

## SPECIFIC LEAF AREA AND PHOTOSYNTHETIC PARAMETERS OF TREE SPECIES IN THE FOREST UNDERSTOREY AS A FUNCTION OF THE MICROSITE LIGHT ENVIRONMENT IN CENTRAL AMAZONIA

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**MARENCO, R. A. & VIEIRA, G. 2005. Specific leaf area and photosynthetic parameters of tree species in the forest understorey as a function of the microsite light environment in central Amazonia.** The effect of the microsite light environment (MLE) on specific leaf area (SLA), light-saturated photosynthesis ( $A_{\max}$ ), maximum transpiration ( $E_{\max}$ ) and stomatal conductance ( $g_{s-\max}$ ) was examined in three tree forest species (late successional *Minquartia guianensis* and *Scleronema micranthum*, and *Goupia glabra*, a pioneer species) growing in the forest understorey. Logging of large trees 15 years ago had no significant effect on either SLA or photosynthetic parameters. On a per area basis, species did not differ in gas exchange parameters. However, when photosynthesis was expressed on a per mass basis ( $\mu\text{g C g}^{-1} \text{DM s}^{-1}$ ), higher photosynthetic rates were observed in *Goupia* (1.07) than in *Scleronema* (0.71) or *Minquartia* (0.57). SLA ( $\text{m}^2 \text{kg}^{-1}$ ) was greater in *Goupia* (24.4) than in *Scleronema* (18) or *Minquartia* (15.9).  $A_{\max}$ ,  $E_{\max}$  and  $g_{s-\max}$  increased as the MLE in the understorey became brighter, particularly in *Goupia*. Leaf respiration in the light ( $0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and the apparent quantum yield ( $33 \text{mmol CO}_2 \text{mol}^{-1} \text{photon}$ ) were similar in all examined species. Regardless of logging disturbance, examined species acclimated to the MLE according to their successional status. *Goupia*, but not *Minquartia* or *Scleronema*, responded to its light environment mainly by changing SLA, indicating that physiological processes are involved in the acclimation of late successional species to the forest understorey.

Key words: Diffuse light – *Goupia glabra* – leaf respiration – *Minquartia guianensis* – *Scleronema micranthum* – photosynthesis – selective logging – stomatal conductance – transpiration

**MARENCO, R. A. & VIEIRA, G. 2005. Luas daun spesifik dan parameter fotosintesis spesies pokok di tingkat bawah kanopi hutan sebagai fungsi persekitaran cahaya mikrosit di Amazon tengah.** Kesan persekitaran cahaya mikrosit (MLE) terhadap luas daun spesifik (SLA), fotosintesis tepu cahaya ( $A_{\max}$ ), transpirasi maksimum ( $E_{\max}$ ) dan konduktans stomata ( $g_{s-\max}$ ) dikaji dalam tiga spesies pokok hutan (spesies sesaran lewat *Minquartia guianensis* dan *Scleronema micranthum* serta spesies perintis, *Goupia glabra*) yang tumbuh di tingkat bawah kanopi hutan. Pembalakan pokok besar 15 tahun dahulu tiada kesan signifikan terhadap SLA mahupun parameter fotosintesis. Berdasarkan luas, spesies tidak berbeza dari segi parameter pertukaran gas. Bagaimanapun, apabila fotosintesis dikira berdasarkan jisim ( $\mu\text{g C g}^{-1} \text{DM s}^{-1}$ ), kadar fotosintesis yang lebih tinggi dicerap dalam *Goupia* (1.07) berbanding *Scleronema* (0.71) atau *Minquartia* (0.57). SLA ( $\text{m}^2 \text{kg}^{-1}$ ) lebih tinggi dalam *Goupia* (24.4) berbanding

*Scleronema* (18) atau *Minquartia* (15.9).  $A_{\max}$ ,  $E_{\max}$  dan  $g_{s-\max}$  meningkat apabila MLE di tingkat bawah kanopi menjadi lebih terang, khususnya dalam *Goupia*. Respirasi daun dalam cahaya ( $0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) dan hasil kuantum ketara ( $33 \text{ mmol (CO}_2\text{) mol}^{-1}$  foton) serupa dalam semua spesies yang dikaji. Tanpa mengira gangguan pembalakan yang terjadi, spesies yang dikaji menyesuaikan iklim terhadap MLE mengikut status sesaran masing-masing. Tidak seperti *Minquartia* dan *Scleronema*, *Goupia* bergerak balas terhadap persekitaran cahayanya terutamanya dengan menukar SLA. Ini menunjukkan proses fisiologi terlibat dalam penyesuaian iklim spesies sesaran lewat di tingkat bawah kanopi hutan.

## Introduction

In the Amazon region, large areas of pristine rain forest are annually converted to agricultural land or disturbed by selective logging. Some negative impacts of selective logging include reductions in timber stand quality and regeneration problems for highly valued timber species. Selective extraction of large trees has several effects on the understorey vegetation. Natural fall of trees in undisturbed rainforest may create small openings, which account for about 10% of the understorey area (Guariguata & Pinard 1998). These openings are essential for maintaining forest functioning. However, drastic reduction of forest canopy due to selective logging greatly increases irradiance levels in the forest understorey, which causes both ecological and ecophysiological effects on understorey vegetation. From an ecophysiological point of view, most studies have examined the exposure of shade plants to high irradiance in gaps or under controlled conditions (e.g. Bazzaz & Carlson 1982, Krause & Winter 1996, Thiele *et al.* 1998). In the short-term, photoinhibition of photosynthesis is commonly observed when shade plants are submitted to high irradiation levels in natural gaps (e.g. Krause & Winter 1996). Although selective logging is a common practice in neotropical forest, little is known about the medium or long-term effects of canopy disturbance on tree species growing in the forest understorey. Three months after logging, Clearwater *et al.* (1999) observed few photoinhibitory effects in seedlings growing in partly open and open sites, and photosynthetic rates were higher in wide open than in partly open environments.

Considering light requirements for seedlings and young tree establishment, rain forest understorey plants can be classified into gap-requiring and shade-tolerant species. The majority of species in pristine rain forests are shade tolerant, as gap-requiring species comprise less than 15% in such ecosystems (Whitmore 1989). Even when gap-requiring species are less abundant in undisturbed forests, they have an important role in forest regeneration after forest disturbance. Seeds of gap-requiring species generally germinate in light gaps and produce seedlings that show high growth rates and photosynthetic capacities. Shade tolerant species are slower-growing species, show reduced photosynthesis and low leaf respiration rates, and become light saturated at low irradiance levels. Shade plant acclimation to low irradiance occurs at both the leaf and whole plant level. Alterations include changes in thylakoid structure and leaf morphology, and modifications in growth patterns and assimilate partitioning (Anderson *et al.* 1988, Marengo & Reis 1998, Maxwell *et al.* 1999).

In tropical rain forest, the light environment drives plant succession because the filling of tree-fall gaps and openings depends on the ability of climax and pioneer species to compete for light and other available resources. Several studies have examined the effect of changes in light availability on photosynthetic parameters for species differing in successional status grown either under controlled conditions (e.g. Bazzaz & Carlson 1982) or in plantations (e.g. Marengo *et al.* 2001). The effect of sunflecks on stomatal functioning and leaf gas exchange parameters in rainforest trees growing in the forest understorey has been characterized (e.g. Küppers *et al.* 1996, Valladares *et al.* 1997, Allen & Pearcy 2000a, b). Also, short-term effects of exposure to high irradiance have been studied either in gaps (e.g. Krause & Winter 1996) or after selective logging (Clearwater *et al.* 1999). However, our understanding of how young trees growing in the forest understorey perform following long-term selective logging is far from complete. Also, there is little information on the effects of the natural microsite light environment on leaf gas exchange parameters of young rain forest trees differing in successional status growing in the forest understorey. This information may be useful in forest management programs, and may help explain community dynamics in the understorey of tropical forests. We hypothesized that the medium-term response to selective logging may affect leaf gas exchange parameters of saplings of canopy trees in the forest floor, and that variation in light availability at individual microsites for these species has less effect on photosynthesis, transpiration and respiration in tropical trees of late successional status. In this paper we examine the effects of diffuse light (percentage of transmittance, T) on gas exchange parameters and specific leaf area in *Minquartia*, *Scleronema* and *Goupia* in an undisturbed forest and in plots selectively logged in 1987 in the central Amazon.

## Materials and methods

### *Site description and species*

This study was conducted at the Tropical Forest Research Station located about 80 km north of Manaus, on experimental plots known as ZF2 (02° 38' S, 60° 09' W). The region is characterized by a humid climate with a brief dry season (50 to 100 mm rainfall per month) from July to September. Mean annual temperature is 26.5 °C and mean annual rainfall is about 2500 mm. Vegetation is representative of a heterogeneous lowland rainforest, with an aboveground biomass of around 325 Mg ha<sup>-1</sup>. The soil is poor in nutrients and deeply weathered (oxisols) with a clay texture, and a pH of 4.2 to 4.5. The forest canopy averages about 30 m in height.

The study species were *Minquartia guianensis* (Olacaceae), *Scleronema micranthum* (Bombacaceae) and *Goupia glabra* (Celastraceae). These species (hereafter, *Minquartia*, *Scleronema* and *Goupia*) are native to the Amazonian forest. *Minquartia* and *Scleronema* are late successional shade-tolerant species, which may grow well in acid soils that are poor in nutrients. *Minquartia* wood is hard and highly durable (Hunter 1991). *Goupia* is a fast-growing early successional species (pioneer) often found in central Amazonia. It rapidly colonizes open areas, has straight stems and

produces a durable timber. For this study, four saplings per species of 0.6 to 3 m in height were selected at random in both undisturbed and partly logged plots of 0.4 ha. Exploited plots had been subjected to selective logging in 1987, when about 50 m<sup>3</sup> ha<sup>-1</sup> of roundwood was extracted, i.e. 8 to 10 trees ha<sup>-1</sup> each at least 50 cm in diameter at breast height (dbh) (Higuchi *et al.* 1997).

### *Leaf gas exchange parameters*

Net photosynthetic rates ( $A$ ), stomatal conductance ( $g_s$ ), transpiration ( $E$ ), and leaf respiration in the dark ( $R_n$ ) were measured with a portable open gas exchange system with infrared gas analyzer (LI-6400, Li-Cor, Lincoln, NE). Water-use efficiency (WUE) was computed as  $A/E$ . Data was collected in June and July 2001 on fully expanded leaves of similar age and appearance. Before collecting data for this study, we verified that the midday-depression commonly reported for sun plants was absent in shade plants of the forest understorey. Thus, gas exchange parameters were measured in two leaves per plant between 0800 and 1700 h. Photosynthetic light response curves were determined for photosynthetic photon flux density (PPFD) levels between 0 and 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . For data analysis, trees were used as replicates and observations on individual leaves treated as subsamples. Taking into account *in situ* ambient conditions during measurements, CO<sub>2</sub> and H<sub>2</sub>O vapor within the leaf chamber were maintained at 380  $\mu\text{mol mol}^{-1}$  and 22 to 24  $\mu\text{mol mol}^{-1}$  respectively. No attempt was made to control leaf temperature in chamber. Temperature ranged from 24 to 25 °C in the forest understorey. For each light response curve, leaf respiration in the light ( $R_d$ ) and the initial slope or apparent quantum yield ( $\alpha$ ) were obtained from the A-PPFD relationship at low light intensity (i.e. 0 to 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). All gas exchange measurements were taken after steady rates of photosynthesis and transpiration were observed, usually within 20 to 30 min after exposure to an altered light intensity. A non-rectangular hyperbola model was used to describe the data obtained from light response curves, as follows:

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

where

$\alpha$  = initial slope or apparent quantum yield

$\Theta$  = convexity parameter that describes the degree of curvature at the shoulder of the light response curve

$I$  = PPFD at the leaf surface and

$A_{\max}$  = rates of light-saturated photosynthesis.

The irradiance compensation point ( $I_c$ ) was estimated by the  $R_d/\alpha$  ratio.  $R_d$  was calculated as the  $y$ -intercept of the linear segment of the light response curve (Villar *et al.* 1994).

### *Specific leaf area and understorey irradiance*

After photosynthetic measurements, leaves (two to six per plant) were collected for specific leaf area (SLA) determinations, which was calculated as the leaf area to

leaf mass ratio. Leaf area was measured with a leaf area meter (LI-3000, Li-Cor, Lincoln, NE). Transmittance (i.e. the fraction of sky visible), expressed as a percentage (%T), was determined using a plant canopy analyzer (LAI-2000, Li-Cor, NE) under overcast sky conditions to avoid the inaccuracy in such measurements that is associated with strong solar radiation. Transmittance was recorded for each sapling by collecting six to eight readings at each microsite. Each reading was collected at a distance of about 1.5 m from the stem, forming a circle around the plant. The height of the sensor above the ground corresponded to the height of leaves used for gas exchange measurements. The mean of these readings was used to determine %T at each microsite. To circumvent problems associated with suitable outside canopy measurement, a second sensor (LAI-2000), operating in remote mode, was used to log irradiance at a nearby open site while recording data under the canopy. Finally, in order to characterize the understorey light environment, daily irradiance was recorded over five days, i.e. three on control plots and two on exploited plots, at randomly chosen microsities. Irradiance was recorded at 5 min intervals using a line quantum sensor (LI-191SA Li-Cor, Lincoln, NE) connected to a datalogger (LI-1000, Li-Cor, Lincoln, NE).

### Statistical analysis

Parameters were analysed using two-way analyses of variance, with levels of logging as the main plots (1 df) and species as subplots (2 df). Means among species were compared by a Duncan's test (Steel & Torrie 1981). Regression analysis was used to examine the effect of level of irradiance in the understorey (%T) on variables studied.

## Results and discussion

### Effect of selective logging and species

Partial logging 15 years ago did not significantly affect ( $p > 0.05$ ) light availability (%T) in the forest understorey (Table 1), and as a result, none of the variables examined were affected by the 1987 selective logging. Therefore, data was pooled

**Table 1**  $F_{\text{ratio}}$  and P values for the percentage of transmittance (%T) and leaf gas exchange parameters according to a two-way ANOVA (1 df for logging and 2 df for species)

Source of variation	df	%T	$A_{\text{max}}$ $\mu\text{mol m}^{-2} \text{s}^{-1}$	$E_{\text{max}}$ $\text{mmol m}^{-2} \text{s}^{-1}$	$g_{\text{s-max}}$ $\text{mmol m}^{-2} \text{s}^{-1}$	SLA $\text{cm}^2 \text{g}^{-1}$	
Logging (L)	1, 6	$F_{\text{ratio}}$	1.65	0.36	0.15	0.51	0.53
		P	0.22	0.57	0.72	0.50	0.50
Species (S)	2, 12	$F_{\text{ratio}}$	1.94	0.76	0.33	0.39	17.00
		P	0.18	0.50	0.53	0.52	0.0003
Interaction (L × S)	2, 12	$F_{\text{ratio}}$	0.38	0.72	0.56	0.31	2.24
		P	0.53	0.50	0.51	0.54	0.15

df : error a, 6 df; error b, 12 df

to analyse effects of species on the variables studied. We attributed the lack of an effect of selective logging on variables studied to the fast growth of pioneer species (e.g. *Goupia*, *Cecropia* spp. and *Jacaranda copaia*) that rapidly filled gaps created by adult tree logging. *Jacaranda* trees about 30 m in height were often found in exploited plots, creating a light environment in these plots similar to that of undisturbed plots. It has been found that light levels in large rain forest gaps (> 400 m<sup>2</sup>) created by the fall of canopy trees may be reduced by about 50% after one year (Denslow *et al.* 1998). Similarities in availability of light in control and exploited plots may help explain the lack of an effect of the earlier selective logging on examined variables. This is because light availability is probably the most important factor limiting plant growth of understorey saplings in many tropical forests. It is also a key factor in determining seedling survival and the dynamics of forest succession (Chazdon *et al.* 1996).

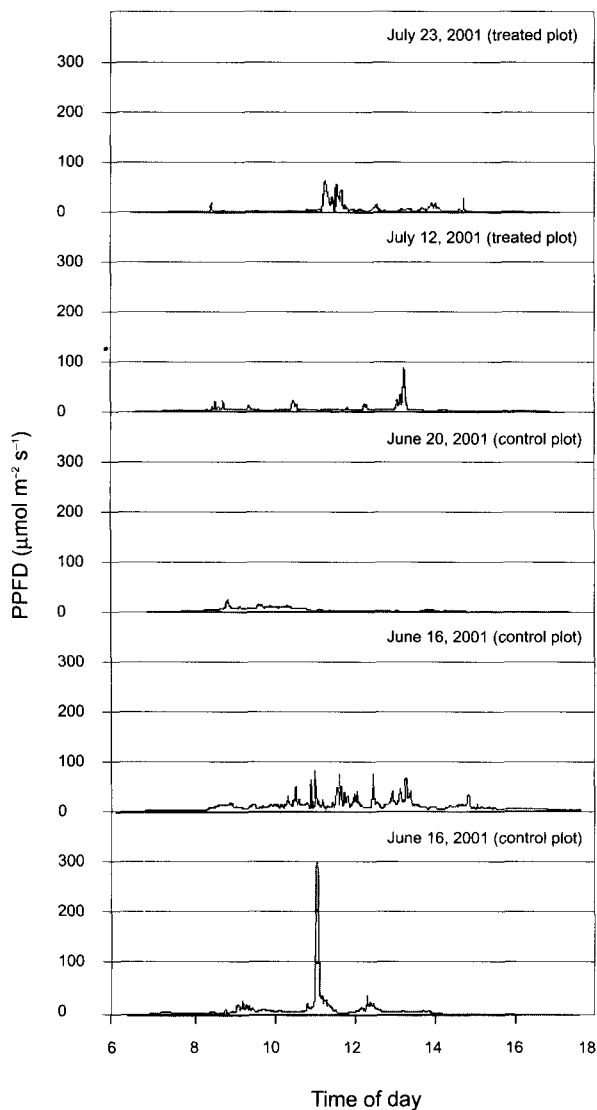
*Effect of the microsite light environment in the forest understorey  
on SLA and gas exchange parameters*

Instantaneous irradiance and daily PPFD in the understorey were about 7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 0.30  $\text{mol m}^{-2} \text{day}^{-1}$  respectively, with sunflecks puncturing the forest understorey irrespective of any previous disturbance caused by selective logging 15 years before (Figure 1). Light-saturated photosynthesis ( $A_{\text{max}}$ ), maximum transpiration ( $E_{\text{max}}$ ) and maximum stomatal conductance ( $g_{\text{s-max}}$ ) significantly increased as the understorey forest became brighter (Figures 2a–d). The effect of the light environment (%T) on these parameters was greater in *Goupia* than in *Scleronema* or *Minquartia* (Figures 2a–c). In addition, when  $A_{\text{max}}$  was expressed on a per mass basis ( $A_{\text{max-mass}}$ ), *Goupia* fixed more carbon than the other species at the same light intensity (Figure 2d).

The relationship between  $A_{\text{max}}$  and %T was stronger in *Minquartia* ( $r^2 = 0.87$ ) and *Goupia* ( $r^2 = 0.64$ ) than in *Scleronema* ( $r^2 = 0.27$ ) (Table 2). Nevertheless, slopes of regression lines of gas exchange parameters against %T were usually steeper in *Goupia*, the pioneer species, than in *Minquartia* or *Scleronema* (Table 2, Figure 2) because its high responsiveness to irradiance increases in the microsite environment. Regression coefficients (b) of  $E_{\text{max}}$  and  $g_{\text{s}}$  as a function of %T were about twice as great in *Scleronema* than in *Minquartia*. SLA was about 30% greater in *Goupia* (24.5  $\text{m}^2 \text{kg}^{-1}$  dry matter) than in *Scleronema* (18  $\text{m}^2 \text{kg}^{-1}$  dry matter) or *Minquartia* (15.9  $\text{m}^2 \text{kg}^{-1}$  dry matter, Table 3). The relationship between %T and SLA was significant only for *Goupia* ( $p = 0.03$ , Figure 2e, Table 2).

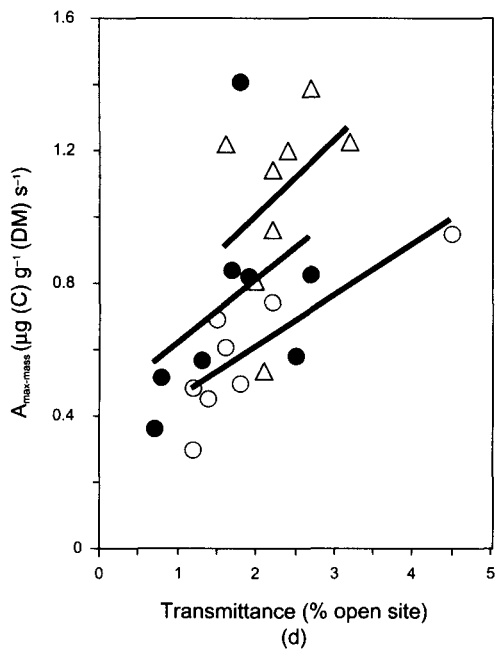
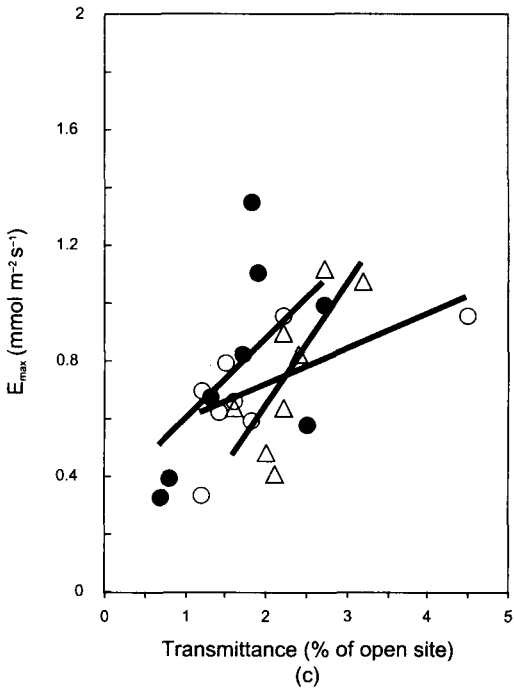
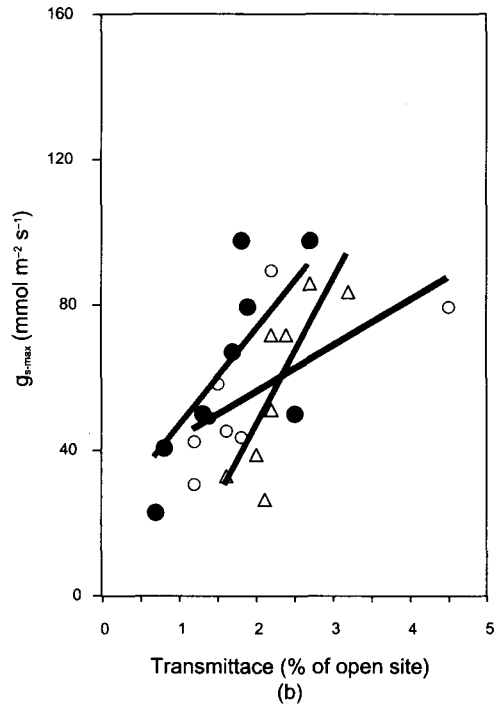
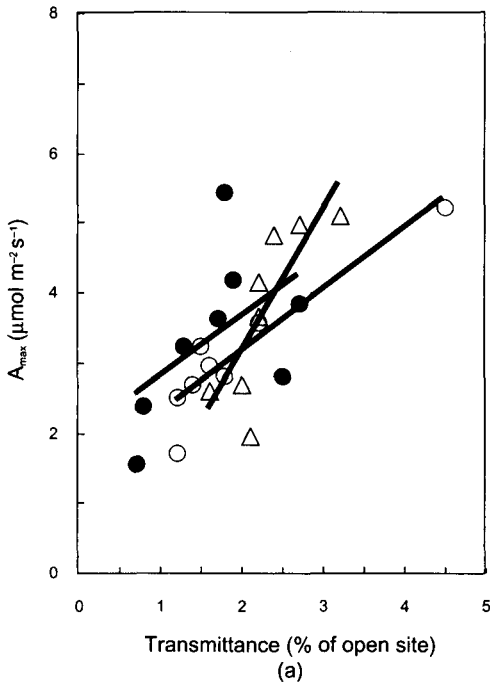
The average PPFD in the forest understorey (around 7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of diffuse light) observed in this study is in agreement with values reported for the understorey of other tropical rain forests, i.e. usually less than 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Fetcher *et al.* 1994). As light availability in the understorey is rather low, species growing in this environment presumably depend on an efficient use of sunflecks for carbon gain.

However, because the response of photosynthesis to light changes is rather slow, an efficient sunfleck utilization depends on a previous induction period, which is a function of both stomatal opening and ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity (Percy & Pfitsch 1995). Rubisco responds faster than  $g_{\text{s}}$  to changes

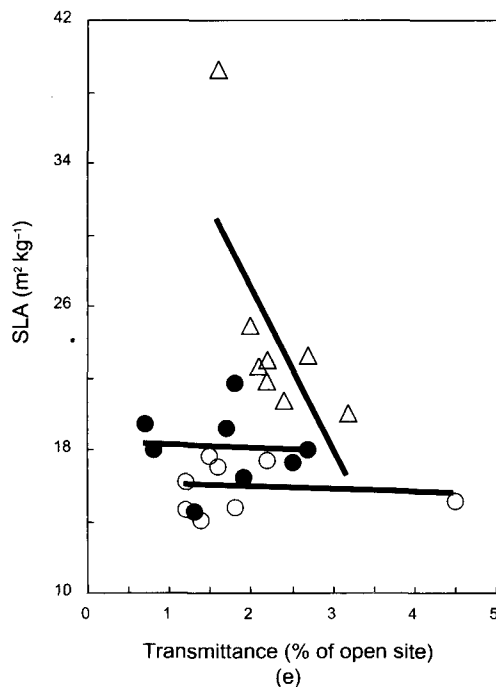


**Figure 1** Light availability in the forest understorey in central Amazonia. Data collected on an undisturbed forest (control plots) and in plots subjected to selective logging in 1987 (treated plots).

in irradiance. We found that stomatal conductance often reached steady-state within 20 to 30 min after changes in light intensity, which is consistent with results reported by Allen & Pearcy (2000a). However, it is worth noting that irradiance of sunflecks was often lower than  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 1). That is their light intensity was frequently within the linear region of the light response curve (Figure 3a inset). In this region the photosynthetic machinery has a rapid response to light (Allen & Pearcy 2000b, Rijkers *et al.* 2000). Thus, although  $A_{\text{max}}$  values are usually not reached during short sunfleck exposures, a significant amount of carbon is assimilated during such events, because they contribute to keep the photosynthetic machinery of





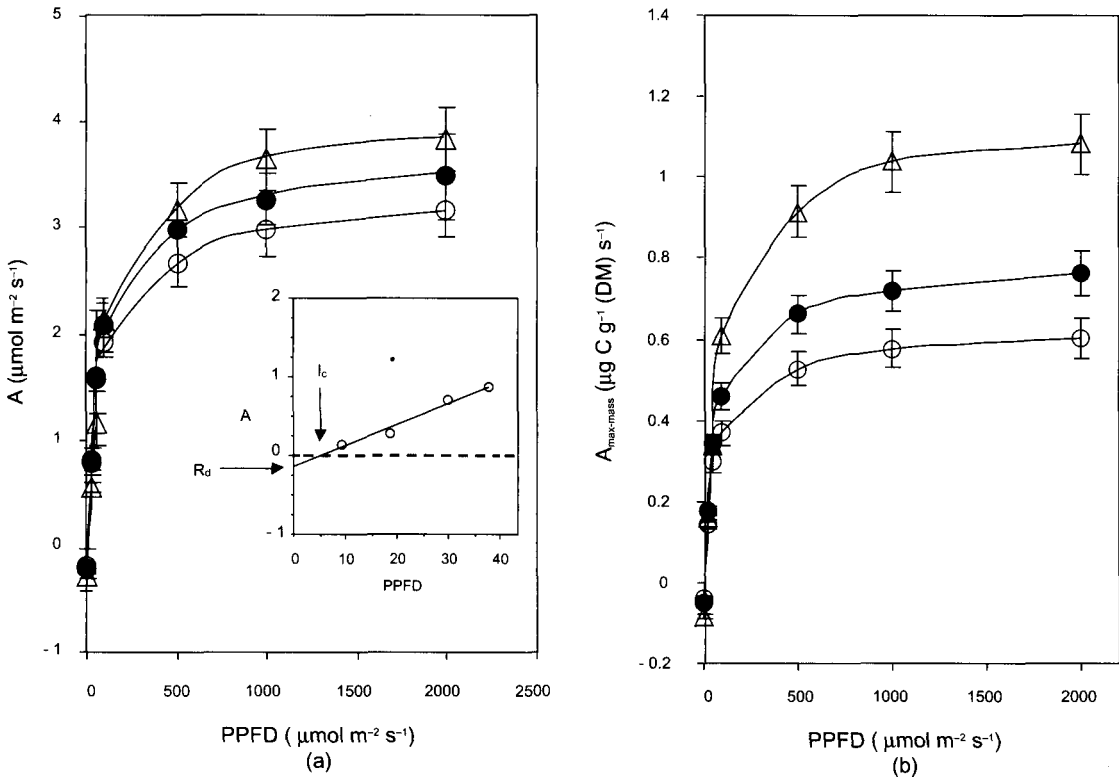


**Figure 2** Light-saturated photosynthesis ( $A_{\max}$ ), maximum stomatal conductance to water vapour ( $g_{s-\max}$ ), maximum transpiration ( $E_{\max}$ ), and specific leaf area (SLA) as a function of percentage of transmittance in the understorey. Species are *Minquartia* (open circles), *Scleronema* (solid circles), and *Goupia* (open triangles). Each line indicates the regression for a species. Regression coefficients and  $r^2$  values are shown in Table 2. Each data point is the mean of two leaves per plant.

understorey species induced, leading to an efficient use of the available light (Pearcy *et al.* 1994).

SLA values found in this study are consistent with results obtained in central Amazonia by Roberts *et al.* (1996), and more recently by Marengo and Maruyama (2003). These authors reported SLA values ranging from  $16 \text{ m}^2 \text{ kg}^{-1}$  for *Swietenia macrophylla* to  $31 \text{ m}^2 \text{ kg}^{-1}$  for *Cedrella odorata*, two mid-successional species. In this study, *Goupia* showed high leaf plasticity since its SLA sharply decreased as the light environment at an individual microsite became brighter (Figure 2e, Table 3).

We found that *Minquartia* and *Scleronema* responded similarly to variation in %T, which may be attributed to the fact that both species belong to the same successional group. *Goupia*, on the other hand, appeared to be more sensitive to change in irradiance in the understorey environment, which is consistent with the capability of pioneer species to respond faster to changes in light regimes (Koike *et al.* 2001). In addition, higher  $A_{\max}$  values of less obscure microsites are also consistent with greater availability of soil inorganic nitrogen in those environments (Denslow *et al.* 1998). In *Goupia*, all photosynthetic parameters (i.e.  $A$ ,  $E$ ,  $g_s$ ) sharply increased with increases in %T. Figures 2 (a)–(c) show that  $A_{\max}$ ,  $E_{\max}$  and  $g_s$  values of *Goupia*



**Figure 3** Net photosynthesis on a per area basis (A) and on a per unit mass basis (B) as a function of irradiance (PPFD). Species are *Minquartia* (open circles), *Scleronema* (solid circles), and *Goupia* (open triangles). The inset in the left panel shows an expanded scale for irradiance PPFD at low light intensity. For panel A, average values of photosynthetic parameters are as follows: apparent quantum yield ( $\alpha$ ) = 0.033 mol(CO<sub>2</sub>) mol<sup>-1</sup> (photons), curvature factor ( $\Theta$ ) = 0.80, leaf respiration in the light ( $R_d$ ) = 0.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and light compensation point ( $I_c$ ) = 6  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .  $I_c$  and  $R_d$  are indicated by arrows in the inset. Each data point is the mean of eight plants and two leaves per plant ( $\pm$  SE).

tended to remain low in deeply shaded microsites, but rapidly increased as these microsites became less dark.

There was no species variation in  $A_{\text{max}}$  values on a per area basis. This can be attributed to the effect of microsite light environment (MLE) on specific leaf area, particularly in *Goupia*. The specific leaf area of *Goupia* reflected the changes in microsite irradiance in the understorey, with thinner leaves at low light availability and thicker ones in less dim microsites. It may be noted in Figure 2(a) that small changes in transmittance (i.e. 2 to 3% of irradiance in the open site) more than doubled  $A_{\text{max}}$  values of *Goupia*, from 2 to about 5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , likely as a result of a sharp decline in SLA and a greater amount of Rubisco per unit leaf area (Chow *et al.* 1988). The same was true for  $g_s$  and  $E_{\text{max}}$  in this species. Under intense shading (1 to 2% T), *Scleronema* showed higher  $A_{\text{max}}$  values than *Minquartia*. This trait may be an important adaptive mechanism for survival and acclimation in deeply shade habitats, and suggests that carbon assimilation basically depends on responsiveness to sunflecks, which may involve rapid Rubisco activation. Effects of microsite

**Table 2**  $F_{\text{ratio}}$ , significance level ( $p$ ), and regression coefficient ( $r^2$ ) for regressions fitted between parameters examined and the percentage of transmittance (%T) ( $n = 8$ )

Species	x-axis	y-axis	$F_{\text{ratio}}$	p value	Slope ( $b$ )	$r^2$
<i>Minquartia</i>	%T	$A_{\text{max}}$	82.89	0.00001	0.873	0.87
<i>Minquartia</i>	%T	$E_{\text{max}}$	4.83	0.04	0.123	0.43
<i>Minquartia</i>	%T	$g_s$	10.24	0.0064	12.63	0.47
<i>Minquartia</i>	%T	SLA	0.10	0.75	-1.21	0.01
<i>Minquartia</i>	%T	$A_{\text{max-mass}}$	25.0	0.001	0.567	0.69
<i>Scleronema</i>	%T	$A_{\text{max}}$	5.18	0.0371	0.85	0.27
<i>Scleronema</i>	%T	$E_{\text{max}}$	5.36	0.0345	0.28	0.32
<i>Scleronema</i>	%T	$g_s$	12.80	0.0033	26.53	0.50
<i>Scleronema</i>	%T	SLA	0.06	0.81	-2.06	0.01
<i>Scleronema</i>	%T	$A_{\text{max-mass}}$	1.23	0.30	0.69	0.17
<i>Goupia</i>	%T	$A_{\text{max}}$	23.58	0.0004	2.02	0.64
<i>Goupia</i>	%T	$E_{\text{max}}$	11.3	0.0048	0.41	0.57
<i>Goupia</i>	%T	$g_s$	24.74	0.0004	39.75	0.66
<i>Goupia</i>	%T	SLA	13.30	0.0029	-89.59	0.49
<i>Goupia</i>	%T	$A_{\text{max-mass}}$	4.90	0.03	0.172	0.44

irradiance on photosynthetic traits of *Goupia* appear to be mainly associated with changes in leaf morphology. Thus, our results suggest that growth and survival of *Goupia* in the understorey of tropical rain forest are associated with more permanent changes in light regimes, such as gaps created by the fall of trees or other disturbances. Supporting this hypothesis is the fact that this species was not found in microsites receiving less than 2% of the irradiance of open sites. Low  $A_{\text{max}}$  rates at low light intensity (< 2% open) in *Minquartia* and *Scleronema* (Figures 2a and d) suggest a low investment in photosynthetic machinery, and also a low cost for maintenance respiration. Compared with late successional species, *Goupia* showed a higher leaf plasticity since its SLA greatly increased in deeply shade environment. Similar results have been reported for mid-successional *S. macrophylla* and *Cedrella* grown in shade environments (Marenco *et al.* 2001, Marenco & Maruyama 2003).

#### *Effect of microsite light environment on light response curves*

In the light response curves, there was no difference among species in the carbon assimilation rates ( $A$ ), transpiration ( $E$ ), and stomatal conductance ( $g_s$ ) ( $p > 0.05$ , Figure 3a). Nevertheless, when data was expressed on a per mass basis, light saturated photosynthesis ( $A_{\text{max-mass}}$ ) was higher in *Goupia* than in the late successional species (Figures 2e, 3b). Leaf dark respiration ( $R_n$ ),  $R_d$ ,  $\alpha$ , and  $\Theta$  were similar in all species examined. The average compensation irradiance ( $I_c$ ) was  $6 \mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$  (Figure 3a inset), which is very close to the PPFD in the understorey (Figure 1). This suggests that carbon assimilation and survival in the understorey is at least partly explained by leaf plasticity and physiological traits that strengthen the capture and efficiency of light utilization. Average  $R_d$  was  $0.2 \mu\text{mol} \text{m}^{-2} \text{s}^{-1}$ , mean  $\alpha$  was

33 mmol(CO<sub>2</sub>) mol<sup>-1</sup>(photon), whereas average  $\Theta$  was 0.80. Mean  $R_n$  was 0.25  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . WUE ranged from 3.4 to 3.8 g(C) kg<sup>-1</sup>(H<sub>2</sub>O) at saturating light intensity, with no difference between species (Table 3). These values match well to those recorded by Marengo & Maruyama (2003) in early and late successional species. On the other hand,  $g_s$  and  $E_{\text{max}}$  values reported in this study are lower than previously observed for other mid- and late successional species growing under partly shade conditions (Marengo *et al.* 2001). Low  $E$  and  $g_s$  values in the forest understorey are not surprising because stomatal aperture is mainly modulated by light intensity. Thus, in the dimly lit forest understorey, stomata usually remain partly closed and as a result, stomatal conductance and transpiration tend to be low.

Even though mean  $A_{\text{max}}$  values were rather low (Table 3), this does not appear to have negatively affected seedling survival, probably because all species examined showed relatively low  $R_d$  and  $R_n$  values, and probably because they are also highly efficient at assimilating carbon during sunfleck exposure. This is supported by the fact that understorey irradiance (around 7  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , Figure 1) was quite similar to  $I_c$  (6  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). This also indicates that seedling survival in the understorey depends on their efficiency in capturing light and assimilating carbon during sunflecks as suggested by Pearcy *et al.* (1994).

Since no difference was found between selectively logged and control plots with respect to the gas exchange parameters examined, we conclude that the immediate effects of selective logging on photosynthetic parameters of young trees understorey species, pioneer or late successional, are apparently overcome after some years of forest regeneration. Regardless of initial logging disturbance, examined species responded to the microsite light environment according to their successional status. The pioneer *Goupia* was highly responsive to its microsite light environment, mainly as a result of its leaf plasticity. On the other hand, *Minuartia* and *Scleronema* showed less leaf thickness changes suggesting that biochemical processes are likely to be involved in their acclimation to changes in the light environment.

**Table 3** Specific leaf area (SLA), light saturated photosynthesis per unit area ( $A_{\text{max}}$ ), transpiration ( $E$ ), stomatal conductance ( $g_s$ ), water-use efficiency (WUE), and light saturated photosynthesis per mass unit ( $A_{\text{max-mass}}$ ) of tree species growing in the forest understorey

Species	SLA (m <sup>2</sup> kg <sup>-1</sup> )	$A_{\text{max}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$E$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	$g_s$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	WUE (g C kg <sup>-1</sup> H <sub>2</sub> O)	$A_{\text{max-mass}}$ ( $\mu\text{g C g}^{-1} \text{DM s}^{-1}$ )
<i>Minuartia</i>	15.87 ± 0.49 B	2.97 ± 0.11A	0.54 ± 0.037 A	46.58 ± 5.04 A	3.67 ± 0.41 A	0.57 ± 0.05 C
<i>Scleronema</i>	18.07 ± 0.75 B	3.27 ± 0.25 A	0.65 ± 0.047 A	58.87 ± 5.71 A	3.35 ± 0.51 A	0.71 ± 0.08 B
<i>Goupia</i>	24.46 ± 2.18 A	3.65 ± 0.29 A	0.64 ± 0.051 A	54.76 ± 6.58 A	3.80 ± 0.29 A	1.07 ± 0.10 A

Within columns means followed by same letters are not significantly different at  $p = 0.05$ , according to Duncan's test.

Mean of eight plants across microsite light environments ( $\pm$  SE)

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