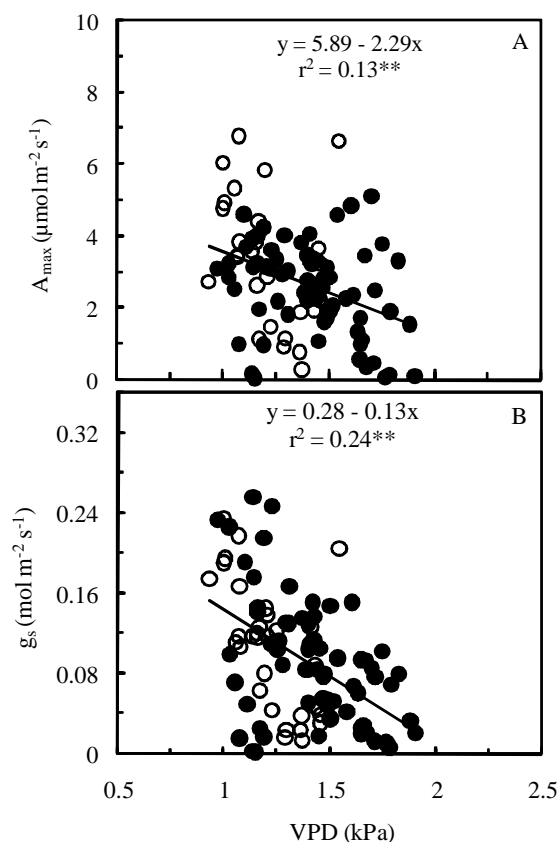
Figure 3 – Relationship between light saturated photosynthesis (A, A_{max}) and stomatal conductance (B, g_s) and vapor pressure deficit (VPD), in January (rainy season, open circle, O) and August (dry season, closed circle, ●) of 2008 in saplings of 10 forest tree species of the Central Amazon. Each symbol represents one leaf (one or two leaves per plant). Experimental conditions as described in Figure 2. **significant at $p < 0.01$.

activity or ATP synthesis (Flexas and Medrano, 2002) A_{pot} should have declined, but it did not. This allows us to conclude that the seasonality may have an effect on g_m. In relation to the seasonal effect on A_{max} is important to take into account that climate models predict changes in the total rainfall in the Amazon as a result of global warming (Cox et al. 2004; Oyama and Nobre, 2003). Besides, differences among species were not observed in A_{max} nor in A_{pot}, so data from both rainfall seasons were pooled to obtain a mean value for each species (Table 3).

At ambient CO_2 concentration (380 µmol mol⁻¹), A_{max} was closely related with g_s ($r^2 = 0.60**$, Figure 5A), which is consistent with results reported by others (Machado et al., 2002; Marenco et al., 2006; Park and Furukawa, 1999). Nonetheless, the correlation between A_{pot} and g_s was very low ($r^2 = 0.01^{ns}$) at saturating CO_2 concentration (Figure 5B), indicating that A_{pot} is little influenced by stomatal opening in the g_s range observed for most of the day (08h00 to 16h00). Except very early in the morning, when most stomata were closed, their resistance to CO_2 diffusion into intercellular spaces was offset by an elevated CO_2 concentration in the leaf chamber. However, when g_s was very low (less than 0.015 mol m⁻² s⁻¹, denoted by diamonds in Figure 5B) the resistance imposed by stomatal closure was not compensated by a high CO_2 concentration in the leaf chamber, which led to a reduction in photosynthetic capacity. Thus, a g_s of 0.015 mol m⁻² s⁻¹ most likely reflects a threshold below which leaf conductance is mainly due to cuticular conductance (g_c). Because A_{pot} remained quite constant for most of the day, the effect of FSV, SLA, LT and leaf nitrogen on photosynthetic rates were examined with respect to A_{pot} rather that A_{max}, which was strongly dependent on g_s. FSV was positively related to leaf thickness

Table 3 – Light saturated photosynthesis (A_{max}), photosynthetic capacity (A_{pot}), specific leaf area (SLA), fresh leaf thickness (FLT), dry leaf thickness (DLT), and leaf nitrogen content determined in saplings of native tree species of the Central Amazon. Each value represents the mean of two seasons (A_{max}, A_{pot} and SLA) or one season (leaf thickness and leaf nitrogen).

Species	A_{max}	A_{pot}	SLA	FLT	DLT	Leaf nitrogen
	------------- µmol m⁻² s⁻¹ -------------		m² kg⁻¹	----------------- mm -----------------		g m⁻²
C. duckeana	2.9 a	8.0 a	16.3 bc	0.23 a	0.18 a	1.3 bc
E. guianensis	3.6 a	8.3 a	14.2 c	0.18 cd	0.13 bc	1.4 ab
E. amplum	4.2 a	9.6 a	19.0 ab	0.22 ab	0.16 ab	1.1 bcd
L. oblongifolia	2.7 a	7.1 a	15.3 bc	0.23 a	0.16 ab	1.2 bcd
P. guianensis	3.5 a	8.8 a	16.9 abc	0.15 d	0.11 c	1.0 cd
R. racemosa	2.7 a	8.0 a	20.8 a	0.21 ab	0.15 ab	0.9 cd
S. guilleminiana	2.0 a	8.6 a	13.5 c	0.20 abc	0.15 ab	1.7 a
T. unifoliolata	2.3 a	8.1 a	18.7 ab	0.16 cd	0.11 c	0.9 d
V. calophylla	2.5 a	8.1 a	15.9 bc	0.16 cd	0.13 bc	1.2 bc
Z. juruana	2.9 a	8.7 a	15.4 bc	0.17 bcd	0.12 bc	1.3 bc
Mean	3.3	8.3	16.6	0.19	0.14	1.2
CV (%)	22.9	51.5	17.8	14.0	20.8	20.0

Means followed by the same letters within columns do not differ according to Tukey test at 5% probability.
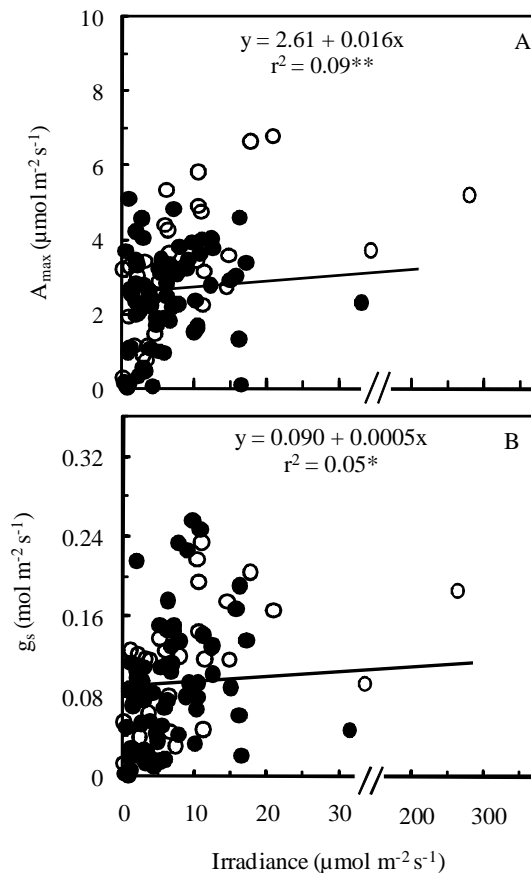
Figure 4 – Relationship between light saturated photosynthesis (A, A_{max}) and stomatal conductance (B, g_s) and instantaneous irradiance recorded at the forest understory during gas exchange measurements, in January (rainy season, open circle, O) and August (dry season, closed circle, ●) of 2008 in saplings of 10 forest tree species of the Central Amazon. Each symbol represents one leaf (one or two leaves per plant). Experimental conditions as described in Figure 2. *significant at $p < 0.05$; **significant at $p < 0.01$.

Figure 5 – Relationship between light saturated photosynthesis (A, A_{max}) and photosynthetic capacity (B, A_{pot}) and stomatal conductance (g_s) in January (rainy season, open circle, O) and August (dry season, closed circle, ●) of 2008 in saplings of ten native forest tree species of the Central Amazon. A_{pot} was measured at a [CO_2] of 2000 μmol mol^{-1} and saturating light. Other experimental conditions as described in Figure 2. The diamonds (◇) in Figure 5B show the values of A_{pot} soon after dawn, when g_s was very low. Each symbol represents one leaf (one or two leaves per plant). ns: not significant ($p > 0.05$), **significant at $p < 0.01$.

(Figures 6A, B) and A_{pot} (Figure 6C), whereas its relationship with SLA was negative (Figure 6D). DLT ranged from 0.11 mm in *P. guianensis* and *T. unifoliolata* to 0.18 mm in *C. duckeana* (Table 3), with an increase of about 35% in fresh leaves (Table 3), in both cases, a positive correlation between leaf thickness and A_{pot} was found (Figure 7).

The effect of FSV on A_{pot}, LT and SLA shows that even small changes in intensity of light in the forest floor can alter the performance of the photosynthetic apparatus. This is in agreement with results reported by others (Ellsworth and Reich, 1993; Oguchi et al., 2005; Weston et al., 2000), who observed increases in LT in leaves exposed to brighter environments. The relationship between LT and A_{pot} concurs with previous findings (McMillen and McClendon, 1983; Niinemets, 1999; Reich et al., 1998). Even when A_{pot} and LT and SLA were strongly related (Figures 7, 8), we cannot attribute increases in A_{pot} only to variations in LT or SLA, as pho-
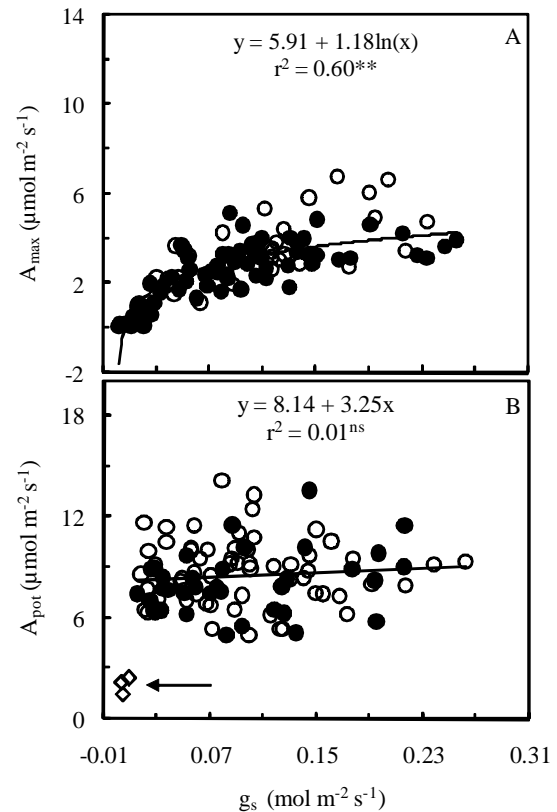
tosynthetic compounds are less effectively used in thicker leaves, perhaps because of a lower leaf conductance in these leaves (Niinemets, 1999).

FSV values increased from 0.014 in January (rainy season) to 0.020 in August (dry season) (Table 2), confirming results obtained previously by Marenco and Vieira (2005). We attributed the difference in FSV values between the evaluated rainfall seasons to differences in leaf area index between the rainy and dry season (5.1 *versus* 4.7, Table 2) or to the higher solar radiation recorded in the dry season (Table 2). High irradiance in the dry season can result in greater carbon assimilation during this part of the year as suggested by Huete et al. (2006). However, a higher light intensity in the forest canopy in the dry season apparently does not contribute to increase the photosynthetic capacity of saplings at the forest floor, although across species, we found an effect of FSV on A_{pot} irrespective of the seasonal rainfall regime, perhaps due to an effect of the R/Fr ratio on
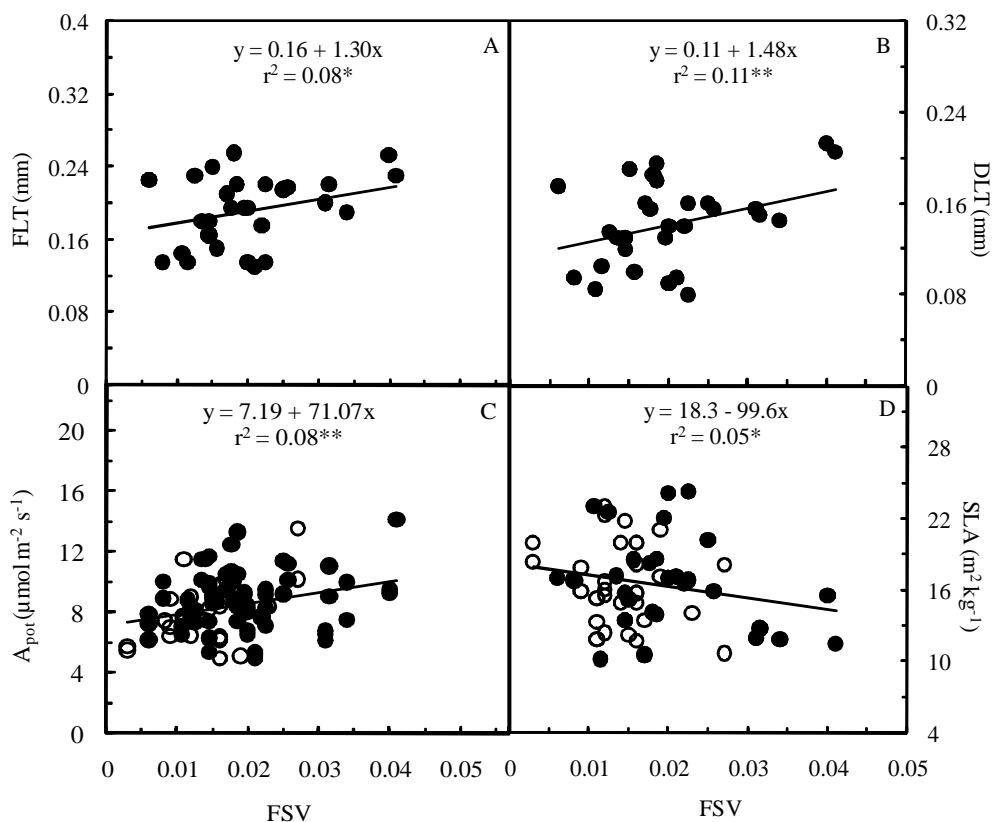
Figure 6 – Fresh (A, FLT) and dry leaf thickness (B, DLT), photosynthetic capacity (C, A_{pot}) and specific leaf area (D, SLA) as a function of the fraction of sky visible (FSV) in January (rainy season, open circle, O) and August (dry season, closed circle, ●) of 2008 in saplings of ten forest tree species of the Central Amazon. Experimental conditions as described in Figure 5. Each symbol represents one leaf (one or two leaves per plant). *significant at $p < 0.05$; **significant at $p < 0.01$

photosynthetic rates. For *Acmena ingens*, for example, under low irradiance (≤ 20 % of full sunlight) g_s and A_{max} where lower in plants grown under a reduced R/Fr ratio (0.2) than in control plants (R/Fr of sunlight, 1.2) (Turnbull, 1991).

SLA ranged from 13.5 m^2 kg^{-1} in *S. guilleminiana* to 20.8 m^2 kg^{-1} in *R. racemosa*, whereas the leaf nitrogen content varied between 0.9 g m^{-2} for *T. unifoliolata* and *R. racemosa* to 1.7 g m^{-2} for *S. guilleminiana* (Table 3). SLA values found in this study are within the range (15 and 24 m^2 kg^{-1}) observed by Marenco and Vieira (2005) for saplings of canopy tree species. FSV had a positive effect on LT, and a negative one on SLA ($p < 0.05$). The positive effect of leaf nitrogen on A_{pot} (Figure 9) is consistent with the results reported by Hikosaka (2004; 2005). However, although significant, the relationship between A_{pot} and leaf N was weak ($r^2 = 0.14$, $p < 0.05$) (Figure 9), indicating that a substantial fraction of the leaf nitrogen is partitioned into non-photosynthetic structures. On the other hand, differences in determination coefficients (r^2) between DLT and SLA against FSV (0.11** *versus* 0.05* for SLA, Figure 6B, D) occur because SLA depends not only on LT, but also on leaf density (Niinemets, 1999), which suggests that FSV has a lower effect on leaf density. Although LT is affected by growth irradiance, we can not explain the wide variations in SLA

among species only by differences in microsite brightness (inferred by FSV values) at the forest floor. This suggests that the genetic background of each species plays a major role in determining adaptive strategies to the physical and ecological environment (soil fertility and acidity, herbivory, etc.), which thereby leads to changes in LT and SLA under a given growth conditions (Lee et al., 2000; Peeters, 2002). Increase in LT (decline in SLA) is often related to higher photosynthetic rates per unit leaf area (McMillen and McClendon, 1983; Yun and Taylor, 1986), because of a greater accumulation of photosynthetic proteins. However, it may also involve an increase in the amount of molecules and compounds not directly related to carbon assimilation but with a key role for plant defense against herbivory and for increasing resistance against other physical hazards (Coley, 1988; Wright and Cannon, 2001).

Although the rainfall regime only slightly affected soil moisture, some photosynthetic traits (perhaps g_m) seem to be responsive to rainfall-related environmental attributes, which eventually lead to an effect on A_{max}. In the forest understory, A_{max} and g_s of saplings appear to be highly sensitive to diurnal variation, and even when stomatal functioning is affected by environment factors (e.g., light and VPD), somehow endogenous factors also seem to have a role in stomatal movements. However,
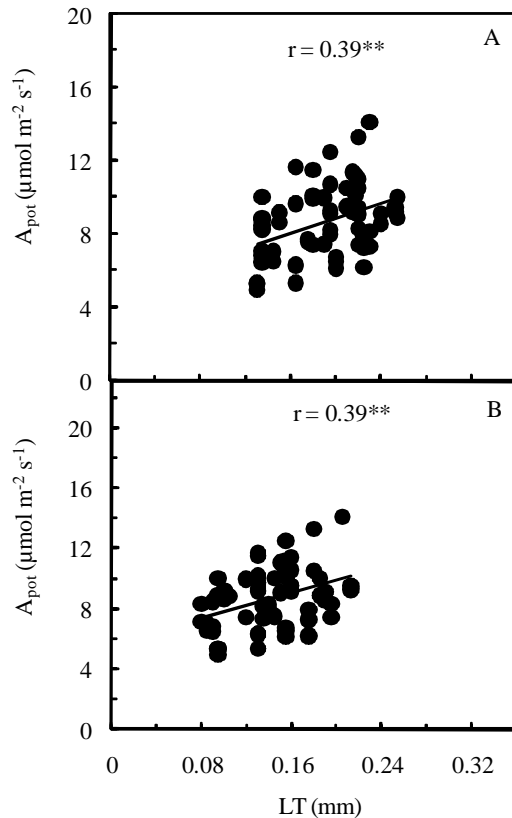
Figure 7 – Relationship between photosynthetic capacity (A_{pot}) and fresh leaf thickness (A, FLT) and dry leaf thickness (B, DLT) in August (dry season) of 2008 in saplings of ten forest tree species of the Central Amazon. Experimental conditions as described in Figure 5. Each symbol represents one leaf (one or two leaves per plant). **significant at $p < 0.01$.
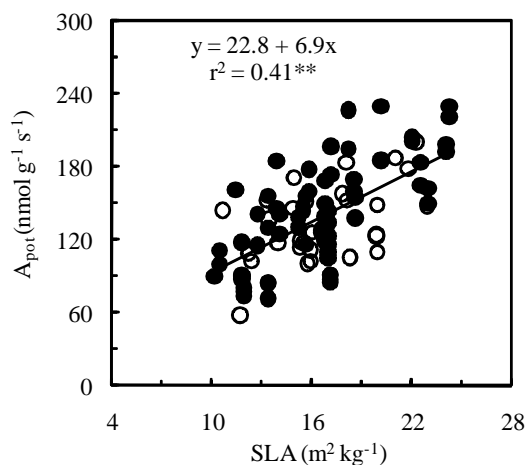

Figure 8 – Relationship between photosynthetic capacity (A_{pot}) and specific leaf area (SLA) in January (wet season, open circle, O) and August (dry season, closed circle, ●) of 2008 in saplings of forest tree species of the Central Amazon. Experimental conditions as described in Figure 5. Each symbol represents one leaf (one or two leaves per plant). **significant at $p < 0.01$.
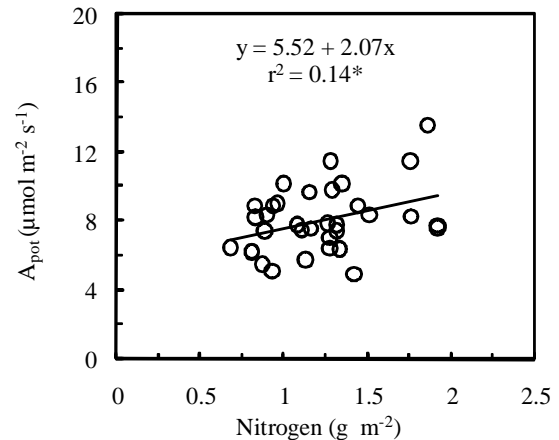

Figure 9 – Relationship between photosynthetic capacity (A_{pot}) and leaf nitrogen content in January (wet season) of 2008 in saplings of ten forest tree species of the Central Amazon. Experimental conditions as described in Figure 5. Each symbol represents one leaf (one or two leaves per plant). *significant at $p < 0.05$.

the dry season of 2008 was not strong enough to unambiguously negate any potential effect of rainfall seasonality on the photosynthetic capacity of saplings. Further studies are needed to elucidate how a prolonged dry season may affect the diurnal pattern of photosynthesis, Rubisco activity, and electron transport rates, which may ultimately affect tree growth in the Central Amazon. Finally, even though irradiance in the forest floor is usually very low, it remarkably affects leaf physiology and leaf anatomy, as photosynthetic capacity, LT and SLA responded to variations in the fraction of sky visible in the forest understory.

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