

Photosynthetic analyses of two native Atlantic Forest species in regenerative understory of eucalyptus plantation

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ABSTRACT

Gas exchange, chlorophyll *a* fluorescence, and photosynthetic pigments of *Xylopia sericea* A. St.-Hil. and *Siparuna guianensis* Aubl. were evaluated during the rainy season and the dry season (2009-2010) in three understories with different ecological conditions (irradiance, water availability, and temperature) located in the União Biological Reserve (known as REBIO União), at Rio de Janeiro State, a natural forest understory, eucalyptus understory under regeneration, and understory of eucalyptus plantation with 18-year-old trees that were removed 1 year before. The lowest values of F_v/F_m e F_m/F_o were observed in the exposed understory for both seasons, with lower values in the dry season, suggesting that reduced water availability potentializes the photoinhibitory process. For both species of the exposed understory it is suggested the occurrence of photoprotection, given that an increased proportion of carotenoid pigments in relation to the chlorophylls were verified. Both species still exhibited dynamic photoinhibition after 1 year of exposure to full sunlight (exposed understory) in both seasons, but more markedly so in the dry season, though they belong to early stages of ecological succession. Based on the results, it is suggested that these species are indicated for planting in degraded areas and that the cutting of eucalyptus trees as management practice should be performed in a gradual manner, during the rainy season, in order to minimize stress on these species.

Keywords: *Corymbia citriodora*, dehydration, photoinhibition, *Siparuna guianensis*, *Xylopia sericea*

Abbreviations: *A*: net photosynthetic rate; *C_i*: internal CO₂ concentration; DMSO: organic solvent dimethylsulfoxide; *E*: transpiration; *ETR*: electron transport rates; *g_s*: stomatal conductance; *IWUE*: intrinsic water-use efficient; MANOVA: multifactorial analysis of variance; NPQ: non-photochemical dissipation; PSII: photosystem II; qP: photochemical dissipation; ROS: reactive oxygen species.

INTRODUCTION

The elevated incidence of solar radiation and the low water availability of the soil are foremost among the factors that limit the establishment and productivity of the plants. The excessive increase in the incidence of light above the utilization capacity of photosynthesis can promote a condition of stress known as 'photoinhibition' (Barber and Anderson, 1992). Photoinhibition can be detected in alterations in the assimilation of CO₂ and in the emission of chlorophyll *a* fluorescence, characterized by a reduction in the amount of photosynthesis that occurs accompanied by alterations in photosystem II (PSII) activities (Krause and Weis, 1991).

Plants exposed to high levels of irradiance experience a reduction in the quantum efficiency of PSII and consequent changes in the directing of photochemical energy by means of NPQ (Castro et al., 1995; Demmig-Adams et al., 1996; Santos Jr. et al., 2006; Gonçalves et al., 2007). Some species under this condition may present increased photosynthetic assimilation (Lichtenthaler and Burkart, 1999) and higher levels of carotenoids, which aid in the protection against photoinhibition (Demmig-Adams et al., 1989).

According to Baker (1993), plants subjected to moderate water stress do not exhibit decreased quantum yields of PSII. However, under severe stress conditions, inhibitory effects generally occur, characterized by significant drops in quantum yield. The effect of the water deficit combined with the high rates of irradiance can lead to a significant reduction in photosynthetic assimilation and *E* as a result of stomatal closing (Prado et al., 2004).

The Atlantic Forest is one of the global biodiversity hotspots (Myers et al., 2000). While the state of Rio de Janeiro, Brazil, maintains 16.7% of its original coverage of Atlantic Forest (SOS Mata Atlântica, 2001), a large portion of this remaining area is distributed in isolated fragments located in hilly regions and mountain ranges with few forested areas in the low-lying regions. By the beginning of the 21st Century, Brazil had assumed the ranking as the sixth country in the world in terms of area occupied by monocultures of exotic tree species, such as *Eucalyptus* and *Pinus*, that totaled 5 million ha (Bacha and Barros, 2004).

Despite the expectation that the cultivation of such monocultures will continue to expand as a result of increased demands for energy and wood (Fonseca

et al., 2009), there have been efforts to discourage the presence of exotic species from protected areas, such as the União Biological Reserve (REBIO União), at Rio de Janeiro, where the process of natural regeneration of understory is occurring in abandoned plantations of eucalyptus (*Corymbia citriodora*). In these understory, *Xylopia sericea* A. St.-Hil. (*Annonaceae*) and *Siparuna guianensis* Aubl. (*Siparunaceae*) — both in the initial phase of ecological succession — are among the species with the highest value of importance (Evaristo et al., 2011) and are also common in the forest border areas of the REBIO União. In accordance with the management plans of the REBIO União, the removal of eucalyptus trees has been initiated, a practice that has promoted the appearance of forest clearings and has exposed the understory to new microclimatic conditions. Within this context the ecophysiological characteristics of *X. sericea* and *S. guianensis* were evaluated in three forest areas with distinct light intensity conditions (forest understory, eucalyptus understory, and exposed understory in eucalyptus plantations) and water availability (the rainy and dry seasons), in order to answer the following questions: (1) do the plants still undergo photoinhibition 1 year after the clearing of tree canopies? (2) do the species present different photosynthetic responses as a result of environment? (3) is there seasonal variation in the photosynthetic capacities of the species in these three environments?

Such information will be useful for management plans for abandoned monocultures of tree species and will aid in the evaluation of the use potential of these species in the ecological restoration of degraded areas in tropical climates.

MATERIAL AND METHODS

Study area, plant material and sampling period: REBIO União (22° 27' 30" S and 42° 02' 14" W) occupies an area of 2,550 ha, with approximately 2,200 ha of Atlantic Forest and 220 ha of eucalyptus plantations (*C. citriodora*). The climate in the region is tropical humid, with an average annual temperature of 25°C and rainfall of approximately 1,920 mm year⁻¹, with 85% of the rainfall concentrated between October and April (Figure 1). According to the IBGE (1992), the vegetation has lowland and submontane formations and is classified as Dense Tropical Rainforest. According to Miranda et al. (2007) the soil of the plantations is dystrophic red-yellow podzolic.

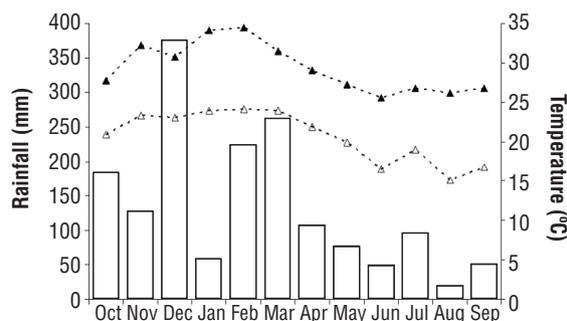


Figure 1. Meteorological data recorded between October 2009 and September 2010 with an automatic weather station (Davis, GroWeather, EUA) in the REBIO União, Brazil. Precipitation: Δ minimum temperature; \blacktriangle maximum temperature.

Individuals of *X. sericea* (1.5 to 2.0 m in height) and *S. guianensis* (1.5 to 2.5 m in height) were selected in three environments with differing lighting and tree canopy conditions in this reserve:

1. Forest Understory (FU): understory on the border of secondary forest. Area with highest species richness and dense canopy formed by native tree species; understory composed principally of bushes, small trees, and plants. This environment presents the lowest light intensity;
2. Eucalyptus Understory (ECU): understory of the eucalyptus (*C. citriodora*) plantation of 41 years that has received no silvicultural intervention for 13 years. Canopy basically composed of eucalyptus trees. The floristic diversity of this understory is low, with *X. sericea* and *S. guianensis* comprising the most common species (Evaristo et al., 2011). Among the environments, it presents an intermediary level of light intensity;
3. Exposed Understory (EXU): understory of the eucalyptus (*C. citriodora*) plantation with 15-year-old trees that were removed 1 year before execution of the present study. The understory has thus been exposed to full sunlight since then, making it the environment with the highest degree of light intensity.

Six individuals of each species were analyzed in both the FU and EXU, and nine individuals were selected in the ECU. Two data collections were performed in the rainy season (November 2009 and February 2010) and two collections were performed in the dry season (July and

September of 2010). Thus, a total of 12 measurements on FU and EXU and 18 measurements on ECU were carried out for both seasons for the photosynthetic analyses, as described below.

Gas exchange: A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), C_i ($\mu\text{mol mol}^{-1}$), g_s ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and E ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were determined using a portable, closed system infrared gas analyzer (Ciras-2, PP System, UK). Measurements were performed between 0800 h and 1030 h (period corresponding to the maximum g_s), used with a clamp-on leaf cuvette that exposed 170 mm^2 of leaf area. The saturating lights for both species were determined by the response curve of photosynthesis to light; they were of $700 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *X. sericea* and $1,100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *S. guianensis*. The leaf chamber conditions were: $380 \mu\text{mol mol}^{-1} \text{ CO}_2$, $28 \pm 3^\circ\text{C}$, and 70% humidity. The $IWUE$ ($\mu\text{mol CO}_2 / \text{mol}^{-1} \text{ H}_2\text{O}$) was calculated by A/g_s ratio. Each measurement was carried out on two newly matured leaves per plant and was repeated on each plant for each site.

Chlorophyll a fluorescence: These measurements were carried out at between 1100 and 1200 h using a pulse amplitude modulation fluorimeter (FMS 2, Hansatech Instruments Ltd., Norfolk, UK). Prior to measurements, intact and healthy leaves were dark adapted using the leaf-clips for 30 min and then exposing the dark-acclimated leaf surface to modulated irradiance (measuring beam of weak far-red irradiance, approximately $6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 660 nm) to obtain the minimum fluorescence yield (F_o) when all PSII reaction centers are open. A saturating white irradiance pulse of 0.8-second duration and intensity of $6,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ was then applied to temporarily close all photosystem reaction centers to determine the maximum fluorescence yield (F_m) of the dark-adapted sample. The samples were then illuminated for 30 seconds with actinic irradiance ($300 \mu\text{mol m}^{-2} \text{ s}^{-1}$). After the illumination (when the fluorescence yield reached a stable and low steady-state level, F_s), the maximal fluorescence yield (F_m') was determined by applying a saturating white irradiance pulse for 0.8 seconds. Then the actinic irradiance was turned off and a far-red illumination was quickly turned on to obtain complete re-oxidation of the primary electron acceptor of PSII to determine the minimal fluorescence yield (F_o') when all PS II reaction centers are open in steady state irradiance. Light-adapted variable fluorescence (ΔF) was obtained as $\Delta F = F_m' - F_s$. The following chlorophyll a fluorescence emission parameters were recorded: F_o (minimum fluorescence), F_m (maximum fluorescence), F_o/F_m (maximum quantum yield of PSII), $\Delta F/F_m'$ (effective quantum yield of PSII), qP (coefficient of photochemical quenching of fluorescence), and NPQ (non-photochemical quenching of fluorescence). All procedures were adapted from Genty et al. (1989) and Van

Kooten and Snel (1990). $\Delta FF_m'$ was used to estimate the apparent ETR , according to Bilger et al. (1995). The ratio of fluorescence yields for open and closed states (F_m/F_o) were calculated. Each measurement was carried out on two newly matured leaves per plant and was repeated on each plant for each site.

Photosynthetic pigment contents: Three discs with 63.6 mm² each were taken from the same leaves analyzed for gas exchange and chlorophyll *a* fluorescence from the FU, ECU, and EXU sites. Three discs were sliced and placed in plastic tubes in the dark with a liquid containing 5 mL of DMSO. After 5 days, the extract was analyzed in a spectrophotometer at wavelengths of 480, 649, and 665 nm. The photosynthetic pigments were quantified according to Wellburn (1994) for chlorophyll *a*, chlorophyll *b*, and carotenoids. The total chlorophyll, chlorophyll *a/b*, and total chlorophyll/carotenoids ratios were calculated. All the laboratory procedures were carried out in a low light environment. The values were expressed in nmol mm⁻².

Statistical analysis: A descriptive analysis of data was made and the normality and homogeneity of variances were tested. The data of gas exchange, chlorophyll *a* fluorescence, and photosynthetic pigments were analyzed by MANOVA (Zar, 1996). The factors considered were species, site, and season. After that, the means were compared using Tukey's test. Pearson's correlation coefficients (*r*) were calculated between the *A* and g_s (Zar, 1996).

RESULTS

Gas exchange: The MANOVA results (Table 1) indicated that C_i and $IWUE$ exhibited interaction between two factors (season *versus* site), while *A*, *E*, and g_s

showed interaction of three factors (season *versus* site *versus* species).

In both seasons, for *X. sericea* the values of *A* were lower in the FU when compared with the ECU, while the values of the EXU did not differ from the other environments (Figure 2A). Comparing the different environments, it is possible to verify that a standard similar to that observed for *A* was only verified for $IWUE$ in the dry season (Figure 2E). In the rainy season, the *X. sericea* plants of the ECU presented higher averages of C_i , *E*, and g_s (Figures 2B, C, and D), while $IWUE$ was higher in this environment in the dry season (Figure 2E). The gas exchange variables of the other environments did not show seasonal differences ($p > 0.05$).

For *S. guianensis*, the *A*, *E*, and g_s variables were higher in the EXU plants in relation to the other environments during the rainy season (Figures 2F–I). In the EXU, the seasonal variations were more visually apparent, as plants presented lower values of *A*, C_i , *E*, and g_s in the dry period (Figures 2F, G, H and I). In the environment with intermediary conditions (ECU), only C_i and g_s presented lower values in the dry season (Figures 2G and I). The ECU and EXU plants exhibited higher $IWUE$ values in the dry season (Figure 2J).

When comparing species, it is possible to observe that *S. guianensis* presented higher averages of *A* (Figures 2A and F), *E* (Figures 2C and H), and g_s (Figures 2D and I) in relation to *X. sericea* in the EXU during the rainy period. The $IWUE$ variable was higher in *S. guianensis* in the FU and in the EXU during the dry period (Figures 2E and J). *X. sericea* exhibited a higher C_i value than *S. guianensis* in the dry season, both in the FU and the EXU (Figures 2B and G).

Table 1. Results of multivariate analysis of variance (MANOVA) performed for the gas exchange of the species in REBIO União, Brazil.

Effect	<i>A</i>		C_i		<i>E</i>		g_s		$IWUE$	
	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Species	9.21	0.0028*	30.99	0.0000*	1.23	0.2683	0.64	0.4262	27.66	0.0000*
Season	7.35	0.0075*	54.15	0.0000*	32.25	0.0000*	60.28	0.0000*	55.91	0.0000*
Site	14.78	0.0000*	2.07	0.1301	7.72	0.0006*	6.92	0.0013*	1.70	0.1862
Species*Season	4.06	0.0455*	8.04	0.0052*	11.09	0.0011*	8.93	0.0033*	10.55	0.0014*
Species*Site	13.12	0.0000*	2.73	0.0687	9.35	0.0002*	6.38	0.0022*	1.50	0.2265
Season*Site	7.71	0.0006*	5.46	0.0051*	4.03	0.0197*	14.66	0.0000*	7.31	0.0009*
Species*Season*Site	3.08	0.0486*	1.43	0.2415	5.87	0.0035*	5.64	0.0043*	2.53	0.0828

*Significant difference ($p \leq 0.05$)

Species: *Xylopia sericea* and *Siparuna guianensis*; seasons: rainy and dry; sites: FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

A: net photosynthetic rate; C_i : internal CO₂ concentration; *E*: transpiration; g_s : stomatal conductance; $IWUE$: intrinsic water-use efficient.

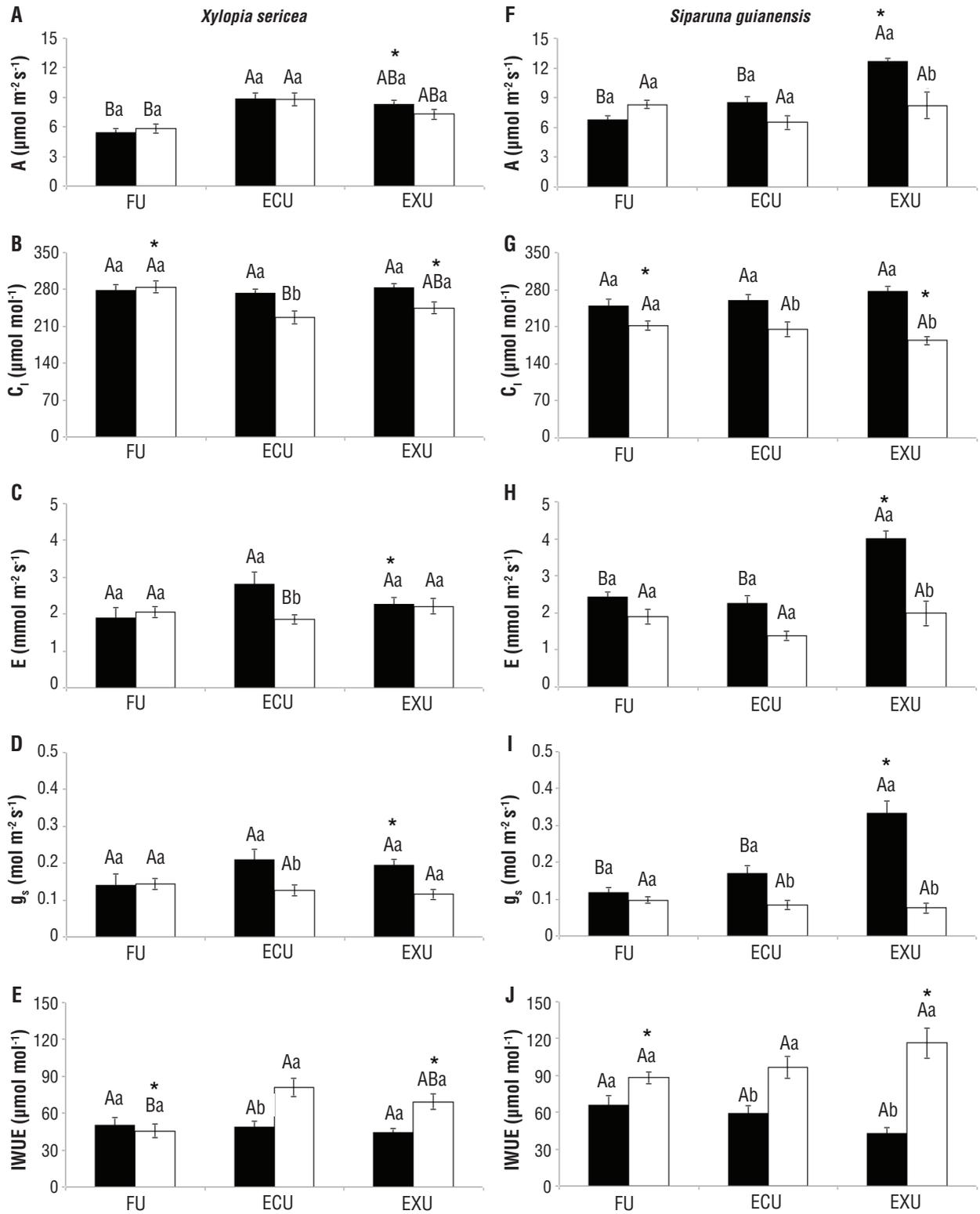


Figure 2. Gas exchange of *Xylopia sericea* (left column) and *Siparuna guianensis* (right column) in REBIO União, Brazil. (A and F) Net photosynthetic rate (A), (B and G) internal CO₂ concentration (C_i), (C and H) transpiration (E), (D and I) stomatal conductance (g_s), and (E and J) intrinsic water-use efficient (IWUE). FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12). Rainy season (■); Dry season (□). Upper case letters compare the three environments in the same season. Lower case letters compare the two seasons in the same environment. Asterisks (*) indicate differences among species of the same environment and season. The data represent mean±standard error. Distinct letters indicate significant differences (p≤0.05).

The correlation between A and g_s (Table 2) was tested to determine how much of the carbon assimilation is dependent on the stomatal opening. There was a significant positive correlation between these parameters in the dry period for *S. guianensis* in all three environments and for *X. sericea* in the ECU and in the EXU. In the rainy season only *X. sericea* presented this significant correlation in the FU and the ECU (Table 2).

Chlorophyll a fluorescence: The MANOVA results (Table 3) indicated that the parameters $\Delta F/F_m'$ and qP showed interaction between three factors (season *versus* site *versus* species). The F_v/F_m and F_m/F_o ratios and the NPQ showed interaction for season *versus* site, while *ETR* exhibited interaction for the species *versus* site.

For the *X. sericea* of the EXU, the lowest values of $\Delta F/F_m'$ were registered in the dry season and lower

values of F_v/F_m and F_m/F_o were registered in both seasons in relation to the other environments (Table 4). During the dry season qP presented a lower average in the FU plants. The NPQ indicated that there was higher dissipation in the FU and EXU plants in *X. sericea* when compared to the ECU plants, during the rainy period. In the dry season, however, this parameter was higher in the EXU plants.

With respect to seasonal variation, *X. sericea* only exhibited significant differences in F_v/F_m and F_m/F_o values in the EXU plants, with the values for these variables being lower in the dry season. In the ECU plants, a higher average qP was registered in the dry period in relation to the rainy one, while the effective quantum yield ($\Delta F/F_m'$) and the *ETR* were higher in the EXU plants in the rainy period when compared with the dry one (Table 4).

Table 2. Correlation between net photosynthetic rate (A) and stomatal conductance (g_s) of *Xylopiya sericea* and *Siparuna guianensis* in REBIO União, Brazil

	FU		ECU		EXU	
	r	p-value	r	p-value	r	p-value
<i>Xylopiya sericea</i>						
Rainy	0.90	0.0001*	0.83	0.0001*	0.51	0.0906
Dry	-0.01	0.9753	0.67	0.0022*	0.61	0.0334*
<i>Siparuna guianensis</i>						
Rainy	0.34	0.2836	0.43	0.0759	0.13	0.6942
Dry	0.60	0.0396*	0.79	0.0001*	0.97	0.0001*

*Positive correlation.

FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

Table 3. Results of multivariate analysis of variance (MANOVA) performed for the chlorophyll fluorescence a parameters of the species in REBIO União, Brazil.

Effect	F_v/F_m		F_m/F_o		$\Delta F/F_m'$		ETR		qP		NPQ	
	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Species	11.53	0.0009*	30.59	0.0000*	0.54	0.4616	58.39	0.0000*	1.28	0.2601	25.34	0.0000*
Season	51.19	0.0000*	39.51	0.0000*	31.46	0.0000*	10.97	0.0012*	0.50	0.4794	42.96	0.0000*
Site	137.74	0.0000*	258.84	0.0000*	26.25	0.0000*	19.86	0.0000*	25.13	0.0000*	16.34	0.0000*
Species*Season	0.39	0.5334	0.04	0.8473	3.91	0.0499*	0.01	0.9533	5.34	0.0222*	0.01	0.9555
Species*Site	1.65	0.1958	0.38	0.6813	1.33	0.2687	7.56	0.0007*	1.42	0.2452	8.80	0.0002*
Season*Site	46.33	0.0000*	36.96	0.0000*	31.94	0.0000*	2.42	0.0922	7.66	0.0007*	5.08	0.0073*
Species*Season*Site	0.52	0.5985	0.07	0.9325	4.34	0.0146*	1.20	0.3052	8.70	0.0003*	0.67	0.5129

*Significant difference ($p \leq 0.05$)

F_v/F_m : maximum quantum yield of PSII; F_m/F_o : ratio of fluorescence yields for open and closed states; $\Delta F/F_m'$: effective quantum yield of PSII; *ETR*: apparent electron transport rate; qP: coefficient of photochemical quenching of fluorescence; NPQ, nonphotochemical quenching of fluorescence. Species: *Xylopiya sericea* and *Siparuna guianensis*; seasons: rainy and dry; sites: FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

Table 4. Chlorophyll *a* fluorescence parameters of *Xylopia sericea* and *Siparuna guianensis* in REBIO União, Brazil.

Sp.	Env.	Chlorophyll <i>a</i> Fluorescence Parameters					
		F_v/F_m	F_m/F_o	$\Delta F/F_m'$	ETR	qP	NPQ
<i>Xylopia sericea</i>	FU						
	Rainy	0.813±0.004 Aa	5.4±0.1 Aa	0.64±0.01 Aa	80.5±1.8 Aa	0.86±0.01 Aa	0.30±0.04 Aa
	Dry	0.815±0.005 Aa	5.5±0.1 Aa	0.63±0.02 Aa	79.7±1.9 Aa	0.85±0.01 Ba	0.38±0.06 Ba
	ECU						
	Rainy	0.811±0.004 Aa	5.3±0.1 Aa	0.65±0.01 Aa	82.0±1.2 Aa	0.86±0.01 Ab	0.16±0.01 Ba
	Dry	0.808±0.007 Aa	5.3±0.2 Aa	0.67±0.01 Aa	84.5±1.2 Aa	0.90±0.01 Aa	0.27±0.03 Ba
<i>Siparuna guianensis</i>	EXU						
	Rainy	0.759±0.007 Ba	4.2±0.1 Ba	0.63±0.01 Aa	79.3±1.2 Aa	0.90±0.01 Aa	0.35±0.05 Ab
	Dry	0.614±0.023 Bb	2.8±0.1 Bb	0.53±0.02 Bb	66.7±2.7 Bb	0.90±0.01 Aa	0.59±0.03 Aa
	FU						
	Rainy	0.828±0.002 Aa	5.8±0.1 Aa	0.60±0.01 Ba	76.2±1.4 Ba	0.81±0.02 Ca	0.44±0.05 Aa
	Dry	0.828±0.002 Aa	5.8±0.1 Aa	0.63±0.01 Aa	80.0±1.1 Aa	0.85±0.01 Aa	0.47±0.05 Ba
<i>Siparuna guianensis</i>	ECU						
	Rainy	0.824±0.002 Aa	5.7±0.1 Aa	0.67±0.01 ABa	83.8±0.8 ABa	0.89±0.01 Ba	0.34±0.02 Ab
	Dry	0.820±0.004 Aa	5.6±0.1 Aa	0.63±0.01 Aa	79.2±1.1 Aa	0.87±0.01 Aa	0.51±0.04 ABa
	EXU						
	Rainy	0.784±0.074 Aa	4.6±0.1 Ba	0.68±0.01 Aa	85.6±1.0 Aa	0.94±0.01 Aa	0.35±0.03 Ab
	Dry	0.665±0.068 Bb	3.3±0.2 Bb	0.51±0.03 Bb	63.7±4.1 Bb	0.87±0.01 Ab	0.58±0.05 Aa

Upper case letters compare the three environments in the same season for each species. Lower case letters compare the two seasons in the same environment. Distinct letters indicate significant differences ($p \leq 0.05$). Data represent mean±standard error.

FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

Sp.: species; Env.: environment; F_v/F_m : maximum quantum yield of PSII; F_m/F_o : ratio of fluorescence yields for open and closed states; $\Delta F/F_m'$: effective quantum yield of PSII; ETR: apparent electron transport rate; qP: coefficient of photochemical quenching of fluorescence; NPQ: nonphotochemical quenching of fluorescence.

Siparuna guianensis exhibited a lower F_m/F_o average in the EXU plants in relation to the plants in the other environments, while F_v/F_m , $\Delta F/F_m'$, and ETR only responded in this manner in the dry season (Table 4). In the rainy season, $\Delta F/F_m'$ and ETR exhibited intermediary values in the ECU, being higher in the EXU plants in relation to those in the FU. *S. guianensis*, in the EXU, demonstrated higher qP during the rainy season. There was higher NPQ in the EXU plants in comparison with those in the FU, with intermediary values in the ECU plants in the dry season (Table 4).

When comparing *S. guianensis* values between the rainy and dry seasons significant differences were only verified for F_v/F_m , F_m/F_o , $\Delta F/F_m'$, ETR, and qP in the EXU plants, with the highest averages registered during the rainy season. The NPQ was higher in the dry season in the ECU and EXU plants (Table 4).

In the EXU plants, the F_v/F_m values were lower than 0.78 in both species and seasons. Comparisons of the species reveal no significant difference between *X. sericea*

and *S. guianensis* for any of the chlorophyll *a* fluorescence variables (Table 4).

Photosynthetic pigments: The MANOVA results (Table 5) indicated that chlorophyll *a*, chlorophyll *a/b* ratio, total chlorophyll/carotenoids ratio, and total chlorophyll showed interaction between three factors (season *versus* site *versus* species). The carotenoids showed seasonal factors interact with the site, while chlorophyll *b* showed interaction with the factors species and site.

The plants of both species presented lower levels of chlorophylls and total chlorophyll/carotenoids ratios in the EXU plants during both seasons of the year (Table 6). Lower values of chlorophyll *a*, carotenoids, and total chlorophyll were observed in the rainy season as compared to the dry season in the ECU plants. In *S. guianensis* in the EXU levels of carotenoids were higher during the dry period in relation to the rainy period. In species comparisons, plants in the EXU during the dry season presented pigment levels that were superior in *S. guianensis* (Table 6).

Table 5. Results of multivariate analysis of variance (MANOVA) performed for the content of photosynthetic pigments of the species in REBIO União, (RJ), Brazil.

Effect	Chl a		Chl b		C _{x+c}		Chl a/b		Chl _{Total} /C _{x+c}		Chl _{Total}	
	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Species	40.35	0.0000*	23.81	0.0000*	4.37	0.0383*	0.00	0.9807	32.45	0.0000*	33.25	0.0000*
Season	25.12	0.0000*	0.82	0.3664	17.84	0.0000*	41.10	0.0000*	5.51	0.0202*	17.02	0.0001*
Site	74.12	0.0000*	30.22	0.0000*	8.87	0.0002*	8.70	0.0003*	109.74	0.0000*	52.59	0.0000*
Species*Season	9.08	0.0030*	12.86	0.0005*	6.33	0.0129*	4.45	0.0366*	1.63	0.2035	11.03	0.0011*
Species*Site	7.33	0.0009*	7.27	0.0010*	2.59	0.0782	0.95	0.3884	7.76	0.0006*	7.19	0.0010*
Season*Site	5.19	0.0066*	0.20	0.8227	10.13	0.0001*	4.36	0.0144*	5.54	0.0048*	4.27	0.0156*
Species*Season*Site	5.48	0.0050*	0.60	0.5509	1.95	0.1456	4.31	0.0151*	3.48	0.0332*	3.70	0.0270*

*Significant difference ($p \leq 0.05$).

Species: *Xylopiia sericea* and *Siparuna guianensis*; seasons: rainy and dry; sites: FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

Chl: chlorophyll; C_{x+c}: carotenoids.

Table 6. Content of photosynthetic pigments (nmol mm⁻²) of *Xylopiia sericea* and *Siparuna guianensis* in REBIO União (RJ), Brazil.

Sp.	Env.	Photosynthetic Pigments					
		Chl a	Chl b	C _{x+c}	Chl a/b	Chl _{Total} /C _{x+c}	Chl _{Total}
<i>Xylopiia sericea</i>	FU						
	Rainy	0.31±0.014 Aa	0.11±0.006 Aa	0.06±0.003 Aa	2.9±0.1 Aa	7.4±0.2 Aa*	0.42±0.020 Aa
	Dry	0.32±0.020 Aa	0.10±0.007 Aa	0.06±0.004 ABa	3.1±0.1 ABa	7.1±0.1 Aa	0.42±0.027 Aa
	ECU						
	Rainy	0.29±0.005 Ab	0.11±0.005 Aa	0.06±0.001 Ab	2.7±0.1 Ab*	7.3±0.2 Aa	0.40±0.009 Ab
	Dry	0.36±0.015 Aa	0.11±0.007 Aa	0.07±0.003 Aa	3.5±0.1 Aa	6.5±0.1 Ab	0.47±0.022 Aa
<i>Siparuna guianensis</i>	EXU						
	Rainy	0.20±0.012 Ba	0.07±0.002 Ba	0.06±0.006 Aa	2.8±0.1 Aa	4.8±0.3 Ba	0.27±0.014 Ba
	Dry	0.17±0.008 Ba*	0.06±0.003 Ba*	0.05±0.002 Ba*	3.0±0.1 Ba	4.4±0.3 Ba	0.23±0.010 Ba*
	FU						
	Rainy	0.31±0.006 Aa	0.11±0.002 Aa	0.05±0.002 Aa	2.9±0.0 Aa	8.4±0.2 Aa*	0.42±0.008 ABa
	Dry	0.36±0.010 Aa	0.12±0.006 Aa	0.06±0.002 Ba	3.1±0.1 Aa	7.7±0.2 Aa	0.48±0.015 Aa
<i>Siparuna guianensis</i>	ECU						
	Rainy	0.33±0.010 Ab	0.11±0.004 Aa	0.06±0.002 Ab	3.1±0.1 Aa*	7.3±0.1 Ba	0.44±0.013 Ab
	Dry	0.39±0.017 Aa	0.12±0.007 Aa	0.08±0.004 ABa	3.3±0.1 Aa	6.7±0.1 Ba	0.51±0.023 Aa
	EXU						
	Rainy	0.24±0.009 Ba	0.09±0.004 Aa	0.06±0.002 Ab	2.7±0.1 Aa	5.4±0.1 Ca	0.33±0.012 Ba
	Dry	0.24±0.015 Ba*	0.08±0.005 Ba*	0.08±0.006 Aa*	2.9±0.1 Aa	4.0±0.2 Cb	0.32±0.020 Ba*

Upper case letters compare the three environments in the same season for each species; lower case letters compare the two seasons in the same environment; distinct letters indicate significant difference ($p \leq 0.05$). Data represent mean±standard error.

*Difference between the species within the same environment and season.

Sp.: species; Env.: environment; Chl: chlorophyll; C_{x+c}: carotenoids; FU: Forest Understory (n=12); ECU: Eucalyptus Understory (n=18); EXU: Exposed Understory (n=12).

DISCUSSION

The values of the gas exchange variables registered in the present study for *X. sericea* and *S. guianensis* are situated within the parameters observed for other tropical tree species (Baker et al., 1997; Eschenbach et al., 1998; Marenco et al., 2001; Costa and Marenco, 2007; Gonçalves et al., 2009; Silva et al., 2010). The species *X. sericea* and *S. guianensis* exhibited high values of correlation between A and g_s in the dry season, suggesting

that their stomata respond significantly to the variations in light and water availability. Nevertheless, in the rainy season, only *X. sericea* presented positive correlation between A and g_s . The absence or low correlation between A and g_s demonstrate that both the g_s and photosynthesis are parameters that respond concomitantly to a series of factors that interact in a coordinated yet highly complex manner (Costa and Marenco, 2007). The high irradiance and low CO₂ concentration stimulate the opening of stomata, while the excessive E and low humidity cause

a reduction in leaf water potential that can lead to the closing of stomata (Hsiao, 1973; Marengo et al., 2006). Because of this, it is common to register an absence or low correlation between A and g_s in natural lighting and air humidity conditions.

With respect to the environmental variation, E presented a pattern similar to the responses observed for g_s . *X. sericea*, however, did not respond in the same way as *S. guianensis*, demonstrating that the responses to variations in lighting differ between the species. According to Marengo and Lopes (2007), this is justified by the fact that the control of stomatal movement and of E results from the interaction of diverse exogenous factors, such as light, CO_2 , temperature, and water tension, as well as endogenous ones, such as nutrition and the presence of hormones in the plant.

In *S. guianensis* in the EXU the stomatal closing represented a principal cause of the reduction in the photosynthetic rate and in the E under conditions of water deficit. This reduction resulted in the decreased availability of CO_2 in the substomatal chambers. Similar results were reported for young *Carapa guianensis* plants submitted to the suspension of irrigation (Gonçalves et al., 2009). The reduction of the E and g_s in *S. guianensis* resulted in higher intrinsic efficiency in the use of the water ($IWUE$) during the dry season. These results suggest that, for *S. guianensis*, the lower availability of water was an important stress factor in the plants submitted to higher irradiance (EXU) in the dry season. However, when water was not a limiting factor, a better photosynthetic performance was observed in this species in conditions of higher light intensity. Similar results were reported by Silva et al. (2010) in studies carried out on the pioneer species *Byrsonima sericea* during the dry and rainy season in the REBIO União.

The decline in the photosynthetic assimilation in *S. guianensis* in the dry season compared with the rainy season in the EXU was accompanied by a decrease in F_v/F_m , F_m/F_o , $\Delta F/F_m'$, ETR , and total chlorophyll/carotenoids ratios, as well as an increase in NPQ and carotenoid levels. These results were observed in conjunction with lower carbon assimilation due to the decrease in g_s . These responses can be seen as an important protective mechanism under conditions of water stress in *S. guianensis*. Similar results were observed by Faria et al. (1996; 1998) in studies of the *Quercus ilex* and *Quercus sùber* species, which emphasized the high degree of coordination between stomatal compartment, photosynthetic capacity, and photoprotective mechanisms. *X. sericea* exhibited a similar response to *S. guianensis* in relation to the parameters F_v/F_m , $\Delta F/F_m'$, and NPQ in the EXU.

The drop in observed values of F_v/F_m , in *X. sericea* and *S. guianensis*, in the EXU plants, is indicative of photoinhibition (Krause and Weis, 1991; Pandey et al., 2005). Reductions in the F_v/F_m ratio are reported as photoinhibition in tropical tree species subjected to elevated levels of irradiance (Dias and Marengo, 2007) and plants exposed to stress (Paiva et al., 2009; Gonçalves et al., 2010). One of the targets of the photoinhibitory process is the dimer D1/D2, a chief structural protein complex of PSII. The ability of a plant to regenerate from such damage will determine its capacity for supporting this stress factor (Krause and Weis, 1991; Barber and Anderson, 1992; Maxwell and Johnson, 2000; Dias and Marengo, 2006).

According to Osmond (1994) when plants are exposed to high light levels that damage the photosynthetic apparatus, the result can be chronic photoinhibition that affects both quantum efficiency as well as maximum photosynthetic rate. The chronic photoinhibition is the process in which the electron flux through the reaction center of PSII is reduced because of the irreversible D1-D2 heterodimer protein inactivation and/or reaction center of PSII disassembly. In strongly photoinhibited leaves, most of the xanthophyll cycle carotenoids are retained as violaxanthin and so low levels of sustained thermal energy dissipation decrease the maximum photosynthetic rate (Alves et al., 2002). On the other hand, the term dynamic photoinhibition (Osmond, 1994) has been adopted to describe the transient and rapidly reversible decreases in maximal PSII quantum efficiency. Dynamic photoinhibition is a photoprotective energy dissipation process involving the xanthophyll cycle in the absorbed light dissipation as heat without changing the rates of photosynthetic electron transport and maintaining the maximal photosynthetic rate (Adams III et al., 2006). Dynamic photoinhibition is typically attributed to midday depressions in the photosynthetic yield occurring between noon and the early afternoon hours. This process involves the regulation of photosynthetic quantum yield in a very predictable manner over the course of the day by thermal dissipation of excess energy from the xanthophyll cycle that represents the non-photochemical quencher (NPQ) (Demmig Adams and Adams III, 1992; Adams III et al., 2006). Thus the results of the present study suggest that both species suffered dynamic photoinhibition in the EXU since a reduction of the net photosynthesis rate (A) was not observed despite the fall in the F_v/F_m .

The F_v/F_m ratio reflects the maximum quantum efficiency of the PSII and it is used as a sensitive indicator of the photosynthetic performance of the plant. According to Bjorkman and Demmig (1987), when a plant is under

stress-free conditions, the F_v/F_m ratio should vary between 0.80 and 0.83. Thus we assume that both EXU species was subject to conditions of stress during both seasons, with that stress being greater during the dry season. Nevertheless, qP values did not demonstrate a significant reduction in the plants analyzed in the exposed understory. Given that qP reflects the proportion of the open state PSII reaction centers, the high values of qP can result either from high rates of electron transfer around PSII or from the occurrence of high non photochemical quenching processes (Chaloub et al., 2010) and thus maintain good photosystem health (Lage-Pinto et al., 2008).

The same response pattern was verified for the F_m/F_o ratio in the studied plants. According to Reigosa and Weiss (2001), this ratio bears a direct relation with the water potential of the plant. Under conditions of severe water stress, this ratio can be reduced to as low as 1 (with no production of F_v). Thus we suggest that both species presented water stress in the EXU in the dry season, a pattern that was unconfirmed in the other environments studied. These data are corroborated by the significant decrease in the quantum yield of the PSII (F_v/F_m) in the EXU during the dry period, which also indicates that the plants have responded to the effects of water stress (Baker, 1993). The relationship between the water deficit and the enhancement of photoinhibition was reported by several authors (Alves et al., 2002, Pastenes et al., 2005, Zhou et al., 2007).

Plants are susceptible to photoinhibition particularly when high light occurs in conjunction with other stressful environmental conditions, such as low water availability. This occurs, for example, when the eucalyptus monodominant plantation trees were removed (EXU), or where there is little canopy vegetation (ECU) to prevent light penetration. In these cases of major light penetration there is rapid evaporation of soil water (Cornic, 1994).

However, plants have different mechanisms to prevent or tolerate photoinhibition. According to Alves et al. (2002), photoprotection can be prevented by accessory pigments, such as carotenoids, which act as a protective system, since they prevent ROS formation. Carotenoids also help in the dissipation of excess absorbed energy as heat. The authors also mention the importance of metabolic pathways such as antioxidant enzymes and a rapid response to excessive irradiation. This response is characterized by an increase in thermal dissipation in the antenna and/or reaction center of PSII associated with the generation of transthylakoidal potential (ΔpH).

The results of the NPQ parameter suggest that during the dry season there was an increase in heat dissipation in

the plants of *X. sericea* in the EXU. In a study of *Phaseolus vulgaris* (L.), Santos et al. (2009) also registered higher NPQ values under conditions of increased light intensity and water stress. In leaves, the dissipation of the energy available through other processes beyond those related to the photosynthetic metabolism of carbon (such as heat) is an important defense mechanism in the presence of water stress or natural conditions (Chaves et al., 2002). The NPQ is among the chief mechanisms used to prevent or reduce the damage caused by the excess of light energy that reaches the photosynthetic apparatus (Maxwell and Johnson, 2000).

The presence of lower levels of chlorophyll *a*, *b*, and total chlorophylls in the EXU is corroborated by the findings of Morais et al. (2007), who also observed lower levels of these pigments in tropical tree species (*Bertholletia excelsa*, *Carapa guianensis*, and *Dipteryx odorata*) exposed to increased light intensity. Chlorophyll is constantly synthesized and destroyed in the presence of light (photo-oxidation), but under high light intensity there is a higher rate of decomposition, with the established equilibrium occurring at a lower concentration (Kramer and Kozlowski, 1979). Thus plants exposed to high light intensities exhibited reduced levels of chlorophyll when compared with plants subjected to moderate lighting (Boardman, 1977). A higher level of carotenoids was observed in the dry season in relation to the rainy season in the ECU for *S. guianensis*. Silva et al. (2010) obtained similar findings for *Byrsonima sericea* in the REBIO União, suggesting that the increase in pigment content in the dry season may have occurred due to lower relative water content in the leaves caused by the decrease in water availability during this season.

The total chlorophyll/carotenoid ratio was lower in the EXU for both species. These results are corroborated by Sarijeva et al. (2007), who studied *Ginkgo biloba* L. and *Fagus sylvatica* L., and by Silva et al. (2010), who studied *Byrsonima sericea* in contrasting light environments. Accumulating more carotenoids is a physiological strategy for the protection of plants against photoinhibition because these pigments efficiently dissipate the excess of solar radiation in a non-destructive manner, avoiding damage to the PSII (Demmig-Adams et al., 1989), which in turn corroborate the non-photochemical (NPQ) dissipation data discussed above. NPQ is basically related to the dissipation of the excess light energy in the form of heat in the level of PSII (Ruban and Horton, 1995).

Though *S. guianensis* in the EXU did not exhibit significant difference in the chlorophyll *a* and *b* contents between the dry and rainy season, the carotenoid levels

were greater during the dry season, while the total chlorophyll/carotenoid ratio was lower. These results suggest that in addition to light intensity, water availability is also an important factor that influences carotenoid content in *S. guianensis*. The species *X. sericea* presented seasonal variation in pigment levels with responses similar to those verified in *S. guianensis* only in the ECU.

Though both species belong to early stages of ecological succession, they still exhibited dynamic photoinhibition after 1 year of exposure to full sunlight (EXU) in both the seasons, but more markedly so in the dry season. In general, both species presented similar photosynthetic responses in relation to environments. Based on these results, in a context of management actions for tropical environments, it is possible to suggest in phases of restoration that: (1) these species are indicated for planting in degraded areas due to its high resistance to dry and high light intensity conditions; and 2) considering that the species present higher degrees of photoinhibition during the dry season, it is recommended that the cutting of eucalyptus trees as management practice should be performed in a gradual manner, during the rainy season, in order to minimize stress on these species.

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