

Leaf gas exchange and carbohydrates in tropical trees differing in successional status in two light environments in central Amazonia

RICARDO A. MARENCO, JOSÉ F. DE C. GONÇALVES and GIL VIEIRA

Coordenação de Pesquisas em Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, Manaus, AM 69011-970, Brazil

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Summary Monoculture and mixed stands of mahogany (*Swietenia macrophylla* King) and tonka bean (*Dipteryx odorata* Willd.) trees were established on degraded land in central Amazonia to compare leaf gas exchange parameters between plants grown in sunlight in an open field and in shade beneath a balsa wood (*Ochroma pyramidale* Cav.) canopy. Shading increased specific leaf area by about 50% in both species. Shading reduced height and diameter growth of *S. macrophylla*, whereas it increased these parameters for *D. odorata*. Light-saturated photosynthesis (A_{\max}), stomatal conductance (g_s) and transpiration (E) were higher in *S. macrophylla* than in *D. odorata*. In *S. macrophylla*, A_{\max} was higher in sun leaves ($12.9 \pm 0.9 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in shade leaves ($10.2 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$), whereas light environment had no significant effect on A_{\max} of *D. odorata*. In both species, CO_2 -saturated photosynthesis (A_{pot}) was higher in sun leaves ($22 \pm 1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in shade leaves ($17\text{--}20 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$). Stomatal conductance and E increased in sun leaves of *S. macrophylla* by 45 and 38%, respectively, whereas light environment did not affect g_s and E of *D. odorata*. Photorespiration rates (P_r) varied from 28 to 36% of net photosynthesis (A) at ambient atmospheric CO_2 concentration (C_a) but declined to around 7% of A at higher C_a . Leaf dark respiration (R_d) and the CO_2 compensation point (Γ) were lower in shade-grown plants than in open-grown plants. Compared with shade-grown plants, total nonstructural carbohydrate (TNC) concentrations increased by 56% in *S. macrophylla* and by 30% in *D. odorata* in the open field. Leaf nitrogen (N_L) concentrations were higher in open-grown plants than in shade-grown plants of both species, and TNC and N_L concentrations were negatively correlated ($r = -0.77$). High TNC accumulation in *S. macrophylla* in the open field suggests that photosynthesis is unlikely to be growth-limiting at this site. We conclude that photosynthetic parameters of *D. odorata* are less affected by light environment than those of *S. macrophylla*, indicating that *D. odorata* has lower physiological plasticity to light than *S. macrophylla*.

Keywords: *Dipteryx odorata*, leaf nitrogen, leaf respiration, photorespiration, photosynthesis, starch, *Swietenia macrophylla*.

Introduction

Despite public concern about the negative impacts of deforestation of tropical forests on biodiversity, soil fertility and global biogeochemical cycles, tropical forests are declining as a result of anthropogenic activities. It is estimated that 10,000 to 15,000 $\text{km}^2 \text{year}^{-1}$ of undisturbed forest were logged in 1996 and 1997 in the Amazon region (Nepstad et al. 1999). If tropical forest destruction continues at high rates it is likely that tropical wood products will be obtained primarily from managed forests or plantations established in secondary habitats (e.g., pasture areas, abandoned pasture and degraded land). However, it is not known how species differing in successional status in the primary Amazonian forest will respond to variations in environmental factors in these open fields. In secondary habitats, variability in the physical environment (e.g., temperature, water and light) is greater than in late-successional habitats (Culf et al. 1996). In general, species adapted to late-successional habitats show lower rates of photosynthesis, respiration and transpiration than plants adapted to early-successional habitats (Bazzaz 1979). Moreover, plants adapted to full sunlight in open fields are better able to deal with variation in irradiance and temperature than late-successional species (Bazzaz and Carlson 1982).

Swietenia macrophylla King (Meliaceae) and *Dipteryx odorata* Willd. (Fabaceae) are found in the primary Amazonian forest. *Swietenia* is a mid-successional species and one of the most valuable neotropical timber species in tropical forests (Whitman et al. 1997). Its growth in diameter is low (3 to 9 mm year^{-1}) under natural forest conditions (Gullison et al. 1996). Current *Swietenia* logging practices are believed to prevent regeneration, reduce genetic variability and may lead to its commercial extinction (Snook 1996). *Dipteryx* is a late-successional species, and its wood, which is among the hardest found in the Amazonian forest, has many industrial uses (Lorenzi 1998).

Ramos and Grace (1990) studied the light responses of *Swietenia* under controlled conditions but little is known about the effects of changes in irradiance and CO_2 concentration on photosynthetic parameters of *Dipteryx* and *Swietenia* under field conditions, particularly in deforested areas or abandoned pastures. Changes in irradiance are usually associated with changes in temperature and rates of photorespiration. An in-

crease in photorespiration with temperature generally causes an increase in the CO₂ compensation point (e.g., Woodrow and Berry 1988). We hypothesized that variation in irradiance has smaller effects on gas exchange in late-successional tropical tree species than in mid-successional tropical tree species. To test this hypothesis, we examined the effect of shading during growth on gas exchange parameters, height growth, leaf nitrogen and nonstructural carbohydrate accumulation in *Swietenia* and *Dipteryx* in a former degraded landscape in the central Amazonia.

Materials and methods

Study site and species

The study was conducted in an experimental plantation located near Presidente Figueiredo (01°51' S, 60°04' W) in Brazilian central Amazonia. The area has a humid tropical climate and an annual precipitation of about 2200 mm, with a wet season from November through June, and a mean temperature of around 27 °C. The soil type is an oxisol with clay texture, low fertility and a pH of 4.5. Eight years before plantation establishment, the site had been cleared and then cultivated until it became agriculturally unproductive and biologically impoverished. In 1998, the secondary vegetation was removed and the area converted to an experimental field.

Six-month-old *Swietenia* and *Dipteryx* seedlings were planted both in monoculture and in a mixed stand with balsa wood (*Ochroma pyramidale* Cav., Bombacaceae), a pioneer species. *Dipteryx* and *Ochroma* were planted in May 1998, whereas *Swietenia* was planted 6 months later to substitute for a species that failed to establish on the site. We assumed that the difference in plant age between *Dipteryx* and *Swietenia* did not affect parameters studied because data were collected from mature leaves of similar age and appearance. Monocultures of each species were planted 3 m apart to obtain a population of about 1000 seedlings ha⁻¹. In the mixed stand, the species were distributed in a polka dot pattern, each at a density of 1000 seedlings ha⁻¹. *Ochroma* was chosen as the companion species because it is one of the faster-growing species in the Amazon region. Thus, a few months after planting, both *Dipteryx* and *Swietenia* were growing beneath the *Ochroma* canopy (hereafter called the shade environment) in the mixed stand. Data for this work were collected from August to November 2000. By this time, *Ochroma* trees had reached 11.1 ± 1.8 m in height (mean ± SD) and 10 ± 2 cm in diameter at 1.3 m height. Optical sensors (LAI-2050, Li-Cor, Lincoln, NE) were used to determine light flux in the shade environment. *Ochroma* had a leaf area index of 2.5, and beneath its canopy irradiance was 13% of full sunlight, about 260 μmol mol⁻¹, with frequent sunflecks of short duration.

Leaf gas exchange parameters

Net photosynthesis, stomatal conductance, transpiration and leaf dark respiration were measured with a portable, open gas exchange system with a Li-Cor, infrared gas analyzer (LI-6400). Data were collected at 3-week intervals from August to

November 2000 on fully expanded leaves of similar age and appearance. For each species, three plants per light environment (shade and open field) were selected at random and gas exchange parameters measured on two leaves per plant between 0900 and 1500 h. For data analysis, trees were used as replicates ($n = 3$) and observations on individual leaves treated as subsamples. Photosynthetic light response curves were determined for photosynthetic photon flux densities (PPFD) between 0 and 2000 μmol m⁻² s⁻¹, with CO₂, temperature and H₂O vapor within the leaf chamber maintained at 380 μmol mol⁻¹, 31 ± 1 °C and 21 ± 1 mmol mol⁻¹, respectively. Photosynthetic CO₂ response curves were determined for CO₂ concentrations between 0 and 2000 μmol mol⁻¹, with irradiance, temperature and H₂O vapor held at 1000 μmol m⁻² s⁻¹, 31 ± 1 °C and 21 ± 1 mmol mol⁻¹, respectively. For each light curve, the initial slope or apparent quantum yield (α), was determined between 0 and 100 μmol m⁻² s⁻¹. The non-rectangular hyperbola model was used to describe data obtained from the light response curves (Lieth and Reynolds 1987):

$$A = \{[(\alpha I + A_{\max} + R_d) - ((\alpha I + A_{\max} + R_d)^2 - 4\alpha I \Theta (A_{\max} + R_d))^{0.5}] / 2\Theta\} - R_d, \quad (1)$$

where α is the initial slope or apparent quantum yield, Θ is the convexity parameter that describes the degree of curvature at the shoulder of the light response curve, A_{\max} is net photosynthetic rate at saturating irradiance (I), and R_d is rate of dark respiration. In addition, the light compensation point (Γ_L) was estimated ($\Gamma_L = R_d/\alpha$). A nonlinear model was fitted to the means obtained from the CO₂ response curves, as follows:

$$A = a\{k - \exp[-b(C_i + c)]\}, \quad (2)$$

where k is a constant and a , b and c are regression coefficients. For each CO₂ response curve, carboxylation efficiency of Rubisco (k_x) was determined for intercellular CO₂ concentrations (C_i) between 0 and 270 μmol mol⁻¹. Photorespiration (P_r) was assumed to equal half the rate of oxygenation (v_o), which was calculated according to Sharkey (1988):

$$v_o = (A + R_d) / [(1/\Phi) - 0.5], \quad (3)$$

where Φ is a dimensionless parameter combination given by (Sharkey 1988):

$$\Phi = 2P[42.7 + 1.68(T - 25) + 0.0012(T - 25)^2] / C_i, \quad (4)$$

where T is temperature (°C) and P is atmospheric pressure (kPa).

Stomatal limitation to photosynthesis (L_s) was calculated as (Sharkey 1985):

$$L_s = (A' - A) / A', \quad (5)$$

where A is net photosynthesis at normal C_i (i.e., about $270 \mu\text{mol mol}^{-1}$) and A' is net photosynthesis when C_i is equal to the atmospheric CO_2 concentration (C_a).

Leaf nitrogen, TNC, specific leaf area and height growth

After photosynthetic measurements, samples of fully expanded leaves of similar age and appearance were randomly collected (one per tree) for leaf nitrogen (N_L), total nonstructural carbohydrate (TNC), and specific leaf area determinations. To reduce variation in starch content of leaves, samples for N_L and TNC determinations were collected between 1500 and 1600 h. To determine effects of irradiance on nitrogen concentration, N_L values on a leaf mass basis were corrected as: $N_L (\text{mg g}^{-1}) = N_{\text{sample}} (\text{mg g}^{-1}) / (1 - \text{TNC} (\text{g g}^{-1}))$, and for N_L on a leaf area basis as: $N_L (\text{g m}^{-2}) = N_{\text{sample}} (\text{g m}^{-2}) / (1 - \text{TNC} (\text{g g}^{-1}))$. Total soluble carbohydrates were extracted from leaves in boiling ethanol (80% v/v), and purified with chloroform. Starch in the ethanol-soluble residue was extracted in 0.5 M NaOH and the precipitate removed by centrifugation (15 min at 1000 g). Glucose content in the sample was assessed colorimetrically at 490 nm after reaction with phenol-sulfuric acid (Passos 1996). The starch content, measured against a glucose standard, was calculated by multiplying the observed value by 0.9 (Marenco et al. 1995). Leaf nitrogen was determined by the Kjeldhal method (i.e., digestion in concentrated sulfuric acid for 2 h at 300 °C, followed by distillation and titration). Specific leaf area (SLA) was calculated as the leaf area to leaf mass ratio. Plant height and diameter at 50 cm height were determined at both sites.

Statistical analysis

The data were subjected to analysis of variance (ANOVA). For data with subsamples (i.e., gas exchange data), sources of variation and degrees of freedom in ANOVA were: light environments (1 df), species (1 df), light environments \times species (1 df), experimental error (8 df), and sampling error (12 df). The experimental error was used in significance tests. Differences between means of measured parameters were tested by Student's t -test (Steel and Torrie 1981). Light or CO_2 response curves were fitted to the means after detecting significant differences between treatments ($P \leq 0.05$). If the effects of treatments (i.e., light environments) were not significant ($P > 0.05$), data for regression analysis were pooled to show the effect of irradiance on photosynthetic rates (e.g., see *Dipteryx* data in Figure 1).

Results

Gas exchange parameters

In *Swietenia*, A_{max} was 26% higher in sun leaves than in shade leaves (Table 1, $P < 0.05$). In *Dipteryx*, A_{max} was around $8.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in both treatments (Table 1, $P > 0.05$), and 17 and 34% lower than in shade and sun leaves of *Swietenia*, respectively (Table 1, $P < 0.05$). Because there was no effect of irradiance on A_{max} of *Dipteryx*, data were pooled across treatments to determine the effect of irradiance on net photo-

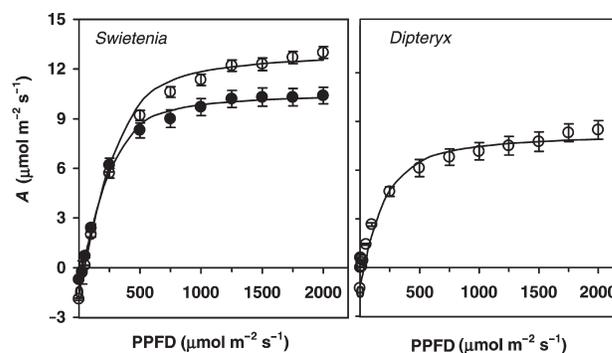


Figure 1. Effects of photosynthetic photon flux density (PPFD) on net photosynthesis (A) in sun (\circ) and shade leaves (\bullet) of *Swietenia* and *Dipteryx* at ambient ($380 \mu\text{mol mol}^{-1}$) CO_2 concentration. Each line represents the non-rectangular hyperbola obtained with the parameters in Table 2. Each value is the mean of three trees for *Swietenia* and six trees for *Dipteryx*. Values are means (\pm SE). For both lines, $R^2 \geq 0.95$.

synthesis (A) (Figure 1). *Swietenia* and *Dipteryx* leaves reached light saturation at about $1250 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 1). Light environment had no significant effect on apparent quantum yield (α) or the convexity parameter (Θ) in either species. Sun and shade leaves of both species had α values of about $0.035 \text{ mol mol}^{-1}$, whereas Θ tended to be 25% higher in *Swietenia* than in *Dipteryx* (Table 2).

In both species, leaf respiration rate (R_d) was lower for shade-grown plants than for open-grown plants (Table 1, $P < 0.05$). The R_d/A_{max} ratio was 0.15 in both species at the open site, but declined to 0.12 and 0.07 for *Dipteryx* and *Swietenia*, respectively, in the shade environment. The light compensation point was 30 and 140% higher in sun leaves than in shade leaves of *Dipteryx* and *Swietenia*, respectively (Table 2).

Stomatal conductance (g_s) and transpiration (E) were higher in sun leaves than in shade leaves of *Swietenia* at ambient CO_2 concentration (Table 3, $P < 0.05$), whereas there was no effect of light environment on either g_s or E in *Dipteryx* (Table 3, $P > 0.05$). Compared with *Dipteryx*, E was 57% higher and g_s was about twice as high in *Swietenia*. However, the light environment did not affect water-use efficiency (WUE), which was about 20% higher in *Dipteryx* than in *Swietenia* (Table 3). Despite differences in g_s , shading had no effect on stomatal limitation to CO_2 diffusion in either species (Table 1, $P > 0.05$). On average, stomata limited photosynthesis by 33 and 45%, in *Swietenia* and *Dipteryx*, respectively.

Potential photosynthetic rates (A_{pot}) were significantly higher in open-grown trees than in shade-grown trees of both species (Table 1, $P < 0.05$). Full sunlight increased A_{pot} by 34% in *Dipteryx* and by 10% in *Swietenia*; however, there were no significant differences in A_{pot} between species at the open site (Table 1, $P > 0.05$). Mean A_{pot} was $22.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in full sunlight, and ranged from 17 to $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ in shade (Table 1).

In both species, carboxylation efficiency was about $0.06 \text{ mol m}^{-2} \text{s}^{-1}$ and was affected by the light environment only slightly (Table 2). Hence, similar rates of light-saturated

Table 1. Light-saturated photosynthesis (A_{\max}), CO₂-saturated photosynthesis (A_{pot}), leaf respiration (R_d), photorespiration (P_r) and stomatal limitation to photosynthesis (L_s) in *Swietenia* and *Dipteryx* grown in two light regimes. Different capital and small letters following each mean indicate a significant difference between species in the same light environment ($P \leq 0.05$, Student *t*-test) and between light environments in the same species ($P \leq 0.05$), respectively. Each value is the mean of three trees (\pm SD) with individual leaves treated as subsamples.

Parameter	<i>Dipteryx</i>		<i>Swietenia</i>	
	Full sunlight	Shade	Full sunlight	Shade
A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	8.68 \pm 0.5 Ba	8.26 \pm 1.1 Aa	12.9 \pm 0.6 Aa	10.2 \pm 0.8 Ab
A_{pot} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	22.9 \pm 1.2 Aa	17.1 \pm 0.6 Bb	22.0 \pm 0.5 Aa	20.0 \pm 0.6 Ab
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.27 \pm 0.11 Ba	0.97 \pm 0.12 Ab	1.94 \pm 0.10 Aa	0.71 \pm 0.18 Ab
$P_{r,\text{amb}}^1$ at ambient CO ₂ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	3.19 \pm 0.19 Ba	2.95 \pm 0.42 Aa	3.84 \pm 0.18 Aa	2.81 \pm 0.29 Ab
($P_{r,\text{amb}}/A_{\max}$)100 (%)	36.8 \pm 2.4 Aa	35.7 \pm 4.3 Aa	29.7 \pm 1.6 Ba	27.6 \pm 2.3 Ba
$P_{r,\text{high}}^1$ at high CO ₂ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.50 \pm 0.08 Aa	1.24 \pm 0.06 Ab	1.47 \pm 0.03 Aa	1.26 \pm 0.05 Ab
($P_{r,\text{high}}/A_{\text{pot}}$)100 (%)	6.60 \pm 0.47 Aa	7.26 \pm 0.41 Aa	6.60 \pm 0.20 Aa	6.42 \pm 0.28 Ba
Drop in P_r^2 (%)	49.3 \pm 2.8 Ba	46.9 \pm 4.9 Aa	61.3 \pm 4.0 Aa	55.1 \pm 4.1 Aa
L_s to photosynthesis ³ (%)	44.0 \pm 2.6 Aa	46.0 \pm 5.4 Aa	32.0 \pm 1.2 Ba	34.0 \pm 1.4 Ba

¹ Calculated according to Sharkey (1988) as one half of the rate of oxygenation (v_o), where $v_o = (A + R_d)/((1/\Phi) - 0.5)$, A is net photosynthesis and Φ is a parameter determined by temperature, atmospheric pressure and intercellular CO₂ concentration.

² Determined as P_r at ambient CO₂ (380 $\mu\text{mol mol}^{-1}$) minus P_r at elevated (1000 $\mu\text{mol mol}^{-1}$) CO₂ concentration.

³ Calculated as $L_s = 100 (A' - A)/A'$, where A is net photosynthesis at normal C_i and A' is net photosynthesis when $C_i = C_a$.

Table 2. Apparent quantum yield (α), convexity parameter (Θ), light compensation point (Γ_L), CO₂ compensation point (Γ), carboxylation efficiency (k_x) and statistics for modeled curves used for describing photosynthesis in *Swietenia* and *Dipteryx* trees grown in two light regimes. Regression coefficients were obtained for response curves fitted to the means after detecting significant differences between treatments (ANOVA at $P \leq 0.05$); * = $P \leq 0.05$, $R^2 \geq 0.95$; and ** = $P \leq 0.01$, $R^2 \geq 0.98$.

Parameter ¹ /statistic	<i>Dipteryx</i>		<i>Swietenia</i>	
	Full sunlight	Shade	Full sunlight	Shade
α (mol (CO ₂) mol ⁻¹ (quanta))	0.036*	0.036*	0.0367*	0.0322*
Θ (dimensionless)	0.673	0.673	0.837	0.857
Γ_L ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	35	27	53	22
Γ ($\mu\text{mol mol}^{-1}$)	84	82	100	88
k_x (mol m ⁻² s ⁻¹)	0.065*	0.062*	0.058*	0.057*
k (constant)	0.62	0.68	0.60	0.60
Coefficient a	38.2**	27.6**	37.8**	35.3**
Coefficient b	0.0035**	0.0047**	0.0038**	0.0042**
Coefficient c	51.6**	0.0033	32.6**	34.1*

¹ Parameter Θ was calculated according to Lieth and Reynolds (1987); Γ was obtained as $\Gamma = (-\log k/b) - c$; k_x was determined at $C_i < 270 \mu\text{mol mol}^{-1}$; and $\Gamma_L = R_d/\alpha$.

photosynthesis were observed in the CO₂-limited region or the ribulose-bisphosphate-saturated region of the photosynthetic CO₂ response curves (Figure 2).

At ambient C_a , irradiance affected P_r in *Swietenia* but not in *Dipteryx* (Table 1, $P < 0.05$). At ambient C_a , P_r was higher in *Swietenia* than in *Dipteryx* in full sunlight (Table 1, $P < 0.05$), but not in shade (Table 1, $P > 0.05$). Mean P_r was 29 and 36% of net photosynthesis in *Swietenia* and *Dipteryx*, respectively. When C_a was temporarily raised to 1000 $\mu\text{mol mol}^{-1}$ or above, P_r dropped by 48% in *Dipteryx*, and by about 60% in *Swietenia* (Table 1) as a result of declines in rates of oxygenation. In the CO₂-saturated region of the photosynthetic CO₂ response curves ($> 1000 \mu\text{mol mol}^{-1}$, Figure 2), P_r declined to around 7% of net carbon uptake in both species at both sites (Table 1, $P > 0.05$).

Leaf nitrogen, TNC, specific leaf area and height growth

Compared with shade-grown leaves, N_L on a leaf area basis was 40 and 65% higher in open-grown leaves of *Dipteryx* and *Swietenia*, respectively (Table 3, $P < 0.05$). However, no effect of light environment was detected when N_L was expressed on a unit mass basis (Table 3, $P > 0.05$). Within a light environment, N_L concentrations were lower in *Swietenia* leaves than in *Dipteryx* leaves (Table 3, $P < 0.05$). Soluble carbohydrate concentrations, mainly sugars, were at least twice as high in *Swietenia* as in *Dipteryx* leaves (Table 3, $P < 0.05$). Although soluble carbohydrate concentrations were higher in sun leaves than in shade leaves of *Swietenia* (Table 3, $P < 0.05$), light environment did not significantly affect soluble carbohydrate concentrations in *Dipteryx* (Table 3, $P > 0.05$).

Table 3. Leaf nitrogen concentration (N_L), soluble carbohydrate (sugar) concentration, starch concentration, transpiration (E), stomatal conductance (g_s), water-use efficiency (WUE), specific leaf area (SLA) and height growth and diameter growth of *Dipteryx* and *Swietenia* trees in two light environments. Different capital and small letters following each mean indicate a significant difference between species in the same light environment ($P \leq 0.05$, Student t -test) and between light environments in the same species ($P \leq 0.05$), respectively. Each value is the mean of n trees (\pm SD).

Parameter ¹	n	<i>Dipteryx</i>		<i>Swietenia</i>	
		Full sunlight	Shade	Full sunlight	Shade
N_L ($g\ m^{-2}$)	3	3.07 \pm 0.23 Aa	2.20 \pm 0.17 Ab	1.77 \pm 0.39 Ba	1.07 \pm 0.14 Bb
N_L ($mg\ g^{-1}$)	3	20.3 \pm 1.56 Aa	22.1 \pm 1.5 Aa	18.5 \pm 4.1 Ba	17.2 \pm 2.3 Ba
Sugars ($mg\ g^{-1}\ DM$)	5	16.3 \pm 0.8 Ba	15.5 \pm 1.2 Ba	59.4 \pm 3.7 Aa	35.7 \pm 2.9 Ab
Starch ($mg\ g^{-1}\ DM$)	5	126.5 \pm 13.5 Ba	93.6 \pm 12.8 Bb	204.2 \pm 14.7 Aa	132.5 \pm 9.5 Ab
E ($mmol\ m^{-2}\ s^{-1}$)	3	3.42 \pm 0.55 Ba	2.48 \pm 0.64 Ba	5.39 \pm 0.30 Aa	3.90 \pm 0.39 Ab
g_s ($mmol\ m^{-2}\ s^{-1}$)	3	107 \pm 15 Ba	99 \pm 19 Ba	266 \pm 6 Aa	183 \pm 20 Ab
WUE ($mmol\ mol^{-1}$)	3	2.78 \pm 0.48 Aa	3.25 \pm 0.25 Aa	2.39 \pm 0.14 Aa	2.43 \pm 0.16 Ba
SLA ($cm^2\ g^{-1}\ DM$)	6	66.2 \pm 4.3 Bb	100.2 \pm 4.4 Ba	104.2 \pm 2.8 Ab	159.9 \pm 2.4 Aa
Height (m)	33	3.54 \pm 0.99 Ab	5.13 \pm 1.07 Aa	1.21 \pm 0.58 Ba	0.87 \pm 0.37 Bb
Diameter (mm)	33	34.0 \pm 8.9 Ab	38.3 \pm 6.3 Aa	18.2 \pm 8.8 Ba	12.1 \pm 5.5 Bb

¹ Each N_L value was obtained from a pooled sample of at least three leaves collected from different trees. Because TNC values were high, we show the effect of light environment on corrected N_L values: N_L ($mg\ g^{-1}$) = N_{sample} ($mg\ g^{-1}$)/(1 - TNC ($g\ g^{-1}$)); N_L ($g\ m^{-2}$) = N_{sample} ($g\ m^{-2}$)/(1 - TNC ($g\ g^{-1}$)). Measurements of E , g_s and WUE were made on two leaves per tree at near ambient CO_2 concentration ($380\ \mu mol\ mol^{-1}$) and $31 \pm 1\ ^\circ C$. Diameter was determined at 50 cm height.

Compared with shade leaves, starch concentrations were 35 and 54% higher in sun leaves of *Dipteryx* and *Swietenia*, respectively (Table 3, $P < 0.05$). Concentrations of TNC concentrations were 264 and 168 $mg\ g^{-1}$ for *Swietenia*, and 143 and 109 $mg\ g^{-1}$ for *Dipteryx* grown in the open and shade environment, respectively.

Shading reduced plant height and diameter growth of *Swietenia*, whereas it increased these parameters in *Dipteryx* (Table 3, $P < 0.05$). Specific leaf area was about 50% larger for shade leaves than for sun leaves in both species (Table 3, $P < 0.05$).

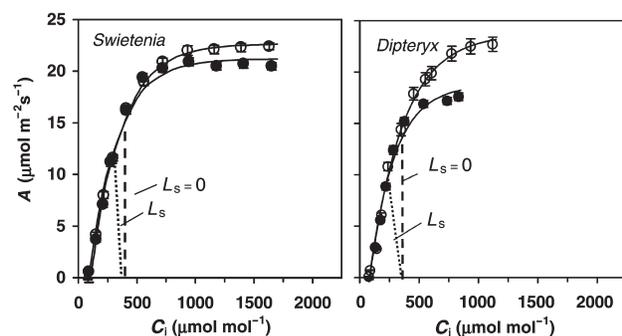


Figure 2. Effects of intercellular CO_2 concentration (C_i) on light-saturated photosynthesis (A) in sun (\circ) and shade leaves (\bullet) of *Swietenia* and *Dipteryx*. Each line is the regression fitted to the means at different C_i values ($A = a[k - \exp(-b(C_i + c))]$). Regression coefficients are shown in Table 2. Dashed lines indicate stomatal limitation to the diffusion of CO_2 from the atmosphere to intercellular spaces (L_s). Vertical lines represent the hypothetical diffusion of CO_2 to intercellular spaces when there is no stomatal limitation ($L_s = 0$). Each value is the mean of three trees (\pm SE). For both lines, $R^2 = 0.99$.

Discussion

Gas exchange parameters

Light-saturated photosynthetic rates measured in this study were within the range observed for other tropical species (Strauss-DeBenedetti and Bazzaz 1996, Maruyama et al. 1997), although A_{max} in *Swietenia* was higher than that measured in plants grown in cabinets at lower PPFDs (Ramos and Grace 1990). The saturating irradiances shown in Figure 1 were higher than values reported for other mid- and late-successional species (Bazzaz and Carlson 1982), suggesting that even shade-grown leaves of the study species developed and acclimated to irradiances higher than those usually found in their natural environments. Our finding that high irradiances did not decrease A_{max} in sun or shade leaves of either species indicates that damage to photosystem II was minimal in all leaves examined, and that both species can acclimate to varying irradiances.

There is evidence that early-successional species and some mid-successional species acclimate to open sites by increasing their photosynthetic capacity (Bazzaz and Carlson 1982, Vieira 1996). Higher photosynthetic rates of sun leaves compared with shade leaves may be attributable to differences in pigment content and leaf anatomy (Terashima and Hikosaka 1995). Similar α values in sun and shade leaves (Table 2) were expected because quantum yield tends to remain insensitive to the light environment during plant growth (Ramos and Grace 1990, Valladares et al. 1997). Therefore, photosynthetic rates in *Swietenia* and *Dipteryx* were similar in the shade environment and at low irradiances, i.e., on cloudy days. The low photosynthetic rates observed in *Dipteryx* are consistent with the finding that late-successional species photosynthesize at lower rates than mid-successional plants (Bazzaz 1979). Fur-

thermore, shade leaves of *Swietenia* showed lower rates of photosynthesis than sun leaves because the rate of photosynthesis tends to decline with increases in shade acclimation (Chazdon et al. 1996). This effect was not observed in *Dipteryx*, probably because late-successional species tend to be less sensitive to changes in the light regime (Bazzaz and Carlson 1982).

The curvature factor (Θ) is related to light saturation of chloroplasts. The transition from a light-limited to a light-saturated region tends to be sharp in shade leaves (i.e., high Θ values) and gradual, low Θ values, in sun leaves (e.g., Lambers et al. 1998). The trend for a high Θ in shade leaves of *Swietenia* (Table 2) is consistent with the results of Valladares et al. (1997) and may be associated with the alignment of chloroplasts along the palisade cells.

Leaf respiration rates were higher in sun leaves than in shade leaves. The R_d values observed for *Swietenia* were higher than those reported by Ramos and Grace (1990). This discrepancy may be attributed to differences in temperature and irradiance during plant development. High leaf respiration rates, which have been positively correlated to acclimation to high long-term irradiances, probably reflect high energy use of photosynthetic components inside the chloroplast and might even prevent photoinhibition in sunny environments (Amthor 1995, Krömer 1995). Maximum rates of gross photosynthesis ($A_{\max} + R_d$) were only eight to 15 times higher than R_d (Table 1). This difference was lower than expected at ambient CO_2 concentrations (Amthor 1995), probably because we collected the data at high temperatures ($31 \pm 1^\circ\text{C}$) when R_d was high. Estimates of the cost of maintaining biomass range from 20 to 60% of photosynthetic production, with much of the cost being associated with macromolecular turnover and maintenance of ion gradients across membranes (Lambers et al. 1998, Amthor 2000). The highest and lowest R_d values were found in sun and shade leaves of *Swietenia*, respectively, suggesting higher physiological plasticity in this species than in *Dipteryx*. Thus, the capacity of *Swietenia* to respond to changes in light environments, with a high metabolic rate at full sunlight and a low metabolic rate in shade, results in high photosynthetic efficiency, an important cultural trait. Because α varied only slightly between light environments, and $\Gamma = R_d/\alpha$, the low Γ values of shade leaves were attributed to their low respiration rates.

The effects of irradiance on g_s and E of *Swietenia* (Table 3) are probably related to the greater CO_2 fixation observed in sun leaves compared with shade leaves and to the higher stomatal density in sun leaves than in shade leaves (e.g., Vieira 1996). High E in sun leaves suggests a high efficiency for water uptake in *Swietenia* at the open site. This is consistent with the results of Gerhardt and Fredriksson (1995) who found deep tap roots in *Swietenia* seedlings grown in a mown pasture. In addition, our g_s values for *Swietenia* were higher than those recorded for this species in a natural forest (Barker and Pérez-Salicrup 2000), indicating that photosynthesis was not limited by water availability in our study. The lack of a light effect on g_s and E in *Dipteryx* suggests that this species is less

efficient than *Swietenia* in controlling either loss of water or CO_2 uptake in open fields. Our g_s values for *Dipteryx* are comparable with previous measurements in other tropical species (e.g., Carswell et al. 2000a), suggesting that low g_s may be important for limiting photosynthetic rates in late-successional tropical trees in this region, at least during drought periods. Both E and A_{\max} were higher in *Swietenia* than in *Dipteryx*, suggesting a higher cooling efficiency in *Swietenia*, which is important in maintaining leaf temperature near optimum temperature for CO_2 assimilation. High transpiration rates in *Swietenia*, especially in the open field, should be taken into account when small seedlings are used in silvicultural projects; however, light environment had no significant effect on WUE in either species (Table 3), largely because, in shade plants, a reduction in A_{\max} was accompanied by a decline in E . On average, WUE was 20% higher in *Dipteryx* than in *Swietenia* (Table 3), perhaps indicating that *Dipteryx* was better able to withstand dry periods.

The light environment did not affect stomatal limitation to CO_2 diffusion in either species. On average, stomata limited photosynthesis by 33 and 45% for *Swietenia* and *Dipteryx*, respectively (Table 1). High L_s values have often been related to water deficit, which may severely inhibit A_{\max} . Because rainfall during the study was around $100 \text{ mm month}^{-1}$, we attribute the high L_s values not to water stress but to the effects of high radiation and temperature and conclude that differences in A_{\max} between species partly reflect differences in their L_s values.

Values of A_{pot} observed in saplings in our study are higher than those measured in the upper canopy of older trees in an undisturbed forest in the same region (Carswell et al. 2000a). We note that differences in A_{pot} between *Dipteryx* and *Swietenia*, which occurred mainly in the shade environment (Table 1, Figure 2), were in the RuBP-limited region, where the capacity to regenerate RuBP is dependent on light-derived chemical energy.

Leaf nitrogen, TNC, specific leaf area and height growth

Foliar nitrogen concentration expressed on a leaf area basis was correlated with photosynthetic capacity of both species (Table 3), which is consistent with previous results (Terashima and Hikosaka 1995, Carswell et al. 2000a). Our N_L values are lower than those reported by Carswell et al. (2000a), perhaps because our plants were grown on former degraded land instead of in a pristine forest, given that foliar nitrogen concentration reflects the amount of nitrogen available in the substrate (Fichtner et al. 1995). Also, *Dipteryx* accumulated more nitrogen than *Swietenia*, probably because it is a legume capable of forming a symbiotic association with N_2 -fixing organisms. It also suggests that *Dipteryx* allocated a higher proportion of nitrogen to leaf components not directly associated with photosynthesis.

Although the TNC concentrations in our study species were about twice as high as those reported for other tropical trees (Körner and Arnone 1992), they fall within the range observed for other tropical plants grown at low nitrogen supply (Fich-

tner et al. 1995, Mooney et al. 1995). In addition, N_L and TNC concentrations were negatively correlated ($r = -0.77$, $P < 0.01$), indicating that the low TNC values found in *Dipteryx* may be related to its high N_L concentrations. This is consistent with previous reports in which a large amount of starch has been associated with a low rate of nutrient supply (Mooney et al. 1995, Carswell et al. 2000b). Because starch concentration increases when availability of photosynthates exceeds the demand for growth (Fichtner et al. 1995, Marengo et al. 1995), the high TNC concentrations suggest that photosynthesis is unlikely to be growth-limiting in these secondary habitats. Leaf soluble carbohydrate (i.e., sugar) concentrations were at least twice as high in *Swietenia* as in *Dipteryx* (Table 3), which is consistent with the higher photosynthetic rates observed in sun leaves of *Swietenia*. The effects of species and light environment on soluble carbohydrates are consistent with the observation that TNC concentrations increase with increasing photosynthetic rate or decreasing nutrient availability (Fichtner et al. 1995).

Changes in the light environment differentially affected gas exchange parameters, height growth and the TNC concentration of tropical trees differing in successional status. Photosynthetic capacity and growth of the mid-successional species *Swietenia* were higher at the open site than in the shade environment. This confirms the importance to *Swietenia* of high irradiances and large gaps to achieve high growth rates and the successful establishment of its seedlings, and indicates that open fields could provide suitable sites for *Swietenia* plantations. In contrast, the late-successional species *Dipteryx* produced taller plants in shade than in the open field, indicating that *Dipteryx* is adapted to colonizing small gaps and performs better in moderately shaded environments than in open fields. Under shading, the low photosynthetic rates of *Dipteryx* are probably offset by other factors such as increased leaf life span and foliage density.

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