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Growth and physiological changes in saplings of *Minquartia guianensis* and *Swietenia macrophylla* during acclimation to full sunlight

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Abstract

Low light availability under a forest canopy often limits plant growth; however, sudden increase in light intensity may induce photoinhibition of photosynthesis. The aim of this study was to evaluate the ecophysiological changes that occur in potted plants of *Minquartia guianensis* and *Swietenia macrophylla* during the acclimation process to full sunlight. We used six full-sun independent acclimation periods (30, 60, 90, 120, 150, and 180 days) and a control kept in the shade. Shading was obtained by placing plants under the canopy of a small forest. The F_v/F_m ratio, net photosynthetic rate (P_N), the maximum carboxylation velocity of Rubisco (V_{cmax}), maximum electron transport rate (J_{max}), specific leaf area (SLA), and growth were assessed at the end of each of the six acclimation periods. Plant exposure to full sunlight caused a sudden decrease in the F_v/F_m ratio (photoinhibition) particularly in *Minquartia*. Photooxidation (necrotic patches) of the leaf tissue was observed in upper leaves of *Minquartia*. The higher P_N values were observed in *Swietenia* under full sun, about 12 μmol(CO_2) m^{-2} s^{-1}. V_{cmax25} values were higher after 90 days of acclimation, about 14 μmol(CO_2) m^{-2} s^{-1} for *Minquartia*, and 35 μmol(CO_2) m^{-2} s^{-1} for *Swietenia*. At the end of a 180-d acclimation period J_{max25} was 35 μmol(electron) m^{-2} s^{-1} for *Minquartia* and 60 μmol(electron) m^{-2} s^{-1} for *Swietenia.* SLA was higher in *Swietenia* than in *Minquartia*. In *Minquartia*, monthly rate of leaf production per plant (MRLP) was positive (0.22 leaf $month^{-1}$) after four months in the open. Whereas, in *Swietenia* MRLP was positive (0.56 leaf $month^{-1}$) after an acclimation period of two months. After six months in the open, height growth rates were 3.5 and 28 mm $month^{-1}$ for *Minquartia* and *Swietenia*, respectively. The greater acclimation capacity of *Swietenia* was associated to an enhanced photosynthetic plasticity under full sun. In *Minquartia*, transition to full-sun conditions and lack of physiological adjustment resulted in severe photoinhibition and loss of leaves.

Additional key words: gas exchange; growth rates; photoinhibition; photosynthesis; Rubisco activity; tropical trees.

Introduction

In tropical rainforest, light is one of the most important factors limiting growth of seedlings and saplings in the forest understorey, which makes sunflecks and gap openings important for tree growth in juvenile stages

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Abbreviations: C_i − intercellular CO_2 concentration; DGR − diameter growth rate; F_m − maximal fluorescence of the dark-adapted state; F_0 − minimal fluorescence of the dark-adapted state; F_v/F_m − maximal quantum yield of PSII; g_s − stomatal conductance; HGR − height growth rate; J_{max} – maximum rate of electron transport (or RuBP regeneration); J_{max25} – maximum rate of electron transport at 25ºC; K_c – Michaelis constant of Rubisco for carboxylation; K_o – Michaelis constant of Rubisco for oxygenation; MRLP − monthly rate of leaf production per plant; O − oxygen concentration in chloroplasts; P_c − net photosynthetic rate limited by Rubisco activity; P_j – net photosynthetic rate limited by RuBP concentration, P_N − net photosynthetic rate; P_{Nmax} – light-saturated photosynthesis; P_{Npot} – potential photosynthesis; P_N/PPFD − light response curves; P_N/C_i – response of photosynthesis to intercellular CO_2 concentration; PPFD − photosynthetic photon flux density, R_D – rate of leaf respiration in the light; SLA – specific leaf area; V_{cmax} – maximum carboxylation velocity of Rubisco; V_{cmax25} – maximum carboxylation velocity of Rubisco at 25ºC; Φ – apparent quantum yield; Θ – convexity parameter of the light response curve; Γ* – CO_2 compensation point in the absence of mitochondrial respiration.

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(Nicotra *et al.* 1999, Valladares and Niinemets 2008). However, sudden increase in light intensity during gap formation may induce photoinhibition of photosynthesis, which may ultimately result in extensive damage in nonacclimated plants (Long *et al.* 1994). Thus, acclimation of shade plants to gap opening or to the open (*e.g.* after transplantation) is critical, as it affects growth rates and eventually determines plant survival and fitness. Photosynthetic plasticity is an important ecophysiological characteristic (Valladares *et al.* 2002, Walters 2005) and from an adaptive perspective, plant responses to variations in irradiance may take days and even months to occur (Kursar and Coley 1999). Photosynthesis of late successional species are less responsive to changes in ambient light (Kammesheidt 2000, Rijkers *et al.* 2000). This indicates that pioneer species may adjust faster to changes in light regime, partly due to faster leaf turnover. In late successional plants (shade-tolerant species), acclimation can be related not only to variation in morphological characteristics but also to changes in physiological plasticity (Givnish 1988). For example, in shade-adapted seedlings of oak (*Quercus robur*, a gap-demanding species) and beech (*Fagus sylvatica*, a shade-tolerant species), the greater tolerance of the gap-demanding species to sudden exposure to full sun light seems to be related to an enhanced physiological plasticity, while shade tolerance depend on increased plasticity in variables linked to capture of light (Valladares *et al.* 2002). Thus, when shade plants are transferred to sunny environments they often increase leaf thickness and specific leaf mass (the mass to area ratio), the inverse of specific leaf area (SLA) (Givnish 1988, Valladares and Niinemets 2008). In several species, a reduction in SLA associated with an increase in irradiance often results in higher photosynthetic rates most likely because of an increase in the amount of Rubisco per unit leaf area (Poorter and Evans 1998, Walters 2005). Photosynthesis may also increase by increasing the area occupied by chloroplasts without significant modification of leaf structure (Oguchi *et al.* 2005).

Acclimation to high irradiance might be directly related to the maximization of total plant carbon accumulation in response to environmental changes. This adjustment may involve simultaneously two functional processes: changes in leaf photosynthetic properties involving physiological and morphological adjustments (Oguchi *et al.* 2005) or changes in plant architecture, which modifies the relationship between photosynthetic and nonphotosynthetic tissues, for example, by affecting the shoot/root ratio (Björkman 1981, Walters 2005). The response of net photosynthetic rate (P_N) to irradiance is commonly described by a nonrectangular hyperbola, which includes the convexity parameter of the light-response curve (Θ) and the apparent quantum yield (Φ). Under natural conditions, P_N is generally limited by light, hence Θ and Φ are important parameters. In C_3 plants Φ is a function of intercellular CO_2 concentration (C_i) and can be reduced by high irradiance due to photoinhibition (Demmig-Adams and Adams 2006). Because there is a linear relationship between Φ and F_v/F_m – the variable to maximal fluorescence (Genty *et al.* 1989), this ratio is commonly used to assess the extent of photoinhibition of a leaf (Kitao *et al.* 2000, Dias and Marenco 2006). Depending on how long a plant takes to recover from photoinhibition, it can be dynamic (recovery from high irradiance stress occurs overnight) or chronic, the plant takes more than a day to recover from photoinhibition at low light conditions (Long *et al.* 1994). In addition, Φ and Θ, maximum carboxylation velocity of Rubisco (V_{max}), and maximum rate of electron transport (J_{max}) are important parameters to describe photosynthetic traits of a plant. Understanding how V_{max} and J_{max} either vary among species or are affected by environmental conditions during growth is important because such parameters are of vital importance for the accuracy of models that aim to describe daily and seasonal photosynthetic carbon gain (Wullschleger 1993).

Manwood (*Minquartia guianensis*) is a late successional tree species that grows in terra-firme rain forests. The wood of this species has many uses in the timber industry, being used in the production of railroad ties, fences, floors and building bridges. It is considered a shade-tolerant climax species, with low photosynthetic rates, slow growth, and low rates of tissue turnover (Marenco and Vieira 2005). Mahogany (*Swietenia macrophylla*) is considered a mid-successional species, with low density in natural forest. It grows well under full sunlight. We tested the hypothesis that during acclimation growth and leaf physiology of intermediate and late successional Amazonian tree species are affected distinctly. Thus, the aim of this work was to assess growth and ecophysiological changes that occur in saplings of *Minquartia* and *Swietenia* during the acclimation process to full sunlight.

Materials and methods

Plant material, growth conditions and treatments: The study was conducted at the V8 campus of the National Institute for Research in the Amazon (INPA) in Manaus - AM, Brazil (03°05'30"S, 59°59'35"W) between June and December of 2008. We used saplings of *Minquartia guianensis* Aubl. (Olacaceae) and *Swietenia macrophylla* King. (Meliaceae). Both species are hereinafter referred to as *Minquartia* and *Swietenia*. They were grown from seeds in 3-kg pots and well watered during the study. The substrate was a mixture of forest soil (90%, collected from the upper 20 cm), sand (7%) and vermiculite (3%), amended with a slow release fertilizer (1.7 g kg^{-1} substrate, Basacote®). The plants grew under natural shading [0.4 mol(photon) m^{-2} d^{-1} for *Minquartia* and

1.4 mol(photon) m^{-2} d^{-1} for *Swietenia,* as this species does not tolerate deep shading] until the beginning of the experiment (about three years for *Minquartia* and six months for *Swietenia*). Shading was obtained by placing plants beneath the canopy of a small forest (areas with deepest shading for *Minquartia*). When plants had reached about 0.20-m height, saplings of both species were subjected to six full sun independent acclimation treatments (30, 60, 90, 120, 150, and 180 d). Plants kept under shade conditions were treated as control. Plants were transferred to full sun starting with the longest acclimation period (180 d), so that all acclimation treatments ended at the same time. At each acclimation period five saplings per species were used. The control was kept under shading at the light levels used before the beginning of the experiment.

Photosynthetic photon flux density (PPFD), temperature and relative humidity were measured using specific sensors (*Li-191SA, Li-Cor*, Lincoln, NE, USA and *Humitter 50Y Vaisala*, Oyj, Finland) connected to a datalogger (*Li-1400, Li-Cor*). Data were collected every 15 min. At the end of each acclimation treatment we determined P_N, g_s, V_{cmax}, maximum rate of electron transport (J_{max} or RuBP regeneration), SLA and F_v/F_m. We also determined monthly height growth rate (HGR), diameter growth rate (DGR), and monthly rate of leaf production per plant (MRLP).

Measurements of chlorophyll (Chl) fluorescence and photosynthetic traits: F_v/F_m was calculated as $(F_m - F_0)/F_m$, where F_m and F_0 denote the maximal and minimal fluorescence of the dark-adapted state, respectively. We measured F_v/F_m weekly from the beginning to the end of each acclimation period using a portable Chl fluorometer (*PEA*, *MK2*, *9600*, *Hansatech*, Norfolk, UK). Fluorescence parameters were determined early in the morning (06:00 to 07:00 h) on intact leaves after 20 min of dark adaptation. F_m was measured using a 1-s saturation pulse (650 nm) of 3,000 μmol(photon) m^{-2} s^{-1} on 4-mm diameter foliar discs. F_0 was obtained using an algorithm that calculates a line fitted for the initial data points. This line is then extrapolated to the start of illumination (*i.e.* time zero).

Measurements of photosynthetic traits were carried out using an infrared gas analyzer (*Li-Cor 6400, Li-Cor*, Lincoln, NE, USA) in five plants and two leaves per plant. Photosynthetic rates were measured in the same leaves used for determining chlorophyll fluorescence. Light-response curves (P_N/PPFD) and the responses of photosynthesis to intercellular CO_2 concentration (P_N/C_i curves) were generated at room temperature (27 ± 1ºC) and relative humidity of 70 ± 2% following Long and Bernacchi (2003). Light-saturated photosynthesis (P_{Nmax}) and g_s were determined at a light intensity of 1,000 μmol(photon) m^{-2} s^{-1} and a [CO_2] of 380 ppm, 70% RH and 27ºC. Whereas, light- and CO_2-saturated photosynthesis (hereinafter termed, potential photosynthesis, P_{Npot}) was determined at light saturation and a [CO_2] of 2,000 ppm. P_N/PPFD data were fitted using the nonrectangular hyperbola model of photosynthesis.

$$P_N = \{[(\Phi\ \mathrm{PPFD} + P_{Nmax} + R_D) - ((\Phi\ \mathrm{PPFD} + P_{Nmax} + R_D)^2 - 4\ \Phi\ \mathrm{PPFD}\ \Theta\ (P_{Nmax} + R_D))^{0.5}]/2\Theta\} - R_D$$

where Φ is the apparent quantum yield; Θ, is the convexity parameter of the light-response curve and R_D the rate of leaf respiration in the light. R_D was determined at low light intensity (7–35 μmol m^{-2} s^{-1}) as the intercept (light intensity zero) of the P_N/PPFD regression line (Villar *et al.* 1994). V_{cmax} and J_{max} were calculated after Farquhar *et al.* (1980), using parameters from Bernacchi *et al.* (2001):

$$P_c = [V_{cmax}\ (C_i - \Gamma^*)]/[C_i + K_c(1 + O/K_o)];$$
$$P_j = [J_{max}\ (C_i - \Gamma^*)]/([4\ C_i + 8\ \Gamma^*)];$$

where P_c and P_j denote net photosynthetic rates limited by either Rubisco activity or RuBP concentration, respectively; Γ* represents the CO_2 compensation point in the absence of mitochondrial respiration (42.75 ppm, at 25°C); *O*, the oxygen concentration in chloroplasts (0.210 mol mol^{-1}, at 25°C); K_c (404.9 μmol mol^{-1}, at 25°C) and K_o (278.4 mmol mol^{-1}, at 25°C) represent the Michaelis constant of Rubisco for carboxylation and oxygenation, respectively. For leaf temperature recorded during gas-exchange measurements, constants associated with the properties of Rubisco (*i.e.* K_c, K_o , Γ*) were obtained using equations of Bernacchi *et al.* (2001). To facilitate comparisons with data reported in the literature, V_{cmax} and J_{max} data were normalized to 25ºC after Medlyn *et al.* (1999).

Plant growth and SLA: Plant height (from the base of the plant to the apex) and stem diameter were recorded at 30-d intervals. Stem diameter was measured (mean of two measurements taken at right angles from each other) with digital calipers at 50 mm from the soil surface. Specific leaf area was determined as the area to dry mass (DM) ratio, in three leaf discs (17-mm diameter) per leaf and five leaves per plant, avoiding major veins. To determine mass, leaf discs were oven-dried at 72°C to constant mass.

Statistical analyses: Treatments (species and acclimation times) were arranged in a completely randomized design with five replications (plants per treatment). Data were subjected to analysis of variance (*ANOVA*). The effect of acclimation time on the studied variables was examined by regression analysis. The *SAEG 9.0* package of the Federal University of Viçosa, Brazil was used for statistical analyses.

Results

Whole-plant response to acclimation: Average irradiance (PPFD) received by saplings during the acclimation period was 15.7 mol(photon) m^{-2} d^{-1}. Mean temperature and relative humidity were 27ºC and 70% in the sun and 26ºC and 90% under shading, respectively. Responses to acclimation treatments varied between species. In *Minquartia*, sudden transfer to full sunlight led to chlorotic lesions in upper leaves, which within a few days evolved into necrotic patches (photooxidation of leaf tissue). Leaves that experienced severe stress for a prolonged period (photooxidation) often underwent premature senescence. In *Swietenia*, leaves also endured photoinhibition, but did not display premature abscission or photooxidation. However, at the end of the most prolonged acclimation period (180 d) saplings of both species had developed new leaves, fully acclimated to the new light environment. Shade leaves of both species remained vigorous and healthy throughout the whole experiment period.

Photosynthetic traits in response to acclimation: P_{Nmax} was significantly higher in *Swietenia* than in *Minquartia* ($p<0.05$). In *Minquartia* the highest P_{Nmax} value (3.0 µmol(CO_2) m^{-2} s^{-1}) was recorded in 180-d-acclimated plants (Fig. 1*A*). In this species, the lower P_{Nmax} values ranged from 1.14 to 1.38 µmol(CO_2) m^{-2} s^{-1}, at 30 and 60 days of exposure to full sun, respectively (Fig. 1*A*). In *Swietenia*, the higher P_{Nmax} values were observed at acclimation periods of 60 to 180 d (3.0–4.0 µmol(CO_2) m^{-2} s^{-1}) and the lower [about 1.25 µmol(CO_2) m^{-2} s^{-1}] in control plants (shade leaves, Fig. 1*A*). In *Minquartia*, but not in *Swietenia*, P_{Nmax} values of control plants were higher than those found in plants acclimated for 30 days (Fig. 1*A*). On average g_s was higher in *Swietenia* [0.07 mol(H_2O) m^{-2} s^{-1}] than in *Minquartia* [0.04 mol(H_2O) m^{-2} s^{-1}] with little difference among acclimation treatments ($p>0.05$, Table 1). P_{Npot} differed significantly ($p<0.05$) both between species and acclimation times. Both species reached higher P_{Npot} values [10 to 12 µmol(CO_2) m^{-2} s^{-1}] after 150 days in the open (Fig. 1*B*). However, *Swietenia* tended to show high P_{Npot} values [about 10 µmol(CO_2) m^{-2} s^{-1}] after an acclimation period of 60 days (Fig. 1*B*). Theta (Θ) values oscillated between 0.65 and 0.75 over acclimation periods, but without differences between species ($p>0.05$, Table 1). The highest Θ value (0.9) was found in shade leaves of control plants. Φ was higher in *Swietenia* than in *Minquartia* ($p<0.05$, Table 1), but regardless of tree species no effect of acclimation times on Φ was found (Table 1).

There were significant differences between species and acclimation times ($p< 0.05$) in both the V_{cmax25} (V_{cmax} normalized at 25°C) and J_{max25} (J_{max} at 25ºC). In *Minquartia*, the lower V_{cmax25} values [6.5 µmol(CO_2) m^{-2} s^{-1}] were observed at 30 and 60 d under full sunlight, and the higher [14.7 µmol(CO_2) m^{-2} s^{-1}] after 120–180 d in the open (Fig. 1*C*). In *Swietenia*, V_{cmax25} values oscillated between [10 µmol(CO_2) m^{-2} s^{-1}] in shade leaves and about 30 µmol(CO_2) m^{-2} s^{-1} after 90–180 d at high irradiance (Fig. 1*C*). In *Minquartia*, J_{max25} values ranged from 20 µmol(electron) m^{-2} s^{-1} at 30–60 d under full sunlight to 35 µmol(electron) m^{-2} s^{-1} following

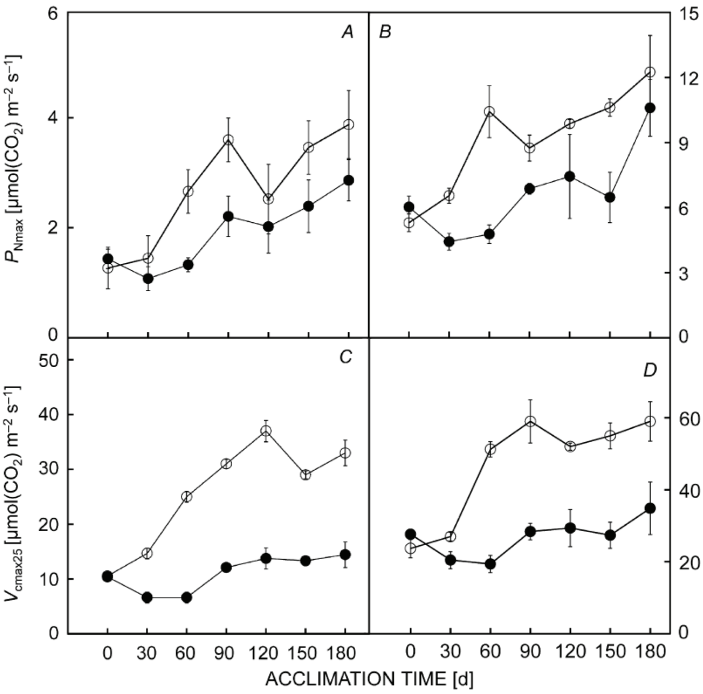

Fig. 1. Light-saturated photosynthesis (P_{Nmax}, *A*), potential photosynthesis (P_{Npot}, *B*), maximum carboxylation velocity of Rubisco at 25ºC (V_{cmax25}, *C*) and maximum electron transport rate at 25ºC (J_{max25}, *D*) in saplings of *Minquartia guianensis* (*filled circles*) and *Swietenia macrophylla* (*open circles*) in response to full-sun acclimation. Each symbol represents the mean of five plants and two leaves per plant (± 1 SD, standard deviation).

Table 1. Stomatal conductance (g_s), convexity parameter of the light response curve (Θ) and apparent quantum yield (Φ) in saplings of *Minquartia guianensis* and *Swietenia macrophylla* in response to full sun acclimation. Each value represents the mean of five plants (± SE). Means followed by *the same letter* within a row (means of species) are not significantly different (*t*-test, $p>0.05$). For p values over acclimation times: ^{NS} – not significant ($p>0.05$); * – significant at $p\leq0.05$.

Acclimation time [d]	g_s [mol(H_2O) m^{-2} s^{-1}]		Θ [unitless]		Φ [mol(CO_2) mol^{-1}(photon)]	
	Minquartia	*Swietenia*	*Minquartia*	*Swietenia*	*Minquartia*	*Swietenia*
0	0.033 ± 0.003	0.04 ± 0.005	0.89 ± 0.01	0.92 ± 0.03	0.02 ± 0.03	0.02 ± 0.03
30	0.04 ± 0.004	0.04 ± 0.0001	0.67 ± 0.03	0.73 ± 0.02	0.01 ± 0.04	0.02 ± 0.02
60	0.04 ± 0.001	0.12 ± 0.04	0.65 ± 0.01	0.67 ± 0.03	0.02 ± 0.03	0.05 ± 0.01
90	0.04 ± 0.004	0.11 ± 0.02	0.66 ± 0.04	0.74 ± 0.04	0.02 ± 0.02	0.04 ± 0.06
120	0.03 ± 0.006	0.07 ± 0.02	0.72 ± 0.01	0.70 ± 0.04	0.03 ± 0.03	0.04 ± 0.06
150	0.02 ± 0.005	0.05 ± 0.002	0.75 ± 0.03	0.75 ± 0.03	0.03 ± 0.02	0.03 ± 0.03
180	0.05 ± 0.006	0.06 ± 0.02	0.67 ± 0.03	0.73 ± 0.02	0.02 ± 0.04	0.03 ± 0.01
Mean	0.04^{b}	0.07^{a}	0.72^{a}	0.75^{a}	0.021^{b}	0.033^{a}
p values	0.5^{NS}	0.5^{NS}	0.0134^{*}	0.0128^{*}	0.25^{NS}	0.13^{NS}

Table 2. Specific leaf area (SLA), monthly rate of leaf production per plant (MRLP), height growth rate (HGR) and diameter growth rate (DGR) in saplings of *Minquartia guianensis* and *Swietenia macrophylla* in response to full-sun acclimation. Each value represents the mean of five plants (± SE). Means followed by *the same letter* within a row (means of species) are not significantly different (*t*-test, $p>0.05$). For p values over acclimation times: ^{NS} – not significant ($p>0.05$); * – significant at $p\leq0.05$; ** – significant at $p\leq0.01$.

Acclimation time [d]	SLA [m^2 kg^{-1}(DM)]		MRLP [leaf $month^{-1}$]		HGR [mm $month^{-1}$]		DGR [mm $month^{-1}$]	
	Minquartia	*Swietenia*	*Minquartia*	*Swietenia*	*Minquartia*	*Swietenia*	*Minquartia*	*Swietenia*
0	23.37 ± 0.73	25.70 ± 1.80	0.20 ± 0.05	0.26 ± 0.10	1.66 ± 0.13	5.3 ± 0.64	0.11 ± 0.01	0.14 ± 0.03
30	16.17 ± 0.46	19.52 ± 0.67	–1.12 ± 0.21	–0.42 ± 0.16	2.54 ± 0.30	5.4 ± 0.88	0.13 ± 0.01	0.20 ± 0.02
60	16.68 ± 0.98	19.63 ± 0.11	–0.83 ± 0.15	–0.08 ± 0.14	3.22 ± 0.36	8.4 ± 0.89	0.14 ± 0.02	0.38 ± 0.03
90	19.71 ± 0.02	19.61 ± 0.02	–0.41 ± 0.13	0.56 ± 0.15	3.23 ± 0.53	11.2 ± 1.18	0.14 ± 0.02	0.49 ± 0.04
120	19.52 ± 0.67	18.31 ± 0.50	–0.12 ± 0.09	0.80 ± 0.09	3.25 ± 0.54	15.2 ± 1.58	0.15 ± 0.02	0.60 ± 0.07
150	17.2 ± 0.61	18.72 ± 0.43	0.22 ± 0.03	0.82 ± 0.10	3.27 ± 0.57	22.6 ± 3.06	0.15 ± 0.03	0.76 ± 0.09
180	17.17 ± 0.92	16.22 ± 0.38	0.31 ± 0.02	1.06 ± 0.12	3.49 ± 0.64	28.0 ± 4.72	0.17 ± 0.07	0.86 ± 0.13
Mean	18.55^{b}	19.67^{a}	-0.25^{b}	0.43^{a}	3.18^{b}	13.73^{b}	0.14^{b}	0.49^{b}
p values	0.018^{*}	0.01^{**}	0.001^{**}	0.001^{**}	0.312^{NS}	0.001^{**}	0.5^{NS}	0.001^{**}

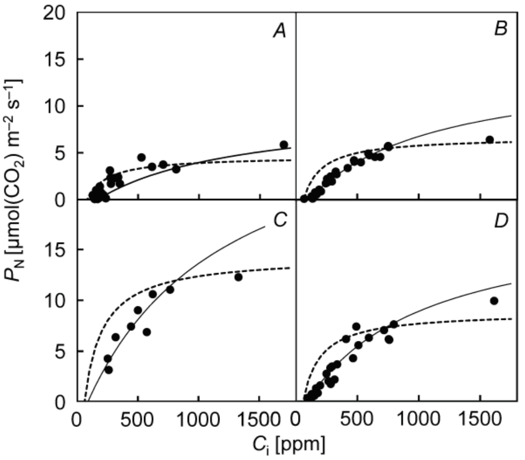

Fig. 2. Photosynthetic rate (P_N) as a function of the intercellular CO_2 concentration (C_i) in saplings of *Swietenia macrophylla (A,C)* and *Minquartia guianensis* (*B,D*) recorded for control plants kept under shading (*A,B*) or in 180-day-acclimated plants (*C,D*). Predicted P_N when carbon assimilation is limited by either Rubisco activity (P_c in equation 1, *solid line*) or electron transport rates (P_j in equation 2, *dashed line*) is also shown. Each point represents the mean of two leaves per plant.

an acclimation period of 180 d (Fig. 1*D*). In *Swietenia*, on the other hand, the lower J_{max25} values were observed in shade leaves of control plants and the higher [about 60 μmol(electron) m^{-2} s^{-1}] after 90–180 d in the open (Fig. 1*D*). That is, following the same trend observed in Rubisco activity. Irrespective of acclimation times, photosynthetic rates (P_N) were limited by Rubisco activity at ambient CO_2 concentration and by electron transport rate at high [CO_2]. As the same trend was observed over acclimation times for the P_N/C_i relationship, only data for control (Fig. 2*A,B*) and 180-d-acclimated plants (Fig. 2*C,D*) are shown.

Chl fluorescence in response to acclimation: In *Minquartia*, the F_v/F_m ratio showed a sharp decrease soon after transfer of plants to high irradiance (Fig. 3*A*). After reaching a minimum (0.25 after 15 d in the open, Fig. 3*A inset*), the F_v/F_m values gradually increased to attain a maximum of 0.75, after an acclimation period of about four months. Saplings of *Swietenia* also suffered from photoinhibition, but in comparison with *Minquartia*, photoinhibition of *Swietenia* was less severe (Fig. 3*B*). In this species the minimum F_v/F_m values was about 0.6; more than double the minimum F_v/F_m value observed in *Minquartia*. At the end of an acclimation period of 80 d for *Swietenia* and 120 d for *Minquartia* leaves recovered from photoinhibition. Then, the F_v/F_m ratio had reached values close to those observed in control plants (Fig. 3).

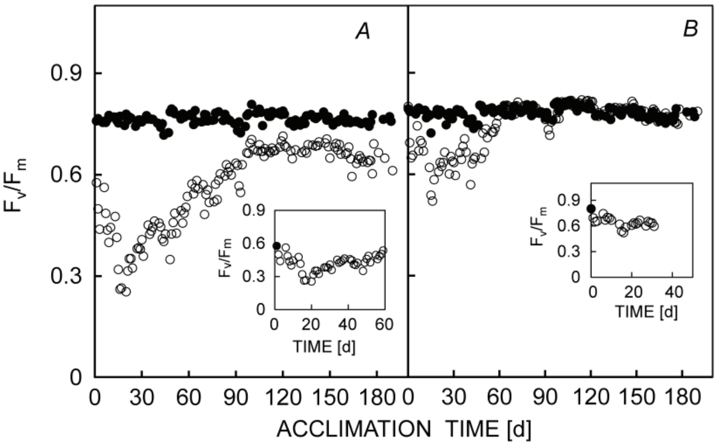

Fig. 3. Maximal quantum yield of PSII (F_v/F_m) in saplings of *Minquartia guianensis* (*A*) and *Swietenia macrophylla* (*B*) as a function of acclimation time, either in control plants (*filled circles*) or full-sun-acclimated plants (*open circles*). Each symbol represents the mean of two leaves per plant.

Specific leaf area and plant growth: SLA was higher in *Swietenia* than in *Minquartia*, and in both species the effect of acclimation time was significant ($p<0.05$, Table 2). Plants acclimated to full sun light produced thicker leaves, and thereby lower SLA values than those of control plants.

MRLP of acclimated *Swietenia* more than tripled the value recorded in control plants after four months in the open (Table 2). Whereas, in *Minquartia* control plants and 180-d-acclimated plants produced leaves almost at the same rate, 0.2–0.3 leaf month^{-1}. In addition, it is worth noting that *Minquartia* consistently lost leaves during the first four months after transfer to full sun, due to premature senescence, which led to a negative MRLP over acclimation periods (–0.25 leaf month^{-1}, Table 2). Whereas, in *Swietenia* loss of leaves after 30 d under full sun was offset or more than compensated by new leaf production in the brighter environment. Indeed, in *Swietenia* leaves per plant significantly increased after 60 d in the open, up to reach 1.1 leaf month^{-1} at the end of the experiment period. Sapling growth rates (diameter and height) of *Swietenia* were higher than those observed in *Minquartia*. DGR ranged from 0.14 to 0.86 mm month^{-1} for *Swietenia* against 0.11 to 0.17 mm month^{-1} for *Minquartia* (Table 2). In the more prolonged acclimation treatment, HGR of *Swietenia* was eight times faster than that of *Minquartia* (28 *vs.* 3.5 mm month^{-1}, Table 2). DGR of 180-d-acclimated plants of *Swietenia* was six times faster than in control plants (0.86 *vs.* 0.14 mm month^{-1}, Table 2); whereas for *Minquartia*, DGR for acclimated and control plants did not differ significantly ($p>0.05$, Table 2). *Minquartia* grew slower than *Swietenia*, which is consistent with growth rates expected for late successional species.

Discussion

Photosynthetic traits: Mean daily irradiance [15.7 mol(photon) m^{-2} d^{-1}] recorded during the experiment period is about 25% lower than that reported by Dias (2009) for a remote area at the top of a 40 m high tower in Central Amazonia. This discrepancy can be attributed to the fact that some tall trees growing around the experiment area cast shadow on acclimating saplings both early in the morning and in the afternoon, which reduced total amount of light received on a daily basis. P_{Nmax} values observed in this study are similar to those found by Silvestrini *et al.* (2007) in species of different successional stages, *Trema micrantha* (pioneer) and *Hymenaea courbaril* (late successional). The lack of a photosynthesis plateau after a given acclimation period (*i.e.* P_{Npot} tended to increase with acclimation time, particularly in *Swietenia*) suggests that even at the end of the more prolonged acclimation period (180 d) the maximum potential for carbon uptake was not reached in *Swietenia* acclimated plants. This hypothesis is consistent with the finding that the highest P_{Npot} value found in *Swietenia* was 45% lower than those observed by Marenco *et al.* (2001) for trees growing in an open field plantation.

In comparison with *Minquartia*, the higher P_{Nmax} values observed in *Swietenia* during the acclimation process can be attributed to the capacity of leaves of this species to endure high irradiance without suffering severe photoinhibitory damage, as has been observed in early and mid-successional species after transfer to high irradiance (Yamashita *et al.* 2000, Kitao *et al.* 2006). Stomatal conductance (g_s) was lower than values often reported for saplings of Amazonian tree species under natural condition (Mendes and Marenco 2010), which suggests that somehow acclimation to high irradiance induces reduction in total pore area, perhaps by affecting stomatal size. In both species, higher Θ values were found in control plants, which suggests a lower investment in Rubisco protein in shade leaves (Ogren 1993). Across species and acclimation times, Θ values observed in this study are within the range of those reported by others (Marenco and Vieira 2005, Magalhães *et al.* 2009). Φ values found in *Swietenia* and *Minquartia* over acclimation times were similar. This is in agreement with Björkman (1981) who suggests that Φ tends to remain unaltered irrespective of light conditions during growth. Φ values found in *Minquartia* are similar to those observed in *Hydrophyllum virginianum, Aesculus glabra*, and *Quercus rubra,* three late successional species (Bazzaz and Carlson 1982). Our Φ values although within the range for measurements conducted at ambient oxygen- and CO_2 concentrations (Björkman 1981) are lower than potential values, about 0.08 mol(CO_2) mol^{-1} (photon) obtainable in a low oxygen (2%) and CO_2-saturated atmosphere (Björkman 1981). Across species, V_{cmax25} and J_{max25} values (Fig. 1*C,D*) are in the bottom range of values often reported for C_3 plants (Wullschleger 1993, Kositsup *et al.* 2010). For example, Manter and Kerrigan (2004) observed that V_{cmax} ranged between 20 and 75 µmol(CO_2) m^{-2} s^{-1} in broad-leaved species. Wullschleger (1993) reported that most J_{max} values range between 50 and 200 µmol(electron) m^{-2} s^{-1}. This indicates that shade leaves of control plants had allocated a low amount of assimilates and nitrogen to synthesize Rubisco protein. On the other hand, leaves of acclimated plants although fully expanded apparently had not reached the potential photosynthetic capacity for the species, perhaps because most nutrients and assimilate available for growth were used for producing new leaves and structural tissues instead of increasing cell structure (*e.g.* enlarging palisade cells or increasing size and number of chloroplasts) of individual leaves. The large difference between species on gas-exchange characteristics (*e.g.* V_{cmax} and J_{max}) indicates that models that describe daily and seasonal carbon gain through assimilation should take into account interspecific differences among species for reliable estimates of ecosystem carbon assimilation. Regardless of the acclimation period, photosynthetic rates measured at ambient [CO_2] were limited by the maximum carboxylation velocity of Rubisco, whereas J_{max} limited carbon assimilation at high [CO_2], which is consistent with the results reported by Sage and Kubien (2007).

Chl fluorescence: The sharp decline in F_v/F_m values after transfer to high irradiance indicates the occurrence of severe damage to PSII reaction centers (Osmond 1994), particularly in *Minquartia*. Less photoinhibitory damage observed in *Swietenia* (higher F_v/F_m values) indicates that photoprotective mechanisms operate more efficiently in *Swietenia*. Photoprotection includes use of energy for electron transport (*e.g.* photosynthesis, photorespiration) and heat dissipation, which is associated with the xanthophyll cycle (Demmig-Adams and Adams 2006). A key plant feature often associated with shade tolerance is the low content of xanthophyll cycle pigments (Valladares and Niinemets 2008). This may explain the drastic decline in F_v/F_m values observed in *Minquartia* just after transition to full sun, as the excess light energy neither used in electron transport nor in heat dissipation determines the rate of photoinhibition (Kato *et al.* 2003). Recovery from photoinhibition over time is most likely related to an increase in levels of pigments related to the xantophyll cycle (Havaux *et al.* 2000) and proteins involved in photosynthesis (Walters 2005). Decreases in F_v/F_m values caused by excessive light were also observed by others (Ribeiro *et al.* 2005, Magalhães *et al.* 2009). In *Cariniana legalis*, Ribeiro *et al.* (2005) observed that the F_v/F_m ratio dropped from 0.7 in low light to about to about 0.30 under high irradiance. At the end of the longest acclimation period, saplings of *Minquartia*, although had reached 80% recovery in the F_v/F_m ratio, were unable attain the same F_v/F_m values recorded in control plants. This suggests that in this species entire recovery from photoinhibition under full sun takes more than six months to occur.

Specific leaf area and plant growth: SLA values reported in this study either for *Swietenia* or *Minquartia* are higher than those often observed in mid-successional or late successional species (Reich *et al.* 1995). Marenco *et al.* (2001) reported SLA values of 10.4 m^2 kg^{-1}(DM) for *Swietenia* growing in an open field, which is 60% lower than SLA values observed after an acclimation period of 180 d. Reich *et al.* (1995) also observed lower SLA values in either mid-successional or late successional species. This leads us to conclude that although leaves produced in the open were acclimated to high irradiance (particularly in *Swietenia*), the maximum photosynthetic capacity of these leaves was lower than expected, even at the end of most prolonged acclimation treatment.

It has been shown that there is an inverse relationship between SLA and nitrogen content (and thereby Rubisco leaf protein) per unit leaf area (Evans and Poorter 2001), which may explain the low photosynthetic rates in shade leaves of control plants. Compared with early successional, late successional species often have lower SLA (Reich *et al.* 1995). Marenco and Vieira (2005) also observed lower SLA in *Minquartia* than in *Goupia glabra* (an early successional species) across a light gradient in the forest understorey. High growth rates in full-sun-acclimated plants concur with previous studies (*e.g.* Felfili *et al.* 1999). During plant development, light regime affects leaf structure and assimilate partitioning and hence, plants grown at low light intensity often have a high shoot/root ratio and thinner and larger leaves (Poorter 1999). We conclude that *Minquartia* and *Swietenia* respond in different ways to sudden exposure to full solar radiation and that the acclimation period to full sun affects distinctively photosynthetic traits of examined species. Sudden plant exposure to high irradiance cause photoinhibition which was most pronounced in *Minquartia*. In this species (but not in *Swietenia*) photoinhibition can evolve to photooxidation of upper leaves, which may lead to premature senescence. In well watered plants, recovery from photoinhibition occurs at the end of an acclimation period of 80 days in *Swietenia*. It is remarkable that in plants of *Minquartia* that undergo severe stress during full-sun acclimation, substantial recovery from photoinhibition (80%) is only observed after 120 d. This information can be useful in afforestation and reforestation projects where seedlings grown under greenhouse conditions are often used to restore forest cover. The high capability of *Swietenia* to adjust leaf physiology in response to exposure to full sunlight makes this species an attractive candidate to be tested in reforestation programs, where species with high acclimation potential are recommended for accelerating forest recovery and successional processes of deforested lands.

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