



HAL
open science

Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance

Sabrina Coste, Jean-Christophe Roggy, Pascal Imbert, Céline Born, Damien Bonal, Erwin Dreyer

► **To cite this version:**

Sabrina Coste, Jean-Christophe Roggy, Pascal Imbert, Céline Born, Damien Bonal, et al.. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance. *Tree Physiology*, 2005, 25 (9), pp.1127-1137. 10.1093/treephys/25.9.1127. hal-01031522

HAL Id: hal-01031522

<https://hal.science/hal-01031522>

Submitted on 1 Jun 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance

SABRINA COSTE,¹ JEAN-CHRISTOPHE ROGGY,^{1,2} PASCAL IMBERT,¹ CÉLINE BORN,¹ DAMIEN BONAL¹ and ERWIN DREYER³

¹ *Unité Mixte de Recherche CIRAD-ENGREF-INRA-CNRS Écologie des Forêts de Guyane, Campus agronomique de Kourou, 97387 Kourou, French Guiana*

² *Corresponding author (roggy.j@cirad.fr)*

³ *UMR Écologie et Écophysiologie Forestières, INRA-UHP, 54280 Champenoux, France*

Received September 24, 2004; accepted January 21, 2005; published online July 4, 2005

Summary Variability of leaf traits related to photosynthesis was assessed in seedlings from 14 tree species growing in the tropical rain forest of French Guiana. Leaf photosynthetic capacity (maximum rate of carboxylation and maximum rate of electron transport) was estimated by fitting a biochemical model of photosynthesis to response curves of net CO₂ assimilation rate versus intercellular CO₂ mole fraction. Leaf morphology described by leaf mass per unit leaf area (LMA), density and thickness, as well as area- and mass-based nitrogen (N) and carbon (C) concentrations, were recorded on the same leaves. Large interspecific variability was detected in photosynthetic capacity as well as in leaf structure and leaf N and C concentrations. No correlation was found between leaf thickness and density. The correlations between area- and mass-based leaf N concentration and photosynthetic capacity were poor. Conversely, the species differed greatly in relative N allocation to carboxylation and bioenergetics. Principal component analysis (PCA) revealed that, of the recorded traits, only the computed fraction of total leaf N invested in photosynthesis was tightly correlated to photosynthetic capacity. We also used PCA to test to what extent species with similar shade tolerances displayed converging leaf traits related to photosynthesis. No clear-cut ranking could be detected among the shade-tolerant groups, as confirmed by a one-way ANOVA. We conclude that the large interspecific diversity in photosynthetic capacity was mostly explained by differences in the relative allocation of N to photosynthesis and not by leaf N concentration, and that leaf traits related to photosynthetic capacity did not discriminate shade-tolerance ranking of these tropical tree species.

Keywords: functional diversity, leaf carbon, leaf nitrogen, nitrogen-use efficiency, photosynthetic capacity, tropical rain forest.

Introduction

Leaf characteristics of tropical trees, such as thickness, density, dry mass per unit area (LMA), anatomy and nitrogen (N) and chlorophyll contents display great diversity from species

to species (Popma et al. 1992, Ellsworth and Reich 1993, Poorter et al. 2000). In general, in tropical rain forests, light availability below the canopy is the most important factor influencing species recruitment because deep shade severely limits growth and survival of understory species (Bazzaz and Pickett 1980, Fetcher et al. 1983). Nevertheless, the eco-physiological traits that allow growth and survival at low irradiances remain a matter of debate. Tolerance of seedlings to shade, which may be one of the features that segregates different ecological groups of species, may be related to a combination of structural properties maximizing leaf area with respect to respiring biomass, and of leaf properties optimizing photosynthesis with respect to N investment (Messier et al. 1999). Tropical rain forest tree species have been classified into several ecological groups based on their supposed light requirements (Bazzaz and Pickett 1980, Swaine and Whitmore 1988), but whether functional leaf traits significantly differ among these ecological groups has not yet been established. In particular, leaf traits like photosynthetic capacity and N allocation to photosynthesis may differ significantly among the different groups. For instance, shade-intolerant or pioneer species are frequently thought to display higher light-saturated net CO₂ assimilation rates (A_{\max}) and photosynthetic N-use efficiencies (PNUE or A_{\max}/N_a , where N_a is the amount of N per unit leaf area) than shade-tolerant or late successional species (Reich and Walters 1994, Reich et al. 1994, Ellsworth and Reich 1996, Niinemets et al. 1998, but see Walters and Reich 1999, Hanba et al. 2002). Similarly, shade-intolerant species are thought to have high photosynthetic capacities (as assessed by maximal ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity, V_{\max} , and electron transport rate, J_{\max}), and a high allocation of leaf N to photosynthetic functions (i.e., to carboxylation and to electron transport) (Niinemets et al. 1998). A high LMA has been widely observed in seedlings of shade-tolerant species among tropical evergreen and deciduous trees (Kitajima 1994, Walters and Reich 1999 but see Niinemets and Kull 1998, Niinemets 1999b). Shade-intolerant species are reported to have thicker leaves (Niinemets et al.

1998, Wilson et al. 2000 but see Davies 1998), a higher total N content (Niinemets 1997, Niinemets et al. 1998) and a higher allocation of N to photosynthesis (Seemann et al. 1987, Evans 1989, Niinemets 1997) (and consequently a smaller allocation of N to chemical defence) than shade-tolerant species. As a consequence, leaves of shade-intolerant species may be more vulnerable to herbivory (Grime et al. 1996). High lignin concentrations in the foliage of shade-tolerant species also suggest that the leaves of these species should contain more carbon and be more expensive to construct than leaves of shade-intolerant species (Niinemets and Kull 1998, Niinemets 1999b).

Relationships between leaf structure and photosynthesis have been the focus of intensive research, and correlations between leaf N content and photosynthetic capacity are frequently observed (Field and Mooney 1986, Evans 1989, Reich and Walters 1994, Reich et al. 1994, 1999). According to Niinemets et al. (1998), the higher foliar N content generally observed in shade-intolerant relative to shade-tolerant species may be responsible for this correlation. Nevertheless, there is still large interspecific diversity in PNUE among shade-tolerant species. The relative ways in which total leaf N content and relative allocation of leaf N to the photosynthetic machinery contribute to the interspecific diversity of photosynthetic capacity remain poorly understood.

To assess the interspecific diversity of leaf traits related to photosynthetic capacity in a range of species differing in shade tolerance, we used the semi-mechanistic leaf photosynthesis model of Farquhar et al. (1980). We estimated in vivo maximal Rubisco activity and electron transport rate, two key parameters for quantifying the photosynthetic capacity of a leaf. The procedure was performed with seedlings from 14 French Guiana tropical rain forest species grown under common conditions in an open greenhouse at Kourou, French Guiana. The adjusted values of V_{cmax} and J_{max} were used to compute the relative allocation of total leaf N to carboxylation (P_c) and

bioenergetics (P_b) (Hikosaka and Terashima 1995, Niinemets and Tenhunen 1997).

The main objectives of our study were: (1) to record inter-specific diversity of leaf structure and photosynthetic capacity in a range of species from French Guiana; (2) to determine potential correlations among these traits, particularly with respect to the photosynthesis–nitrogen relationship; and (3) to test whether some of these traits could, alone or in combination, discriminate among species of different ecological groups.

Materials and methods

Plant material

The study was carried out at Kourou, French Guiana (5°10' N, 52°40' W) from February to May 2002 in a greenhouse. Measurements were made on seedlings from 14 species of the Guiana tropical rain forest (see Table 1 for the sizes of the seedlings used in the experiment). Two-year-old seedlings were transplanted in September 2001 to 20-l liter pots filled with a 1:2 (v/v) mixture of sand and A horizon soil from a nearby forest. Each pot was fertilized every second month with 5 g of complete fertilizer (12:12:17:2 N,P,K,Mg), treated bi-monthly with a commercial insecticide (Cuberol: 5% rotenone), and irrigated to field capacity (0.25 m³ m⁻³) every day. Temperature and relative humidity in the greenhouse were close to ambient (mean temperature: 27.6 °C (min/max: 23.5/31.5 °C), mean relative humidity: 72% (min/ max: 57/ 92%)). The greenhouse roof was equipped with a neutral sheet (black polyethylene, Uco Agrotexiles, Belgium) that transmitted 30% of global irradiance. Irradiance at plant level was within the range of 25 to 45% of full sunlight that supports optimal growth of seedlings of tropical rain forest species (Barigah et al. 1998, Poorter 1999). Around 6–8 seedlings per species were selected based on uniformity in height. The stud-

Table 1. List of study species, with the abbreviations used in the figures, the systematic position, and the ecological group as defined by Favrichon (1994, 1995). Mean shoot height recorded at the end of the experiment is indicated (mean ± SD); n = number of individuals per species.

Species name	Code	Family name	Ecological group	Shoot height ± SD (cm)	n
<i>Amanoa guianensis</i> J.B. Aublet	Ag	Euphorbiaceae	Tolerant	64 ± 17	7
<i>Bagassa guianensis</i> J.B. Aublet	Bg	Moraceae	Intolerant	96 ± 12	7
<i>Carapa procera</i> A.P. De Candolle	Cp	Meliaceae	Intolerant	50 ± 9	7
<i>Cecropia obtusa</i> Trécul	Co	Cecropiaceae	Intolerant	77 ± 9	8
<i>Couepia caryophylloides</i> R. Benoist	Cc	Chrysobalanaceae	Tolerant	–	7
<i>Eperua falcata</i> J.B. Aublet	Ef	Caesalpiniaceae	Mid-tolerant	74 ± 20	7
<i>Eperua grandiflora</i> (J.B. Aublet) Benth	Eg	Caesalpiniaceae	Mid-tolerant	63 ± 20	6
<i>Hymenaea courbaril</i> L.	Hc	Caesalpiniaceae	Mid-tolerant	88 ± 20	7
<i>Licania heteromorpha</i> Benth	Lh	Chrysobalanaceae	Tolerant ¹	40 ± 14	6
<i>Symphonia globulifera</i> L. f.	Sg	Clusiaceae	Mid-tolerant	36 ± 12	7
<i>Tabebuia insignis</i> (Miquel) Sandwith	Ti	Bignoniaceae	Intolerant ¹	37 ± 10	7
<i>Virola michelii</i> Heckel	Vm	Myristicaceae	Intolerant	36 ± 15	7
<i>Virola surinamensis</i> (Rolander) Warburg	Vs	Myristicaceae	Intolerant	99 ± 23	7
<i>Vouacapoua americana</i> J.B. Aublet	Va	Caesalpiniaceae	Tolerant	18 ± 9	7

¹ Shade tolerance ranking according to Béna (1960).

ied species were grouped according to the classification proposed by Favrichon (1994, see also Turner 2001, pp 244) (Table 1). Favrichon based his ecological grouping of trees from French Guiana on dynamic and structural variables like growth, mortality, recruitment height and maximal diameter, recorded on adult and sub-adult trees (diameter at breast height ≥ 10 cm). A principal component analysis (PCA) followed by a factorial analysis of correspondence yielded five groups of species discriminating on the basis of their potential height growth. After consideration of other ecological data (seed dispersal and seed size, gap colonization and wood density) the Favrichon groups were classified as (1) understory shade-tolerant, (2) canopy shade-tolerant, (3) emergent mid-tolerant, (4) canopy shade-intolerant and (5) pioneer. In our study, all species belonged to groups 2, 3 and 4, except the pioneer *Cecropia obtusa* (Table 1).

Estimating leaf photosynthetic capacity

We used the Harley et al. (1992) version of Farquhar's biochemical model of leaf photosynthesis (Farquhar et al. 1980) in which net CO₂ assimilation rate (A ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is expressed as:

$$A = V_c - 0.5V_o - R_d \quad (1)$$

where V_c is Rubisco bisphosphate (RuBP) carboxylation rate, V_o is RuBP oxygenation rate and R_d corresponds to CO₂ production by non-photorespiratory respiration. For a detailed description of the equation set, readers are referred to Le Roux et al. (1999) and to Dreyer et al. (2001). This model permits the estimation of V_{cmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and J_{max} ($\mu\text{mol e}^- \text{ m}^{-2} \text{ s}^{-1}$). The potential limitation arising from triose phosphate utilization was omitted.

Gas exchange measurements

We estimated V_{cmax} and J_{max} from A versus sub-stomatal CO₂ mole fraction (C_i) relationships. Leaf gas exchange was measured with a portable gas exchange system (CIRAS-1, PP-system, Hitchin, U.K.) equipped with a Parkinson leaf chamber (2.5 cm²). All measurements were performed on mature leaves, usually the ultimate leaf of the penultimate shoot flush. Air temperature in the leaf chamber and air–water vapor pressure deficit at the leaf surface were kept as stable as possible, but nevertheless varied significantly because of changes in the external microclimate (means \pm SD = 30 \pm 3 °C and 1.6 \pm 0.2 kPa, respectively). To compensate for the differences in temperature during measurements, all parameters were scaled to a common reference temperature (T_{ref}) of 25 °C (298.16 K). Because of the lack of data available for tropical tree species, we used temperature response parameters computed by Dreyer et al. (2001) for seedlings of temperate forest species. A halogen lamp (Philips 12 V, 20 W) yielded a saturating photosynthetic photon flux (PPF) of 700 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. For each leaf, after full light induction for at least 30 min, an $A-C_i$ curve was generated by 12 stepwise increases in atmospheric CO₂ concentration ($C_a = 40, 100, 200, 300, 400, 500, 600, 700, 900, 1200, 1500, 1800$ and $2000 \mu\text{mol mol}^{-1}$). The procedure

yielded about six values in each fraction of the curve (CO₂-limited or irradiance-limited zone of the response). Values of R_d were recorded in the dark 5 min after switching off the illumination. We estimated A_{max} as the light-saturated net assimilation rate measured at the CO₂ concentration close to 400 $\mu\text{mol mol}^{-1}$ (mean values of C_a and $C_i \pm$ SD = 396 \pm 8.8 and 275 \pm 25 $\mu\text{mol mol}^{-1}$, respectively). While the $A-C_i$ curve data were being gathered, stomatal conductance declined in response to increasing CO₂ concentration; therefore, these values must be interpreted with caution.

Primary model parameters and their temperature dependencies were taken from Dreyer et al. (2001) and are listed in Table 2. For each individual, a nonlinear least squares regression (Newton method, ProcNLIN, SAS v.8.1, SAS Institute Inc., Cary, NC) was used to estimate V_{cmax} and J_{max} by fitting the $A-C_i$ curve to empirical equations as described by Dreyer et al. (2001).

Leaf structure, nitrogen and carbon content

After gas exchange measurements, leaves were harvested and their area measured with an electronic area meter (LI-3000A, Li-Cor, Lincoln, NE). Thickness (μm) of each sampled leaf was obtained as the mean of three measurements with a digital micrometer (Digimatic micrometer, Mitutoyo, Japan), care being taken to avoid the main veins. Leaf dry mass was recorded after drying for 48 h at 70 °C. Total N (N_m ; mmol N g⁻¹) and carbon per unit leaf dry mass (C_m ; mmol C g⁻¹) were measured with an elemental analyzer (NA 1500 NCS, Carlo Erba, Italy). Values of LMA (g m⁻²), N_a and leaf density (LMA/thickness; g cm⁻³) were derived from these data.

Estimation of relative allocation of nitrogen to carboxylation and bioenergetics

Relative allocation of leaf N to Rubisco (P_c ; g N in Rubisco g⁻¹ total leaf N) and to bioenergetics (P_b ; g N in cytochrome f, ferredoxin NADP reductase, and coupling factor g⁻¹ total leaf

Table 2. Primary parameters of the photosynthesis model used in this study: α = apparent quantum yield; K_c = affinity of Rubisco for CO₂; K_o = affinity of Rubisco for O₂; ΔH_a = activation energy; and τ = specificity factor of Rubisco. For details, see Dreyer et al. (2001).

Parameters	Value	Unit
α	0.24	mol e ⁻ mol ⁻¹ photons
K_c (25 °C)	40	Pa
ΔH_a (K_c)	70,000	J mol ⁻¹
K_o (25 °C)	25,000	Pa
ΔH_a (K_o)	15,000	J mol ⁻¹
τ (25 °C)	2710	–
ΔH_a (τ)	–29,000	J mol ⁻¹
ΔH_a (V_{cmax}) ¹	73,000	J mol ⁻¹
ΔH_a (J_{max}) ¹	57,900	J mol ⁻¹
ΔH_a (R_d) ¹	32,000	J mol ⁻¹

¹ Mean value of ΔH_a from seven temperate tree species (Dreyer et al. 2001).

N) were derived from N_a and from V_{cmax} or J_{max} , respectively, as described by Niinemets and Tenhunen (1997) using the parameters provided by them:

$$P_c = \frac{V_{cmax}}{6.25V_{cr}N_a} \quad (2)$$

$$P_b = \frac{J_{max}}{8.06J_{mc}N_a} \quad (3)$$

where V_{cr} is the specific activity of Rubisco ($\mu\text{mol CO}_2 \text{ g}^{-1}$ Rubisco s^{-1}), J_{mc} is the potential rate of photosynthetic electron transport per unit cytochrome f ($\text{mol e}^- \text{ mol}^{-1} \text{ cyt f s}^{-1}$), and the factors 6.25 (g Rubisco g^{-1} N in Rubisco) and 8.06 ($\mu\text{mol cyt f g}^{-1}$ N in bioenergetics) convert N mass to protein mass (Niinemets and Tenhunen 1997). Reference values at 25 °C were 20.78 $\mu\text{mol CO}_2 \text{ g}^{-1}$ Rubisco s^{-1} and 156 mol electrons $\text{mol}^{-1} \text{ cyt f s}^{-1}$, for V_{cr} and J_{mc} , respectively (cf. Niinemets and Tenhunen 1997).

Statistical analysis

All statistical analyses were performed with STATISTICA (Kernel Version 5.5, StatSoft, Tulsa, OK). Normality of the data and homogeneity of variances were examined by the Shapiro-Wilk and Levene tests, and \log_{10} or square root transformations were occasionally applied to normalize the distributions of the data. A principal component analysis was conducted to explore simultaneously species variation in multiple leaf traits. For the PCA, the dependent variables P_c and P_b (calculated from V_{cmax} and J_{max}), as well as density (product of LMA and thickness), were used as inactive variables. Because

data on leaf thickness and density of *Couepia caryophylloides* were unavailable, this species does not appear in the PCA, which reduces the number of shade-tolerant species to three. Differences between groups were analyzed by a one-way ANOVA. All regressions as well as the PCA and the final ANOVA were applied on the computed mean values of variables for each species. All statistical relationships were considered significant at $P < 0.05$.

Results

Inter-specific diversity of photosynthetic capacity

Values of A_{max} ranged from 5.4 to 12.9 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ among species (Figure 1A) (equivalent to 75.1 to 290 $\text{nmol g}^{-1} \text{ s}^{-1}$; data not shown). Both V_{cmax} and J_{max} differed significantly among the 14 species ($P < 0.001$; Figures 1B and 1C). Species means of V_{cmax} varied more than twofold (from 22.1 to 55.3 $\mu\text{mol m}^{-2} \text{ s}^{-1}$). There was a strong positive correlation between J_{max} and V_{cmax} ($r^2 = 0.9$, $P < 0.001$; Figure 2) and the J_{max}/V_{cmax} ratio varied between 1.7 and 2.2, but with only a small species effect ($P = 0.07$; Figure 1C). We observed considerable variability in R_d and no species effect was detected ($P = 0.13$; Figure 1D).

Interspecific diversity of leaf structure and chemical composition

Leaf density and thickness differed significantly among species ($P < 0.001$; Figures 3B and 3C), with more than a twofold range between extreme values. Values of LMA varied from 44.6 to 117 g m^{-2} . Shade-tolerant species had higher LMA

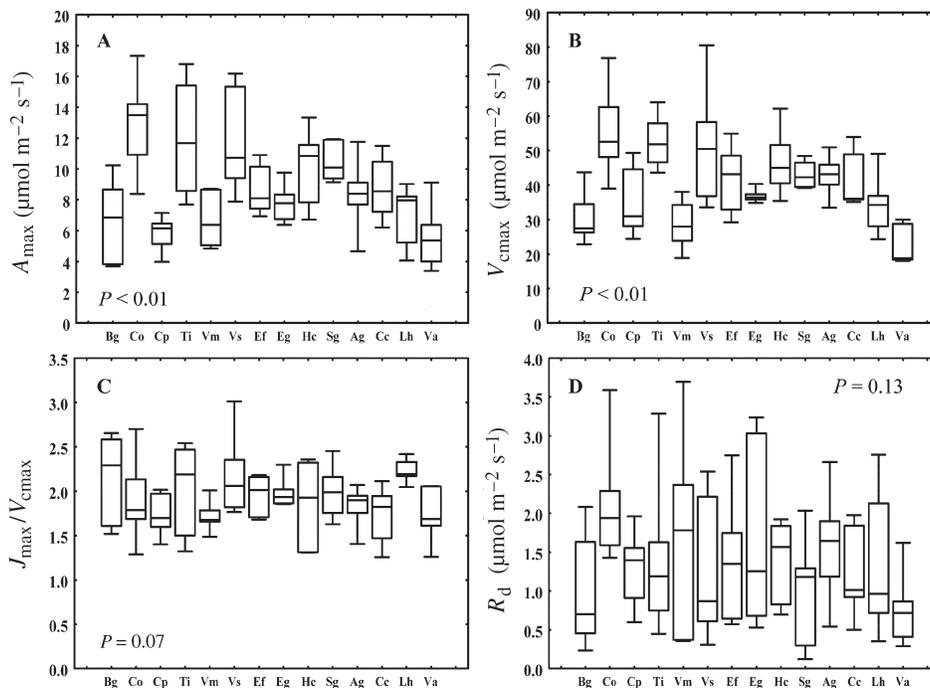


Figure 1. Box and whisker plots of (A) light-saturated net photosynthesis (A_{max}), (B) maximum carboxylation velocity (V_{cmax}), (C) ratio of maximum electron transport rate (J_{max}) to V_{cmax} , and (D) non-photorespiratory respiration (R_d) for 14 species (abbreviations as in Table 1). The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median and the vertical bars indicate the 10th to the 90th percentile ranges. A value of $P < 0.05$ indicates a significant difference among species according to a one-way ANOVA. Shade-intolerant species are on the left, mid-tolerant species in the center and shade-tolerant species on the right of the x-axis.

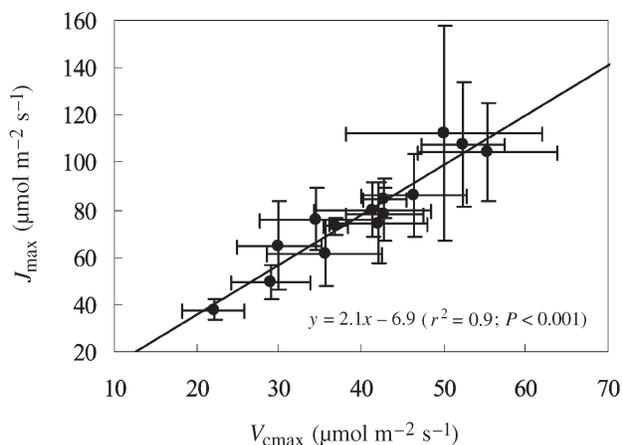


Figure 2. Relationship between the maximum electron transport rate (J_{\max}) and the maximum carboxylation velocity (V_{cmax}) in seedlings of 14 species of the tropical rainforest of French Guiana. Each value represents the mean \pm 95% confidence interval for a given species.

than shade-intolerant species, with the exception of *Vouacoupa americana* (Figure 3A).

Values of C_m , N_m and N_a differed significantly ($P < 0.001$) among species, ranging from 438 to 518 mg g^{-1} , 11.6 to 21.9 mg g^{-1} and 0.93 to 1.93 g m^{-2} , respectively (Figures 3D–F).

Relative investment of leaf nitrogen in carboxylation and bioenergetics

Values of PNUE differed significantly among the 14 species, ranging from 60.9 to 186.8 $\mu\text{mol mol}^{-1} \text{s}^{-1}$ (Figure 3G). In parallel, the estimated P_c and P_b varied significantly among species ($P < 0.001$). *Cecropia obtusa* invested more than 40% of its leaf N in Rubisco and *Vouacoupa americana* only about 16% (Figure 3H). As expected from the tight correlation between J_{\max} and V_{cmax} , the distribution of mean values of P_b among species paralleled that for P_c , but with lower values ranging from 0.03 to 0.08 (Figure 3I).

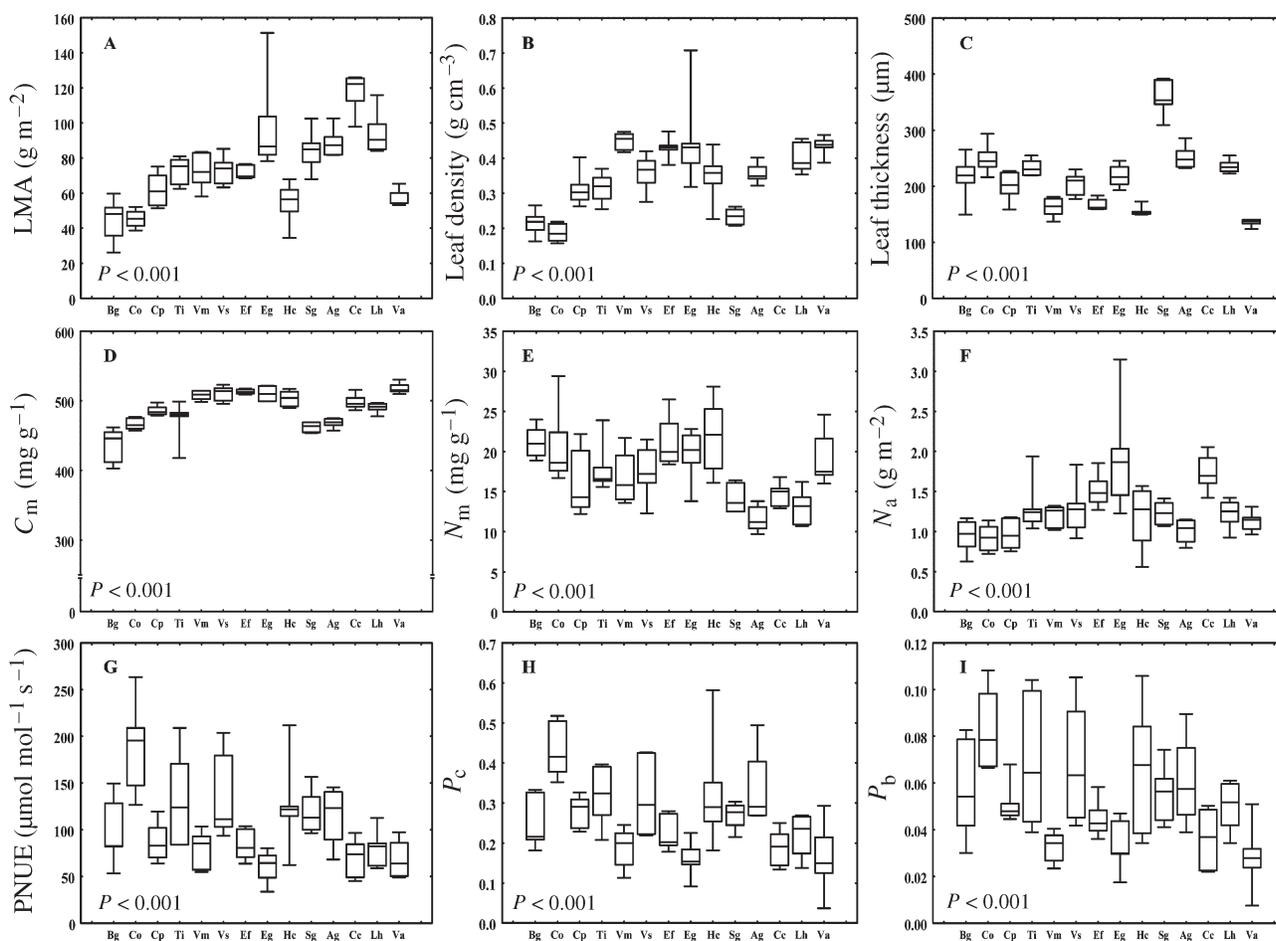


Figure 3. Box and whisker plots of leaf (A) mass per area (LMA), (B) density and (C) thickness, (D) total carbon content per unit leaf dry mass (C_m), total nitrogen content (E) per unit leaf dry mass (N_m), and (F) per unit leaf area (N_a), (G) photosynthetic nitrogen-use efficiency (PNUE), and relative investment of total leaf nitrogen in (H) Rubisco (P_c) and (I) bioenergetics (P_b) for 14 species (abbreviations as in Table 1). The upper and the lower edges of each box indicate the 75th and 25th percentiles, respectively. The horizontal line within each box is the median and the vertical bars indicate the 10th to the 90th percentile ranges. A value of $P < 0.05$ indicates a significant difference among species according to a one-way ANOVA. Shade-intolerant species are on the left, mid-tolerant species in the center and shade-tolerant species on the right of the x-axis.

Relationships between leaf morphology, chemical composition and photosynthetic capacity

We found that N_m was linearly and negatively correlated with LMA ($P < 0.01$; Figure 4): LMA increased more than twofold as N_m dropped from 21.9 to 11.6 mg g^{-1} . In contrast, C_m seemed to be independent of LMA (Figure 4). Results of a multiple regression showed that LMA was not correlated with its two components, leaf thickness and density (data not shown), and that thickness and density were not correlated either. Although N_m was not correlated with either thickness or density, C_m increased with density and decreased with thickness (Figure 4).

No correlations were found between photosynthetic capacity expressed per unit leaf area (A_{max} , V_{cmax} , J_{max} and R_d) and any leaf morphology parameter (LMA, leaf thickness and density) or N_a . Only PNUE, P_c and P_b were tightly correlated with V_{cmax} , J_{max} and A_{max} (Table 3A). Close correlations were found between PNUE and P_c and P_b ($r = 0.95$ and 0.94 , respectively), as well as between V_{cmax} and J_{max} and A_{max} ($r = 0.94$ and 0.93 , respectively). In addition, N_a was negatively correlated with P_c ($P < 0.01$; Figure 5). Similarly, photosynthetic capacity expressed per unit leaf mass was tightly correlated to P_c and P_b ($P < 0.001$). Both V_{cmax} and J_{max} decreased with increases in N_m , LMA and leaf density (but not leaf thickness) (Table 3).

Principal component analysis

A principal component analysis was applied to the variables V_{cmax} , J_{max} , R_d , LMA, leaf thickness, N_a , N_m and C_m , with the dependent variables density, P_c and P_b as supplementary variables. We also included area-based A_{max} and PNUE as non-active variables. The first two axes explained 58% of the ob-

served variability (Figure 6). The distribution of variables on the correlation circle projected on the factor plane (1×2) yielded several clusters. The main contributors to the first principal axis were thickness, V_{cmax} and J_{max} (with factorial coordinates of -0.81 in all cases). In this group, V_{cmax} and J_{max} and the inactive variable A_{max} were strongly inter-correlated. The main contributors to the second principal axis were LMA and N_a , and N_m to a lesser extent (with factor coordinates of -0.94 , -0.70 and $+0.52$, respectively). The intercorrelated supplementary variables P_c , P_b and PNUE were correlated to the first principal axis. Density and C_m were also tightly correlated. Leaf mass per area was negatively correlated to N_m discriminated by Factor 2. Photosynthetic capacity was not related to LMA or total leaf N concentration (axes were orthogonal).

The distribution of the species on the factor plane (1×2) yielded three clusters, one with high photosynthetic capacities and thick leaves, one with moderate photosynthetic capacities and high LMA leaves, and one with low photosynthetic capacities and thin leaves. The shade-tolerant *Vouacapoua americana* (low photosynthetic capacity) and the pioneer *Cecropia obtusa* (high photosynthetic capacity and high PNUE) were independent of these groups. These groups did not match the ecological groups defined by Favrichon (1994) and, furthermore, the three species clusters each contained species from different ecological groups. On the second axis, shade-tolerant species seemed to display lower N_m and higher LMA than mid-tolerant species—except for *Symphonia globulifera* and *Eperua grandiflora*—and shade-intolerant species

A multivariate ANOVA applied to the two groups of variables revealed by the PCA, V_{cmax} , J_{max} , R_d and thickness for the first axis ($P = 0.97$) and LMA, N_a and N_m for the second ($P = 0.11$), confirmed that no difference was observed among the

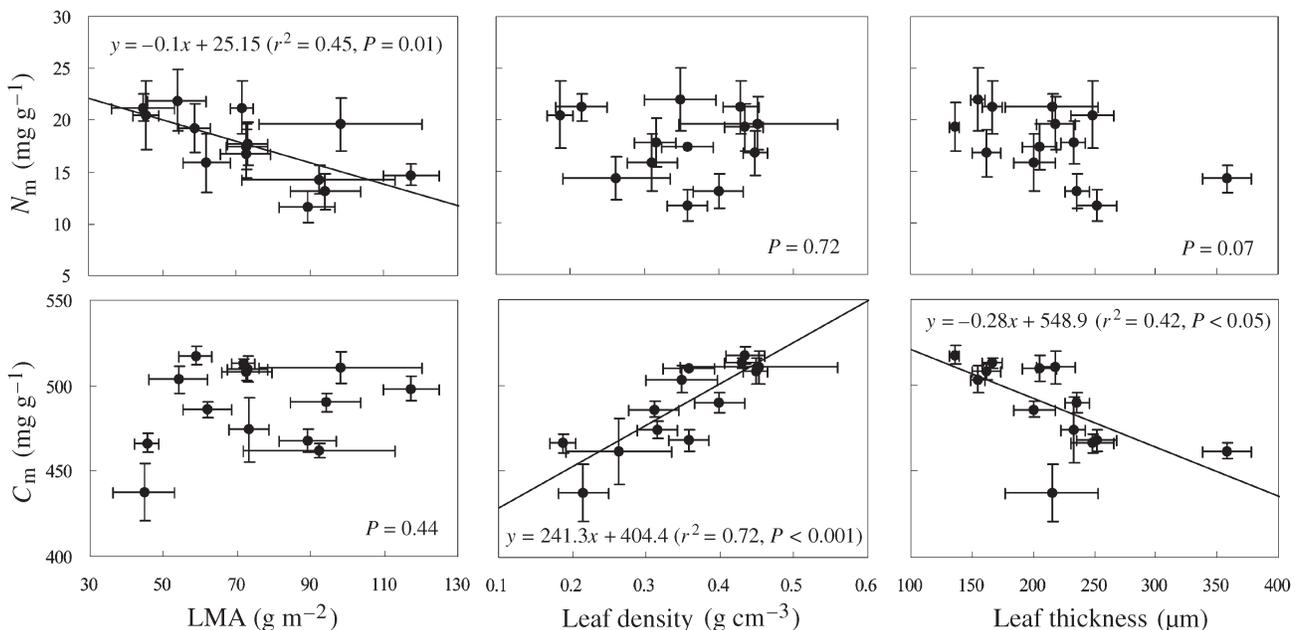


Figure 4. Relationships between leaf mass per area ratio (LMA), leaf thickness or leaf density, and total nitrogen (N_m) or carbon concentration (C_m) per unit leaf dry mass. Simple linear regressions were applied to species means ($\pm 95\%$ confidence intervals) of the variables.

Table 3. Pearson's correlation coefficients between photosynthetic capacity expressed on a leaf area or on a mass basis (light-saturated net photosynthesis rate (A_{\max}), maximal carboxylation velocity ($V_{c\max}$), maximum electron transport rate (J_{\max}) and dark respiration (R_d)) and studied leaf characteristics: total carbon content per unit leaf dry mass (C_m); total nitrogen content per unit leaf dry mass (N_m) and per unit leaf area (N_a); leaf mass per area (LMA); leaf density and thickness; photosynthetic nitrogen-use efficiency (PNUE); and relative nitrogen allocation to Rubisco (P_c) and to bioenergetics (P_b). Simple linear regressions were applied using species means for each variable. Significance levels: ns, $P > 0.05$; *, $P < 0.05$; **, $P = 0.01$; ***, $P = 0.001$; and ****, $P = 0.0001$.

	A_{\max}	$V_{c\max}$	J_{\max}	R_d
<i>Photosynthetic capacity expressed on a leaf area basis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)</i>				
N_a (mg m^{-2})	0.04 ns	0.05 ns	0.05 ns	0.07 ns
LMA (g m^{-2})	-0.04 ns	0.02 ns	0.01 ns	-0.01 ns
Leaf thickness (μm)	0.42 ns	0.39 ns	0.42 ns	-0.001 ns
Leaf density (g cm^{-3})	-0.46 ns	-0.45 ns	-0.43 ns	0.01 ns
PNUE ($\mu\text{mol mol}^{-1} \text{s}^{-1}$)	0.83 ***	0.79 ***	0.75 **	0.39 ns
P_c	0.71 **	0.77 ***	0.7 **	0.41 ns
P_b	0.77 ***	0.8 ***	0.81 **	0.31 ns
<i>Photosynthetic capacity expressed on a leaf mass basis ($\text{nmol g}^{-1} \text{s}^{-1}$)</i>				
N_m (mg g^{-1})	0.55 *	0.55 *	0.55 *	0.54 ns
C_m (mg g^{-1})	-0.32 ns	-0.35 ns	-0.39 ns	-0.14 ns
LMA (g m^{-2})	-0.67 **	-0.70 **	-0.67 **	-0.69 **
Leaf thickness (μm)	0.08 ns	0.03 ns	0.09 ns	-0.19 ns
Leaf density (g cm^{-3})	-0.68 **	-0.71 **	-0.73 **	-0.44 ns
PNUE ($\mu\text{mol mol}^{-1} \text{s}^{-1}$)	0.9 ****	0.87 ****	0.88 ****	0.66 **
P_c	0.81 ***	0.85 ****	0.83 ***	0.63 *
P_b	0.80 ***	0.82 ***	0.86 ****	0.54 *

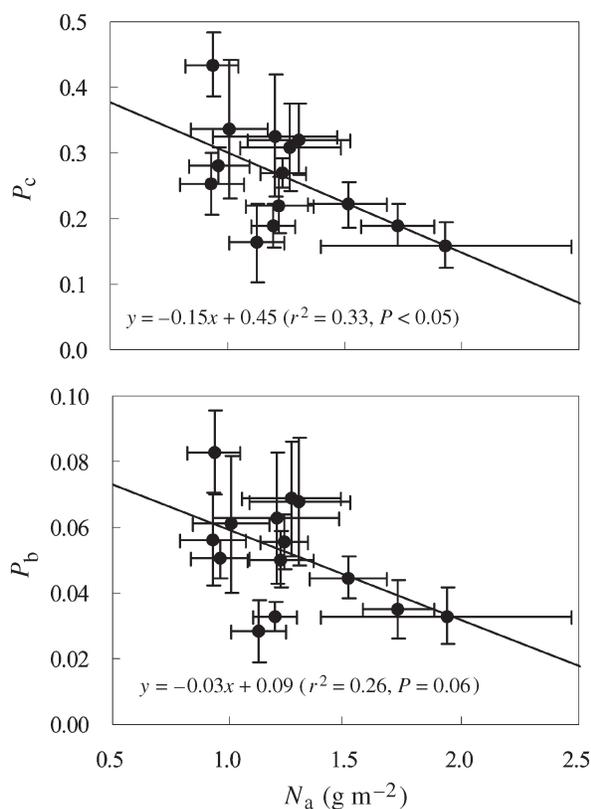


Figure 5. Relationships between the relative investment of total leaf nitrogen in Rubisco (P_c), and to bioenergetics (P_b), and the amount of leaf nitrogen per unit area (N_a). Simple linear regressions were applied to species means ($\pm 95\%$ confidence intervals) of the variables.

three Favrichon groups. A complementary one-way ANOVA of the effect of the ecological groups on the parameters, applied to each studied variable, confirmed this observation. Furthermore, no significant difference was observed between the three groups for all the studied parameters, even when the pioneer *Cecropia obtusa* was removed from the analysis (data not shown).

Discussion

Interspecific variability in leaf traits

Large differences were found in leaf traits among seedlings from 14 tropical rain forest tree species in French Guiana. Leaf structure varied significantly and, in particular, leaf density and thickness displayed a wide range of values. No correlation was found between leaf density and thickness, in agreement with previous studies (Niinemets 1999a, Wilson et al. 1999). The two variables seem to be totally independent even among species from a common biome, indicating that control over leaf density and thickness is exerted by different mechanisms (Niinemets 1999a). Similarly, N_m displayed a wide range of values that fell within the ranges reported by others (Niinemets 1999a, Bonal et al. 2000). Mature trees generally exhibit higher LMA and leaf N than seedlings (Thomas and Winner 2002, Mediavilla and Escudero 2003) and this could explain why our N_m values ranked within the lower range of those presented by Niinemets (1999a). We found that N_m was independent of leaf density and thickness, which contrasts with the observations of Niinemets (1999a) and the general view that

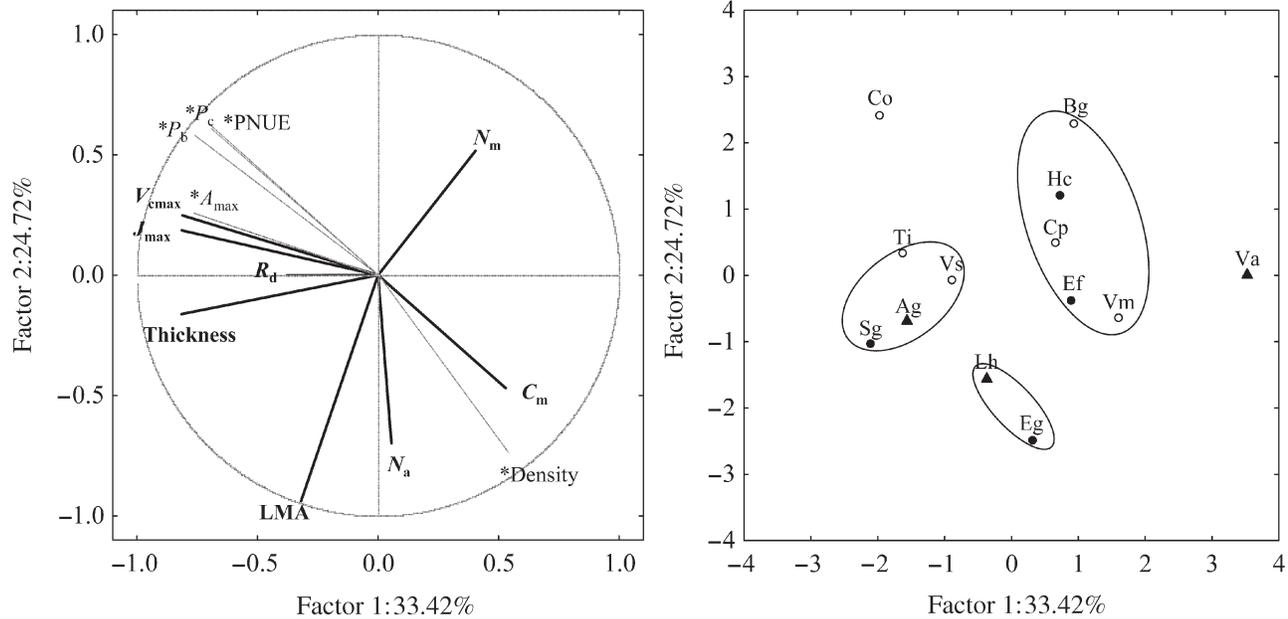


Figure 6. Principal component analysis of the studied species, ordinated according to eight leaf traits (in bold): maximum rate of carboxylation (V_{cmax}); maximum rate of electron transport (J_{max}); dark respiration (R_d); leaf thickness; leaf mass to area ratio (LMA); total carbon (C_m) and nitrogen concentrations per unit leaf dry mass (N_m); and nitrogen content per unit leaf area (N_a). Additional variables (with asterisks) were light-saturated net photosynthesis (A_{max}), leaf density, photosynthetic nitrogen-use efficiency (PNUE) and the relative investment of leaf nitrogen in carboxylation (P_c) and bioenergetics (P_b). Projection of the variables on the factor-planes (1 × 2) and projection of the species on the same plane are shown. Circles envelop points from species belonging to the three ecological groups: shade-intolerant (○), mid-tolerant (●) and shade-tolerant (▲) species (Favrichon 1994).

species with a low N_m usually maximize LMA through increased leaf density or thickness, thereby maximizing N_a . The interspecific variability in C_m was also high and similar to that recorded by D. Bonal (personal communication) for a wider range of French Guiana forest tropical species. We found that C_m was tightly correlated with density: high leaf density may be partly associated with the presence of sclerenchymatous tissues with high lignin contents (Niinemets and Kull 1998, Niinemets 1999b). However, although dense leaves had higher C_m , neither leaf density nor C_m was correlated with LMA. Leaf mass per area is often tightly correlated with leaf life span (Reich et al. 1997, Wright and Cannon 2001, Wright et al. 2004) and a high LMA is supposed to contribute to enhanced leaf resistance to herbivory (Walters and Reich 1999, Rijkers et al. 2000, Hanba et al. 2002). However, there is little information on how leaf density or thickness influences leaf life span in tree species. In a study of 17 perennial dicots, Wright (2001) found that LMA and leaf thickness each explained approximately 30–40% of the variation in leaf life span, whereas leaf toughness (generally correlated with density) explained only 25%. A trade-off between leaf N investment in photosynthesis and leaf life span has frequently been detected (Reich et al. 1991, 1997). In our study, dense leaves displayed low N allocation to photosynthesis (low values of P_c and P_b), but we did not determine if this was associated with long life span.

These large differences in leaf structure and leaf N concentration were paralleled by significant variability (twofold

range) in photosynthetic capacity as measured by V_{cmax} and J_{max} . As expected from earlier findings (Niinemets et al. 1998), V_{cmax} and J_{max} were tightly correlated, and no species-specific feature could be detected between these components of photosynthetic capacity. The residual (nonsignificant) variability may be associated with the method used to estimate the two parameters. For example, the estimate of V_{cmax} may be affected by internal resistance to CO_2 transfer, because V_{cmax} is adjusted on the CO_2 -limited fraction of the curve, and substomatal CO_2 mole fraction (not chloroplastic CO_2) was used for the computation. A significant underestimation of V_{cmax} may result (Ethier and Livingston 2004). The estimate of J_{max} derives from the CO_2 -saturated segment of the curve and is therefore less prone to underestimation. To date, no information is available about the importance of internal resistance to CO_2 transfer in the tested species, and we have no idea whether significant interspecific variability affects this resistance in tropical trees, although significant diversity has been recorded among evergreen trees (Warren and Adams 2004). From recent investigations, it may be concluded that the internal resistance is of the same magnitude as stomatal resistance (Piel et al. 2002). Non-photorespiratory respiration was low and displayed large variation due to measurement errors. A significant interspecific diversity in R_d , related to thickness and N_m , is predicted, but would require more precise estimates with an adapted chamber.

The values of V_{cmax} and J_{max} recorded in our study were

within the range of those reported by Niinemets (1999a) for a large number of species from a wide range of earth biomes with woody vegetation, and close to values recorded in the canopy of rain forest species in central Amazonia (Carswell et al. 2000), but they were lower than those reported by Dreyer et al. (2001) for temperate forest tree seedlings (63 to $90.5 \mu\text{mol m}^{-2} \text{s}^{-1}$). This difference can be explained on the basis of the following considerations: (1) tropical rain forest trees operate at temperatures close to optimum for photosynthesis and with ample water supply almost year-round, whereas temperate species usually operate at less than optimum temperatures during a large fraction of the growth season; and (2) leaf life span is usually, but not always, longer in tropical species than in deciduous, temperate broad-leaved species. As a consequence, higher photosynthetic capacities are required in temperate trees to approach the net CO_2 assimilation rates detected in tropical species.

Leaf structure and photosynthetic capacity are plastic features that depend on the irradiance received during growth (Niinemets and Kull 1998, Lee et al. 2000, Evans and Poorter 2001). Our data were recorded under common conditions and at a comparatively high irradiance (30%) relative to that generally found at the forest floor (usually below 5%; Bazzaz and Pickett 1980, Clark et al. 1996, Poorter 1999). Only the pioneer species *Cecropia obtusa* generally grows in large gaps. Because the plastic responses of leaf traits are poorly known in these species (Rijkers et al. 2000, Kitajima and Hogan 2003), we can only speculate that, based on the results obtained with temperate species (P. Montpied et al., INRA-UHP, Champenoux, France, personal communication), the interspecific diversity we recorded at 30% of full sunlight would probably be maintained at the much lower irradiances on the forest floor. Additional data are needed to document such irradiance \times genotype interactions.

Juvenility effects are known to occur for leaf anatomy and photosynthetic capacity, and adult trees often display rather different leaves (Thomas and Winner 2002, Mediavilla and Escudero 2003). For example, significant changes in leaf structure and function occur during successive architectural stages in *Dicorynia guianensis* Amsh. (Caesalpinaceae) (Roggy et al. 2005). Nevertheless, even though the absolute values of leaf traits may vary, the ranking of species and the degree of diversity is likely to remain independent of tree age; however, this assumption needs to be verified.

Relationships between leaf structure, leaf nitrogen concentration and photosynthetic capacity

Despite the tight correlation observed on a broad scale between leaf N and photosynthetic capacity (Reich and Walters 1994, Reich et al. 1994, 1999, Niinemets 1999a, Wright et al. 2004), there is significant variability in PNUE among co-occurring species (Pons and Percy 1994). This was confirmed in our data set, where there was no correlation between leaf N concentration and photosynthetic capacity when expressed on a leaf area basis, whereas weak correlations were detected when these variables were expressed on a mass basis. This difference was a result of the covariation of leaf N and LMA;

moreover, the relationships were negative, i.e., increasing N and density both resulted in a slight decrease in photosynthetic capacity. No other leaf trait was significantly correlated to photosynthetic capacity expressed on a leaf area basis. These findings led to the conclusion that the diversity of photosynthetic capacity among species was explained by differences in the relative allocation of N to photosynthetic functions. In other words, there was large diversity in PNUE among species.

To document this conclusion, we computed an index for P_c and P_b (Niinemets and Tenhunen 1997). Because of the tight correlation between J_{max} and V_{cmax} , P_c and P_b were also tightly correlated, and so for simplicity, we will concentrate the discussion on P_c , which is tightly correlated with PNUE. The computation of this allocation may yield comparative results, provided that several assumptions are fulfilled: Rubisco specific activity is stable among species, and Rubisco in the leaves is fully activated—which is probably not always the case (Warren et al. 2003, Warren and Adams 2004). The specific activity used in our computation was derived from in vivo data produced by Jordan and Ögren (1984) and is smaller than that produced by von Caemmerer et al. (1994) with transgenic tobacco, and as a result, the computed N investment was probably an overestimate of the real values. We nevertheless kept these values to facilitate comparisons with published results based on the same parameters and computed values of PNUE. Our computations resulted in a large range of values for P_c , with highest values (above 40%) in the pioneer *Cecropia obtusa* and lowest values (around 15%) in *Vouacapoua americana* and *Eperua grandiflora*. In parallel, P_b ranked from 3 to 8%. The P_c values computed by Niinemets (1999a) ranged from 4 to 17% for adult trees. Similarly, our PNUE values (61 – $187 \mu\text{mol mol}^{-1} \text{N s}^{-1}$) were large compared with the literature values (Field and Mooney 1986, Reich et al. 1991). Our data therefore point to large variability in N investment in photosynthesis (i.e., PNUE) among our study species, and this factor was probably the main source of variation in photosynthetic capacity among the tested species.

Do ecological groups of rain forest trees differ in leaf traits?

Based on our data set and the studied parameters, it was difficult to detect a clear-cut segregation among the groups defined by Favrichon (1994), although photosynthetic capacities were weakly discriminating. The pioneer and fast-growing *Cecropia obtusa* differed from the other shade-intolerant species by having a larger photosynthetic capacity, whereas *Bagassa guyanensis* and *Carapa procera* displayed low photosynthetic capacities, comparable with those of the shade-tolerant species. Similarly, the deeply shade-tolerant *Vouacapoua americana* had a much lower photosynthetic capacity than the other shade-tolerant species. Although some of our shade-intolerant species tended to display higher PNUE and lower LMA and N_a than the shade-tolerant species, as observed by others (Reich and Walters 1994, Reich et al. 1994, Ellsworth and Reich 1996, Hikosaka and Hirose 2000, Poorter et al. 2000), no significant inter-group difference was detected. This was well illustrated by the absence of any grouping in the PCA. The large

within-group variability observed for most of the variables makes Favrichon's classification questionable. Favrichon's classification was based on the vegetative development of adult and sub-adult trees, and no criteria relative to seedlings were taken into account (Favrichon 1994). The only pioneer species in our experiment, *Cecropia obtusa*, did not break established classification rules; it had a high photosynthetic capacity, allocated a large fraction of leaf N to photosynthesis and had a low LMA and N_a . However, non-pioneer species like *Tabebuia insignis*, *Virola surinamensis*, *Hymenaea courbaril* and *Symphonia globulifera* had photosynthetic capacities comparable with that of *Cecropia obtusa*. Distribution of the species in the factorial plan confirmed the lack of any potential grouping based on these criteria.

Many studies have predicted that leaves with a high LMA are better defended against herbivore attack than their low LMA counterparts (Grime et al. 1996, Hanley and Lamont 2002) and exhibit longer life spans (Reich et al. 1991, 1992, 1997, 1999, Wright et al. 2004). We found no correlation between LMA (and low N_m) and leaf density or C_m (which may be associated with a larger investment of carbon in defence compounds), and the ecological groups did not differ in this respect.

We conclude that photosynthetic features and functional leaf traits, although they differ greatly among co-occurring rain forest species, are inadequate for characterizing ecological groups. Other traits related to seedling carbon budget, like construction costs of leafy shoots and leaf life spans, probably need to be taken into account. The question of whether tree species can be assigned to clear ecological groups based on their growth and carbon economy at the seedling stage, or whether there is a continuum of growth habits between the extremes, remains a matter of debate.

Acknowledgments

The authors thank Jacqueline Marchand for carbon and nitrogen analyses, Jean-Yves Goret and Elli Lentilus for their help throughout the experiment, and Christopher Baraloto for the supply of seedlings. Useful discussions with Pierre Montpied, Daniel Epron and Eric Marcon are gratefully acknowledged. We also thank Stéphane Ponton, Patrick Heuret and Christopher Baraloto for constructive comments on earlier drafts of the manuscript.

References

Barigah, T.S., P. Imbert and R. Huc. 1998. Croissance et assimilation nette foliaire de jeunes plants de dix arbres de la forêt guyanaise cultivés à cinq niveaux d'éclaircissement. *Ann. For. Sci.* 55:681–706.

Bazzaz, F.A. and S.T.A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.* 11: 287–310.

Béna, P. 1960. *Essences forestières de Guyane*. Imprimerie Nationale, Paris, 489 p.

Bonal, D., D. Sabatier, P. Montpied, D. Tremeaux and J.M. Guehl. 2000. Interspecific variability of $\Delta^{13}C$ among trees in rainforests of French Guiana: functional groups and canopy integration. *Oecologia* 124:454–468.

Carswell, F.E., P. Meir, E.V. Wandelli, L.C.M. Bonates, B. Kruijt, E.M. Barbosa, A.D. Nobre, J. Grace and P.G. Jarvis. 2000. Photosynthetic capacity in a central Amazonian rain forest. *Tree Physiol.* 20:179–186.

Clark, D.B., D.A. Clark, P.M. Rich, S. Weiss and S.F. Oberbauer. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rainforest. *Can. J. Forest Res.* 26:747–757.

Davies, S.J. 1998. Photosynthesis of nine pioneer *Macaranga* species from Borneo in relation to life history. *Ecology* 79:2292–2308.

Dreyer, E., X. Le Roux, P. Montpied, F.A. Daudet and F. Masson. 2001. Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species. *Tree Physiol.* 21: 223–232.

Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96:169–178.

Ellsworth, D.S. and P.B. Reich. 1996. Photosynthesis and leaf nitrogen in five Amazonian tree species during early secondary succession. *Ecology* 77:581–594.

Ethier, G.J. and N. Livingston. 2004. On the need to incorporate sensitivity to CO_2 transfer conductance into the Farquhar-von Caemmerer-Berry leaf photosynthesis model. *Plant Cell Environ.* 27:137–153.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* 78:9–19.

Evans, J.R. and H. Poorter. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* 24:755–767.

Farquhar, G.D., S. von Caemmerer and J.A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* 149:78–90.

Favrichon, V. 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. *Rev. Ecol. (Terre et Vie)* 49: 379–403.

Favrichon, V. 1995. *Modèle matriciel déterministe en temps discret. Application à l'étude de la dynamique d'un peuplement forestier tropical humide*. Ph.D. Thesis, Univ. Claude Bernard, Lyon, France, 251 p.

Fetcher, N., B.R. Strain and S.F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* 58:314–319.

Field, C. and H.A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* On the Economy of Plant Form and Function. Ed. T.J. Givnish. Cambridge University Press, Cambridge, U.K., pp 25–55.

Grime, J.P., J.H.C. Cornelissen, K. Thompson and J.G. Hodgson. 1996. Evidence of a causal connection between antiherbivore defence and the decomposition rate of leaves. *Oikos* 77:489–494.

Hanba, Y.T., H. Kogami and I. Terashima. 2002. The effect of growth irradiance on leaf anatomy and photosynthesis in *Acer* species differing in light demand. *Plant Cell Environ.* 25:1021–1030.

Hanley, M.E. and B.B. Lamont. 2002. Relationships between physical and chemical attributes of congeneric seedlings: how important is seedling defence? *Funct. Ecol.* 16:216–222.

Harley, P.C., R.B. Thomas, J.F. Reynolds and B.R. Strain. 1992. Modelling photosynthesis of cotton grown in elevated CO_2 . *Plant Cell Environ.* 15:271–282.

Hikosaka, K. and T. Hirose. 2000. Photosynthetic nitrogen-use efficiency in evergreen broad-leaved woody species coexisting in a warm-temperate forest. *Tree Physiol.* 20:1249–1254.

- Hikosaka, K. and I. Terashima. 1995. A model of the acclimation of photosynthesis in the leaves of C₃ plants to sun and shade with respect to nitrogen use. *Plant Cell Environ.* 18:605–618.
- Jordan, D.B. and W.L. Ögren. 1984. The CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase. Dependence on ribulose bisphosphate concentration, pH and temperature. *Planta* 161:308–313.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Kitajima, K. and K.P. Hogan. 2003. Increases of chlorophyll a/b ratios during acclimation of tropical woody seedlings to nitrogen limitation and high light. *Plant Cell Environ.* 26:857–865.
- Le Roux, X., S. Grand, E. Dreyer and F.A. Daudet. 1999. Parameterization and testing of a biochemically based photosynthesis model for walnut trees (*Juglans regia*) and seedlings. *Tree Physiol.* 19:481–492.
- Lee, D.W., S.F. Oberbauer, P. Johnson, B. Krishnapilay, M. Mansor, H. Mohamad and S.K. Yap. 2000. Effects of irradiance and spectral quality on leaf structure and function in seedlings of two southeast Asian *Hopea* (Dipterocarpaceae) species. *Am. J. Bot.* 87:447–455.
- Mediavilla, S. and A. Escudero. 2003. Mature trees versus seedlings: differences in leaf traits and gas exchange patterns in three co-occurring Mediterranean oaks. *Ann. For. Sci.* 60:455–460.
- Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can J. For. Res.* 29:812–823.
- Niinemets, Ü. 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Funct. Ecol.* 11:518–531.
- Niinemets, Ü. 1999a. Components of leaf dry mass per area—thickness and density—alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytol.* 144:35–47.
- Niinemets, Ü. 1999b. Energy requirement for foliage formation is not constant along canopy light gradients in temperate deciduous trees. *New Phytol.* 141:459–470.
- Niinemets, Ü. and O. Kull. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. *Tree Physiol.* 18:467–479.
- Niinemets, Ü. and J.D. Tenhunen. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant Cell Environ.* 20:845–866.
- Niinemets, Ü., O. Kull and J.D. Tenhunen. 1998. An analysis of light effects on foliar morphology, physiology and interception in temperate deciduous woody species shade tolerance. *Tree Physiol.* 18:681–696.
- Piel, C., E. Frak, X. Le Roux and B. Genty. 2002. Effect of local irradiance on CO₂ transfer conductance of mesophyll in walnut. *J. Exp. Bot.* 53:1–8.
- Pons, T.L. and R. Pearcy. 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiol. Plant.* 92:636–644.
- Poorter, L. 1999. Growth responses of 15 rainforest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct. Ecol.* 13:396–410.
- Poorter, L., R. Kwant, R. Hernández, E. Medina and M.J.A. Werger. 2000. Leaf optical properties in Venezuelan cloud forest trees. *Tree Physiol.* 20:519–526.
- Popma, J., F. Bongers and M.J.A. Werger. 1992. Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in Mexico. *Oikos* 63:207–214.
- Reich, P.B. and M.B. Walters. 1994. Photosynthesis–nitrogen relations in Amazonian tree species. II: Variation in nitrogen vis-à-vis specific leaf area influences mass- and area-based expressions. *Oecologia* 97:73–80.
- Reich, P.B., C. Uhl, M.B. Walters and D.S. Ellsworth. 1991. Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* 86:16–24.
- Reich, P.B., M.B. Walters and D.S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62:365–392.
- Reich, P.B., M.B. Walters, D.S. Ellsworth and C. Uhl. 1994. Photosynthesis–nitrogen relations in Amazonian tree species. I: Patterns among species and communities. *Oecologia* 97:62–72.
- Reich, P.B., M.B. Walters and D.S. Ellsworth. 1997. From tropics to tundra: global convergence in plant functioning. *PNAS* 94:13,730–13,734.
- Reich, P.B., D.S. Ellsworth, M.B. Walters, J.M. Vose, C. Gresham, J.C. Volin and W.D. Bowman. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80:1955–1969.
- Rijkers, T., T.L. Pons and F. Bongers. 2000. The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Funct. Ecol.* 14:77–86.
- Roggy, J.C., E. Nicolini, P. Imbert, Y. Caraglio, A. Bosc and P. Heuret. 2005. Links between tree structure, and functional leaf traits in the tropical forest tree *Dicorynia guianensis* Amshoff (Caesalpinaceae). *Ann. For. Sci.* In press.
- Seemann, J.R., T.D. Sharkey, J.L. Wang and C.B. Osmond. 1987. Environmental effects on photosynthesis, nitrogen-use efficiency and metabolite pools in leaves of sun and shade plants. *Plant Physiol.* 84:796–802.
- Swaine, M.D. and T.C. Whitmore. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.
- Thomas, S.C. and W.E. Winner. 2002. Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiol.* 22:117–127.
- Turner, I.M. 2001. *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge, U.K., 298 p.
- von Caemmerer, S., J.R. Evans, G.S. Hudson and T.J. Andrews. 1994. The kinetics of ribulose-1,5-bisphosphate carboxylase/oxygenase in vivo inferred from measurements of photosynthesis in leaves of transgenic tobacco. *Planta* 195:88–97.
- Walters, M.B. and P.B. Reich. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytol.* 143:143–154.
- Warren, C.R. and M.A. Adams. 2004. Evergreen trees do not maximize instantaneous photosynthesis. *Trends Plant Sci.* 9:270–274.
- Warren, C.R., E. Dreyer and M.A. Adams. 2003. Photosynthesis–Rubisco relationships in foliage of *Pinus sylvestris* in response to nitrogen supply and the proposed role of Rubisco and amino acids as nitrogen stores. *Trees* 17:359–366.
- Wilson, K.B., D.D. Baldocchi and P.J. Hanson. 2000. Spatial and seasonal variability of photosynthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiol.* 20:565–578.
- Wilson, P.J., K. Thompson and J.G. Hodgson. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytol.* 143:155–162.
- Wright, I.J. and K. Cannon. 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. *Funct. Ecol.* 15:351–359.
- Wright, I.J., P.B. Reich, M. Westoby et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.