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Chlorophyll fluorescence and initial growth of two liana species, *Cuspidaria sceptrum* (Cham.) L.G. Lohmann and *Fridericia florida* (DC) L.G. Lohmann, under changes of natural light conditions

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Abstract

The physiological alterations as well as the growth were evaluated in seedlings of two liana species, *Cuspidaria sceptrum* and *Fridericia florida*, which were transferred from shade to full sunlight conditions. We cultivated one group of seedlings under full sunlight, the second group under natural shade beneath canopy, and the third group was transferred from shade to full sunlight. Reductions on the potential quantum yield of PSII (F_v/F_m) during predawn was detected under full sunlight, but these responses were more pronounced when the plants were transferred from shade to full sunlight. *C. cuspidaria* lost all leaves developed under shade a few days after transfer. However, at 60 d after transfer, new leaves were already developed and their F_v/F_m values were similar to full sunlight plants. *F. florida* was able to maintain its leaves after transfer and exhibited gradual recovery of F_v/F_m over time. The initial photoinhibition influenced growth responses of these liana species, in spite of their heliophyte character as adult plants.

Additional key words: biomass partitioning; light acclimation; nonphotochemical quenching; photoinhibition; relative growth rate; tropical semideciduous forest; specific leaf area; woody vines.

Introduction

Lianas (woody vines) are plants that are rooted in the soil and rely on other plants as support for its growth and ascending to the canopy (Holbrook and Putz 1996, Wyka *et al.* 2013). Lianas decrease the growth of their host trees (Putz 1984, Toledo-Aceves and Swaine 2007) and have the potential to modify the traditional successional process by supressing tree seedling regeneration (Schnitzer *et al.* 2000, Schnitzer and Carson 2010, Martínez-Izquierdo *et al.* 2016). On the other hand, when compared to trees, lianas produce leaf litter enriched with phosphorous which could increase the nutrient availability where these plants are abundant (Cai and Bongers 2007). Furthermore, lianas contribute to the evapotranspiration of seasonal forests (Restom and Nepstad 2001) and serve as a food source for animals and as a structural component of their habitat (Gentry 1991, Morellato and Leitão Filho 1996, Anbarashan and Parthasarathy 2013).

The presence of lianas represents an important characteristic that distinguishes temperate from tropical forests (Putz 1984, Gentry 1991, Schnitzer and Bongers 2011). A comparative study of floristic composition from several tropical semideciduous forests of the Southeast of Brazil found that lianas comprise about 52% to total wood species and that the mean similarity among forest sites was low (Santos *et al.* 2009). As pointed by the authors, these results reveal the importance of these plants for diversity maintenance of tropical semideciduous forests whose ecosystem has been threatened and fragmented by agricultural activities and urban expansion (Toniato and de Oliveira-Filho 2004, Prado Júnior *et al.* 2014).

Light varies continuously both in time and space in tropical semideciduous forests. Under canopy, the light intensity, which reaches the leaves, is extremely reduced and strongly depleted of photosynthetically active radiation and is high in the far-red region (Bazzaz 1979, Souza and Válio 2003). Conversely, the light environment in the interior of these forests may be drastically altered due to gap opening which can be created by the death of canopy trees or even by the fall of branches and leaves (Wirth *et al.* 2001, Nascimento *et al.* 2012, Venturoli *et al.* 2012, Souza *et al.* 2014).

Seedling survival and growth in these environments

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Abbreviations: Chl – chlorophyll; DAT – days after transfer, DM – dry mass, F_v/F_m – potential quantum yield of PSII, $\Delta F/F_m'$ – effective quantum yield of PSII, ETR – electron transport rate, NPQ – nonphotochemical quenching, RGR – relative growth rate, FSU – full sunlight, SH-FSU – shade–full sunlight, SH – shade.

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depend on adjustments at all levels of organization. Under the canopy, it is common to observe increases in the quantum yield of PSII and modifications of biomass distribution that contribute to maintenance of positive carbon balance (Lavinsky *et al*. 2014, Lestari and Nichols 2017). On the other hand, in gaps or forest edges, plants are exposed to high light intensity which promotes increases in relative growth rates and in root biomass (Mazzanatti *et al*. 2016). However, in open areas, the increase in light intensity is followed by higher temperatures and lower relative humidity. Such conditions may predispose plants continuously exposed to full sunlight to stress known as photoinhibition, which comprises a set of complex reactions that can lead to the reduction in photosynthesis or even in growth (Krause *et al*. 2012). Photoinhibition can increase when shaded plants are exposed to sudden increases in light intensity (Lovelock *et al*. 1994, Naramoto *et al*. 2006, Azevedo and Marenco 2012). The possible photoinhibition damage at the moment of gap opening may be minimized if plants exhibit efficient mechanisms of acclimation (Naidu and DeLucia 1997, 1998).

Compared to species that require high levels of light for their growth, as the pioneers, the shade-tolerant species tend to be more susceptible to photoinhibition and have a lower acclimation capacity under high-light intensity conditions (Yamashita *et al*. 2000, Krause *et al*. 2001, Einhorn *et al*. 2004, Dias and Marenco 2006, dos Anjos *et al*. 2012, Rabelo *et al*. 2013). Based on demand for light, lianas have been considered pioneer clearing-dependent plants (Dewalt *et al*. 2000). Indeed, many lianas grow better in clearings. Such distribution pattern gives us indications that these plants require high irradiance for their establishment and development (Lüttge 2008). The capacity to fix more carbon per unit leaf mass mainly during the dry season, to drive electron flow to photorespiration and use water efficiently gives lianas some characteristics that allow them to survive in high-light environments (Sanches and Válio 2008, Cai *et al*. 2009, Zhang *et al*. 2016).

Nevertheless, there are many lianas that germinate, survive, and grow beneath canopies, suggesting that these plants have traits that promote some level of shade tolerance (Sanches and Válio 2002, Cai *et al*. 2007, Celis and Avalos 2013, Avalos and Mulkey 2014, Yuan *et al*. 2016). Regardless, it is unclear how lianas respond to sudden increases in light intensity and the magnitude of probable photoinhibition when lianas are faced with such increases. For instance, some lianas increased the photosynthetic capacity and biomass accumulation when transferred from shade to full sunlight indicating that these species are able to respond quickly to alterations in light conditions (Toledo-Aceves and Swaine 2008, Avalos and Mulkey 2014). Regarding the role that lianas exert on forest dynamics (Schnitzer and Bongers 2011), it is important to understand the physiological and morphological changes during the initial phase of their development, since these responses would impact the succession process of semideciduous forests (Letcher and Chazdon 2012).

Cuspidaria sceptrum (Cham.) L.G. Lohmann and *Fridericia florida* (DC) L.G. Lohmann are two liana species belonging to the Bignoniaceae family. *C. spectrum* occurs in several states of Brazil, in areas of the Cerrado Biome (Brazilian savannas) and dry rocky outcrops, while *F. florida* has a more widespread distribution including the Amazon rainforest and the Atlantic rainforest, and also in Cerrado Biome (Lohmann and Taylor 2014, Vasconcelos *et al*. 2015). Considering that lianas begin their life in the soil of a tropical forest and then ascend to the canopy, these plants may experience extreme differences in light intensity and spectral quality during their growth (Lee and Richards 1991, Celis and Avalos 2013, Avalos and Mulkey 2014). Within this context, the aim of this work was: (*1*) to determine the physiological alterations in these liana species under contrasting natural light environments (shade and full sunlight) in a semideciduous forest and (*2*) to evaluate the magnitude of photoinhibition and growth when the seedlings were transferred from shade to full sunlight conditions, simulating changes in the light conditions that are found during the life history of lianas.

Materials and methods

Experimental conditions: The liana studied are native of semideciduous tropical forests of the Southeast of Brazil (48º12'22''W, 18º57'03''S) (Vargas and Araujo 2014). In these forests, both species occur mainly at edge forests, although juvenile seedlings of *F. florida* are also found in the interior of the forest. When adult, these lianas exhibit tendrils as a way to ascend to the canopy and present fruits that are wind-dispersed (Vargas and Araujo 2014). The climate of this region is classified as Cwa, with a dry season during the winter from April to September and a wet and warm season from October to March (Alvares *et al*. 2013). The average annual rainfall varies from 1,400 to 1,700 mm and the maximum temperatures vary between 27 and 30ºC with a minimum close to 18ºC (Haridasan and Araújo 2005). Ripe fruits were picked up from at least five individuals before their natural dispersal in September 2012. Afterwards, the fruits were brought to the laboratory, and then were cleaned. Seedlings were obtained from seeds germinated in Petri dishes at 25ºC under continuous white fluorescent light. Germinated seeds were transplanted to plastic bags (3 l) with a mixture of forest soil and sand in a proportion of 2:1. These seedlings were maintained in a nursey for initial establishment. In December 2012, when the seedlings presented the cotyledons and the first pair of expanded leaves, they were taken to an urban fragment of tropical semideciduous forest and randomly distributed into three groups of 15 seedlings: one group was set outside of the forest (full sunlight treatment: FSU), the second beneath the canopy of the forest (shade treatment: SH) and the third group consisted of the seedlings that were later transferred from the under canopy to the external forest area (shade–full sunlight treatment: SH-FSU). In this period, ten seedlings were used to determine initial dry mass (t_1) to compose the data of a relative growth rate. The seedlings were transferred from shade to full sunlight in June 2013 at day 173 and were maintained in these conditions for another 85 d. Until day 173, the seedlings survived under light-limiting conditions presenting around six leaves, indicating some level of shade tolerance in both species.

The transfer experiment was conducted in June because a period of acclimation to shade and sun conditions was required. The seedlings were kept well-watered during the whole period of the experiment. Therefore, the absence of rains during dry season did not affect the development of the seedlings.

The PPFD (λ = 400–700 nm) was recorded during the experiment under full sunlight and under canopy using a *LI-191SA* quantum sensor attached to a *LI-250A* datalogger (*Li-Cor, Inc.*, Lincoln, NE) on cloudless days near midday. Ten measurements close to the plants, in both conditions, were made. These measurements were also made during the occurrence of sun flecks in the under canopy. The mean values of PPFD and the standard error under full sunlight were 1,397.47 ± 110.94 µmol(photon) m^{-2} s^{-1} with maximum values of 2,185 µmol(photon) m^{-2} s^{-1}. Under shade conditions, the mean values were 11.24 ± 1.48 µmol(photon) m^{-2} s^{-1} but due to occurrence of sun flecks in the under canopy the PPFD can reach to 197.87 ± 22.02 µmol(photon) m^{-2} s^{-1}. The air temperature and relative humidity were measured with a thermohygrometer (*Instruterm HT-270*, China) on different days throughout the experiment. Under full sunlight, the mean values and standard error of air temperature was 29.74 ± 0.97ºC, while under canopy the air temperature was 24.85 ± 0.82ºC. The relative humidity was 38.4 ± 3.20% and 47.50 ± 2.88% under full sunlight and shade, respectively.

Chlorophyll (Chl) fluorescence: The daily courses of Chl fluorescence measurements were made using a pulse-amplitude photosynthesis yield analyser (*MINI-PAM*, *Walz*, Effeltrich, Germany) equipped with a leaf clip holder (model *2030-B*). The maximum fluorescence (F_m) and minimum fluorescence (F_0) were measured after 30 min of darkening with dark leaf clip (*DLC-8, Walz*) at predawn. From these data, the potential quantum yield of PSII was calculated as [$F_v/F_m = (F_m - F_0)/F_m$]. The maximum fluorescence (F_m’) and steady-state fluorescence (F) in the light-adapted state were measured following the methods described by Bilger *et al*. (1995). Saturated radiation pulses of 700 ms in duration were applied through a fiber-optic cable that was oriented 60º to the leaf surface. The angle and distance between the leaf and the fiber-optic cable were manually adjusted and set with the leaf clip holder. During the measurements of light-adapted parameters, care was taken not to shade the leaves with the fiber-optic probe and the leaf clip holder. The effective quantum yield of PSII was calculated as [$\Delta F/F_m' = (F_m' - F)/F_m'$] (Genty *et al*. 1989). The ETR through PSII was calculated as $ETR = \Delta F/F_m' \times 0.5 \times PPFD \times 0.84$ where PPFD corresponds to the photosynthetic photon flux density radiation incident at the leaf level, which was measured using the micro-quantum sensor of the leaf clip holder [µmol(photon) m^{-2} s^{-1}], 0.5 is a multiplication factor that assumes that the transport of a single electron requires the absorption of 2 quanta (White and Critchley 1999), and 0.84 is the photon absorbance at the leaf surface for wavelengths in the range of 400–700 nm. These measurements were made on plants under FSU and SH in April and August 2013 on five plants per treatment.

After this, in order to assess the magnitude of photoinhibition between shade plants after their transfer to full sunlight, the kinetics of Chl measurements were followed, including F_v/F_m, F_0/F_m, $\Delta F/F_m$’, ETR, and the NPQ, using five plants per treatment. The light intensity during ETR measurements was 1,163.40 ± 64.77 µmol (photon) m^{-2} s^{-1} under full sunlight and 28.89 ± 6.63 µmol (photon) m^{-2} s^{-1} under shade conditions. The NPQ was calculated as ($F_m - F_m$’)/F_m’ according to Maxwell and Johnson (2000), using F_m values at predawn to calculate this quenching parameter. All these measurements were made in totally expanded leaves two nodes below the shoot apex, each from a different plant. Among SH-FSU plants, these Chl fluorescence measurements were made in leaves that expanded under shade conditions, except in *C. sceptrum*, whose leaves, which had developed in shade, fell right after it was transferred to full sunlight. Although the leaf age was not necessarily the same, the Chl fluorescence measurements were always made on the leaves at the same stage of development. The fluorescence measurements were conducted at 3, 5, 19, 33, 47, 61, and 82 d after transfer (DAT) during predawn and midday.

Integrations of ETR and averages of NPQ over time were performed for all the treatments. The values of ETR in of µmol(electron) m^{-2} s^{-1} were converted to mol(electron) m^{-2} day^{-1}, using the sunrise and sunset local times. Then the function $F_{ETR}(t)$ was composed from a linear interpolation of the mean values of ETR data (Press *et al.* 1992). After, for each species, $F_{ETR}(t)$ was integrated in time as

$$\mathrm{ETR}_{int} = \int_{t_i}^{t_f} \mathrm{F}_{\mathbf{ETR}}(\mathrm{t})\mathrm{dt} \qquad (1)$$

where t_i is the third day and t_f is day 82. The confidence intervals were also calculated by direct integration in upper and lower time curves. The upper (lower) curve consists of the mean ETR values added (subtracted) to the standard deviation. For the dimensionless NPQ parameter, the average value $\overline{\mathrm{NPQ}}$ was defined by

$$\overline{\mathrm{NPQ}} = \frac{1}{t_f - t_i} \int_{t_i}^{t_f} F_{\mathrm{NPQ}}(t)dt\,, \qquad (2)$$

where the integral and confidence intervals were solved as described above.

Growth measurements: At the end of the experiment ten plants per treatment were used for growth measurements. The height from the base of the stem to the apex was measured using a millimetre ruler and the number of leaves was registered. The stem diameter was measured at 2 cm above the soil with a digital calliper. After this, all their leaves were collected, scanned, and the leaf area was determined using the *Image J 1.3v* software (http://rsb.info.nih.gov/ij/). The plants were separated into leaves, stems plus petioles, and roots. After washing the root system in running water for total removal of the substrate, each part of the seedling was dried at 70ºC for 48 h and then weighed. From the primary data of dry mass (DM) and leaf area, the following parameters were derived according to

Hunt (1982): specific leaf area (SLA – leaf area/leaf DM), leaf area ratio (LAR – leaf area/total plant DM), leaf mass ratio (LMR – leaf dry mass/total plant DM), stem mass ratio (SMR – stem + petiole DM/total plant DM) and root mass ratio (RMR – root DM/total plant DM). The RGR was calculated as RGR = $\ln(W_2) - \ln(W_1)/t_2 - t_1$, where W corresponds to total plant DM, 1 and 2 are initial and final plant DM, respectively, $t_2 - t_1$ correspond to the interval between harvests.

Statistical analysis: The influence of light conditions on Chl fluorescence measurements and growth parameters were evaluated by one-way analysis of variance (one-way *ANOVA*) followed by *Tukey*'s post-hoc test at 5% level after checking the normality and homogeneity of variance. When necessary, the natural log transformation was performed to satisfy the assumptions of parametric analysis (Sokal and Rohlf 1981).

Results

Chl fluorescence: The daily courses of Chl fluorescence carried out during April (2013) showed that predawn values of F_v/F_m under FSU were 0.67 and 0.69 for *C. sceptrum* and *F. florida*, respectively (Fig. 1*A*,*B*). In August, under the same conditions, both species exhibited F_v/F_m values close to 0.8 during predawn and sunset measurements, with decreases just around midday and afternoon (Fig. 1*C*,*D*). The same was not observed in SH plants, where values of F_v/F_m were high during both periods (Fig. 1). Distinct daily values of $\Delta F/F_m'$ were found among treatments. Low values of $\Delta F/F_m'$ were observed between 11:00 and 13:00 h for both species under FSU, which were significantly lower compared to SH plants (Fig. 2). Maximum ETR values were reached in August under FSU, whose values were *ca*. 116 μmol(electron) m^{-2} s^{-1} for both species (Fig. 2*G*,*H*).

Reductions of F_v/F_m during predawn were found as soon as the seedlings of *C. sceptrum* and *F. florida* were transferred from shade to full sunlight. In *C. sceptrum*, the lower values of F_v/F_m (0.21) were found at 5 DAT and were significantly lower when compared to plants kept continuously under SH and FSU (Fig. 3*A*) (*F* = 149.5, *p*<0.0001). After the first days of the transfer from shade to full sunlight, the leaves of all individuals of *C. secptrum* fell. However, at 61 DAT, *C. sceptrum* had new leaves which were completely expanded. These new leaves presented full recovery of F_v/F_m values, such as those found for SH and FSU plants (Fig. 3*A*). *F. florida* presented the lowest values of F_v/F_m (0.42) at 3 DAT when compared to SH and FSU plants with progressively increasing values during the period of acclimation (Fig. 3*C*) (*F* = 100.56, *p*<0.0001). At 82 DAT, *F. florida* attained similar values of F_v/F_m compared to those plants that were found under SH and FSU (Fig. 3*C*) (*F* = 1.46, *p* = 0.27). At midday, the reduction of F_v/F_m values was more pronounced when compared to predawn values for both species under FSU and for SH-FSU (Fig. 3*B*,*D*). In addition, significant increases in F_0/F_m were observed at the first days after transfer in both species during predawn and midday. The higher values were found in *C. scpetrum* at 5 DAT, but at the end of the experiment the values of F_0/F_m were lower and close to the plants under FSU conditions (Fig. 3*E*,*F*). *F. florida* showed increases in F_0/F_m ratio at 3 and 5 DAT. Then, the values of F_0/F_m were continuously decreasing during the experiment with similar values to the plants under FSU after 61 DAT (Fig. 3*G*,*H*).

Higher values of $\Delta F/F_m'$ were found in both species under SH conditions. These values varied from 0.65 to 0.72 in *C. sceptrum* and 0.58 to 0.75 in *F. florida* (Fig. 4*A*,*B*). When these species were transferred from shade to full sunlight, a sharp decline in $\Delta F/F_m'$ was found with values lower than 0.10 at 5 DAT (Fig. 4*A*,*B*). In *F. florida,* increases in $\Delta F/F_m'$ were observed at 19 DAT, whose values were similar to those plants kept under FSU (Fig. 4*B*). The ETR mean values were between 69.66 and

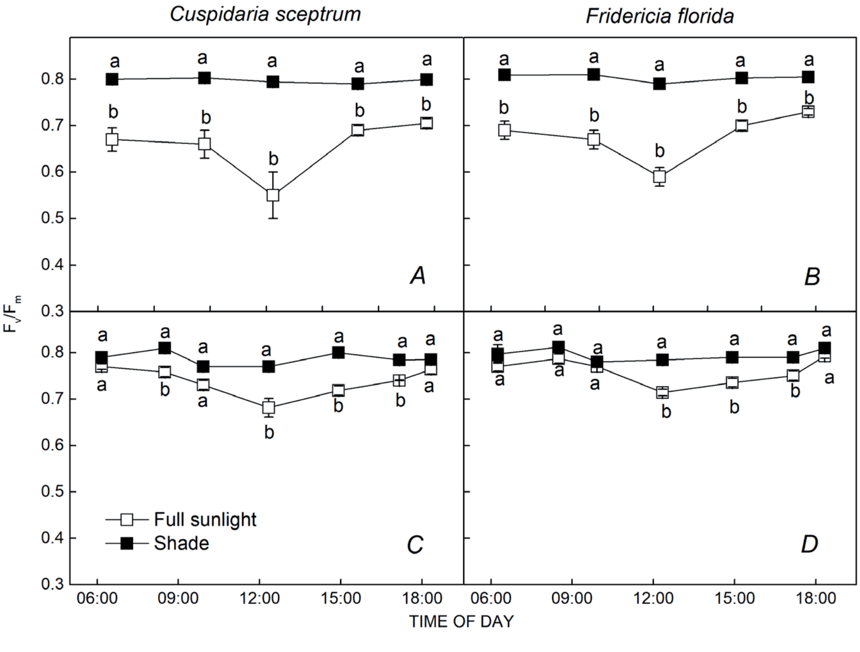

Fig. 1. Daily course of potential quantum yield of PSII (F_v/F_m) in seedlings of *Cuspidaria sceptrum* (*A*,*C*) and *Fridericia florida* (*B*,*D*) under full sunlight (*open square*) and shade (*filled square*) during April 2013 (*A*,*B*) and August 2013 (*C*,*D*). Data represent the mean ± SE in five leaves from different individuals. The values followed by *the same letters* do not differ according to *Tukey*'s test (*P*≤0.05).

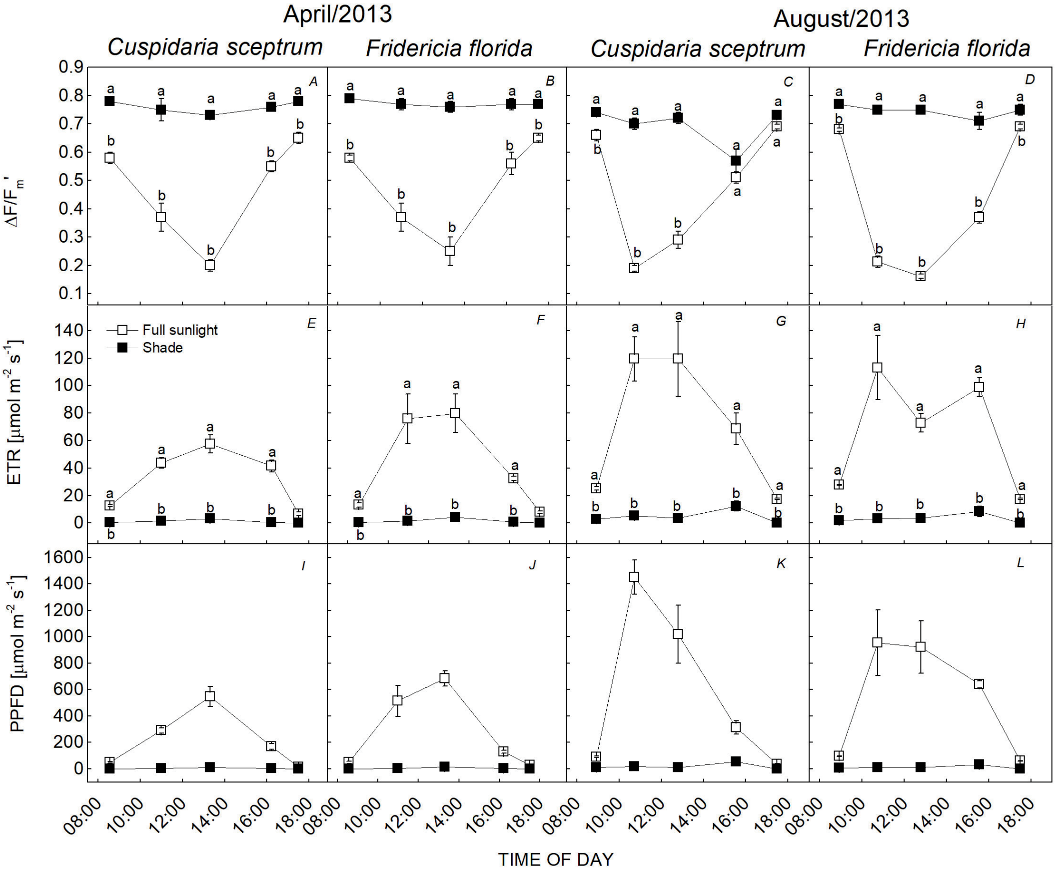

Fig. 2. Daily course of effective quantum yield of PSII ($\Delta F/F_m'$) (*A–D*), electron transport rate (ETR) (*E–H*), and PPFD at leaf level (*I–L*) in seedlings of *Cuspidaria sceptrum* and *Fridericia florida* during April (*A*,*B*,*E*,*F*) and August 2013 (*C*,*D*,*G*,*H*). Data represent the mean ± SE in five leaves from different individuals. The values followed by *the same letters* do not differ statistically according to *Tukey*'s test ($P \leq 0.05$).

163.80 for *C. sceptrum,* and between 72.78 and 133.58 for *F. florida* under FSU (Fig. 4*C*,*D*). When transferred from shade to full sunlight, both species presented marked reduction in ETR on the first DAT. However, at 47 DAT, *F. florida* showed ETR values similar to FSU plants (Fig. 4*D*). In *C. sceptrum*, the recovery of ETR values was found at 61 DAT when new leaves were developed (Fig. 4*C*). At 5 DAT, *C. sceptrum* showed significant reductions in NPQ compared to plants growing under FSU (Fig. 4*E*) ($F = 13.99$, $p = 0.001$). At the end of the experiment, FSU and SH-FSU plants exhibited similar values of NPQ (Fig. 4*E*). Overall, transferred plants of *F. florida* kept values of NPQ similar to FSU plants (Fig. 4*F*).

Growth: Both species presented a reduced height under SH. An increase of this parameter was not observed when these plants were transferred from shade to full sunlight. Compared to SH plants, *C. sceptrum* increased its leaf numbers when it was transferred to full sunlight, whereas in *F. florida* the total number of leaves did not differ between light treatments (Table 1). In both species, the total leaf area was higher under FSU. When these species were transferred from shade to full sunlight, the total leaf area increased by 34% in *C. sceptrum* and by 47% in *F. florida* when compared to SH plants. Stem diameter and stem DM was higher under FSU in both species. However, the change in light intensity induced increases in stem diameter only in *F. florida* (Table 1). Pronounced reductions in leaf, root, and total DM were found for both species kept under SH conditions compared to FSU plants. After transfer, both species exhibited increases in leaf, root, and total DM compared to SH plants, presenting intermediate values when compared to FSU and SH plants (Table 1).

Table 2 shows a comparison of the ETR_{int}, (Eq. 1), $\overline{NPQ}$, (Eq. 2), and total DM of each treatment for both species. In the SH-FSU treatment, the ETR_{int} values for *F. florida* were higher than that for *C. sceptrum*, the same occurring for $\overline{NPQ}$. Conversely, the total DM was lower for *F. florida* compared to *C. sceptrum*.

The biomass partitioning was influenced by light conditions. Under FSU both species allocated less resources to stems ($F = 15.64$, $p = 0.0001$ and $F = 19.51$, $p < 0.0001$ for *C. sceptrum* and *F. florida,* respectively) and more to roots ($F = 9.89$, $p = 0.0009$ for *C. sceptrum* and $F = 19.83$, $p < 0.001$ for *F. florida*) (Fig. 5*A*,*C*). LMR was higher under SH and lower under FSU for *F. florida*, but when these plants were exposed to increased light intensity, no alteration in biomass distribution was found (Fig. 5*B*). In *C. sceptrum*, this pattern was not observed.

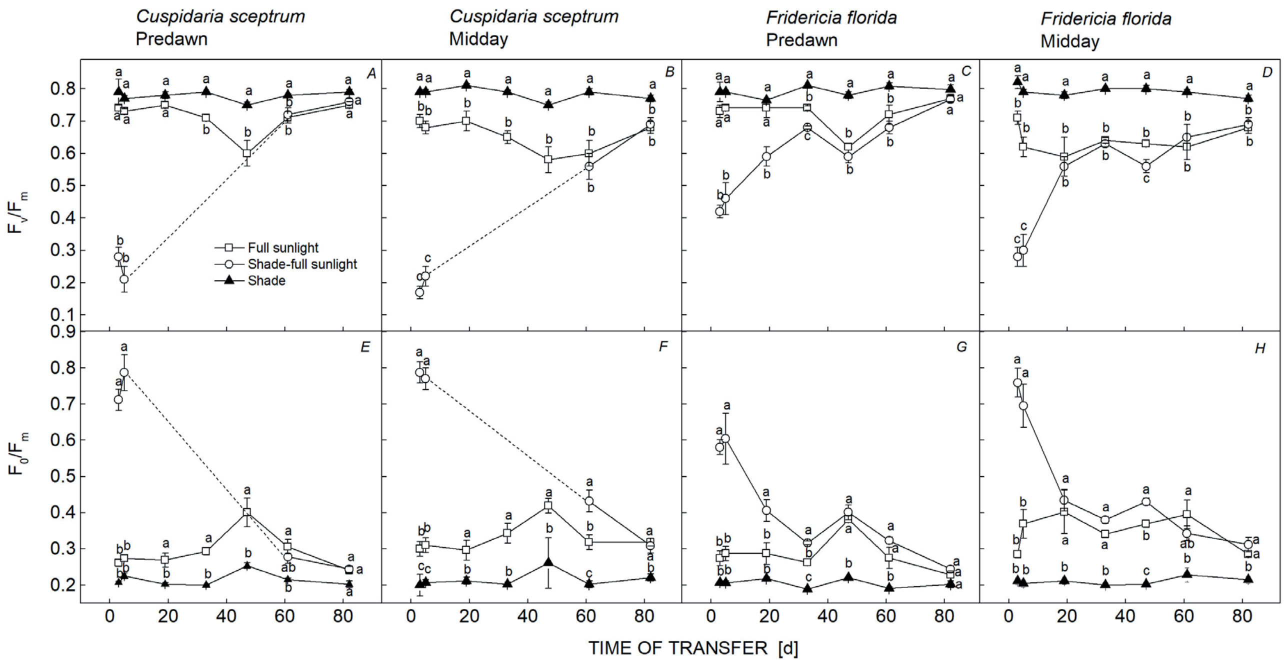

Fig. 3. Changes in the course of time of potential quantum yield of PSII (F_v/F_m) (*A–D*) and in F_0/F_m (*E–H*) in seedlings of *Cuspidaria sceptrum* and *Fridericia florida* permanently under full sunlight (*open square*), transferred from shade to full sunlight (*open circle*), and permanently under shade (*filled triangle*), during predawn (*A,E,C,G*) and midday (*B,F,D,H*). Data represent the mean ± SE in five leaves from different individuals. The values followed by *the same letters* do not differ statistically according to *Tukey*'s test ($P \leq 0.05$).

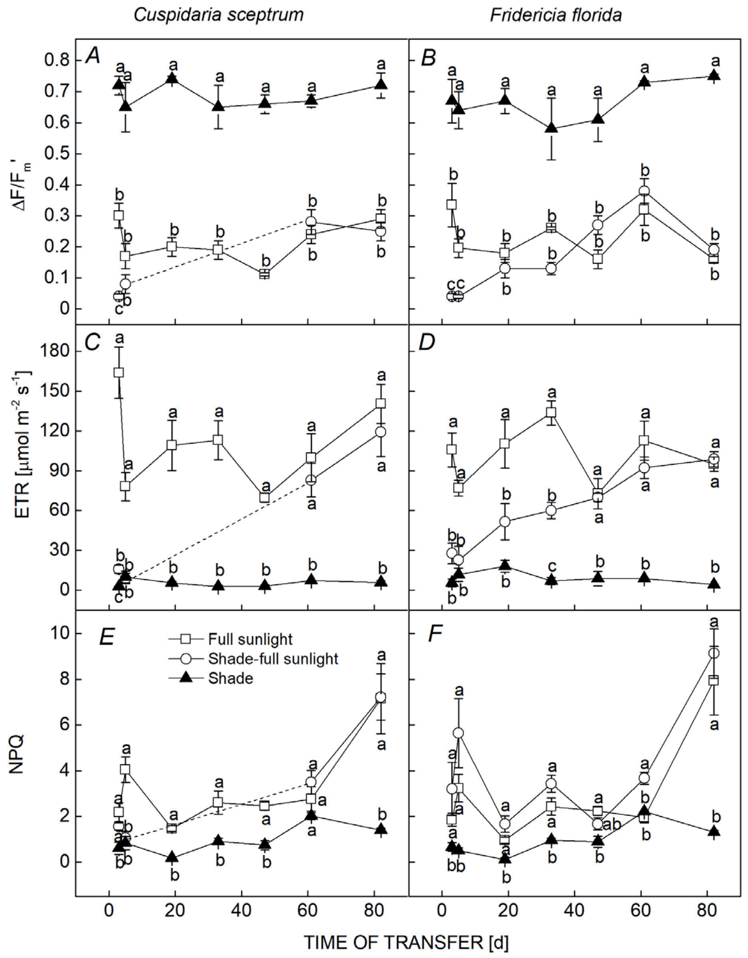

Fig. 4. Changes in the course of time of photosynthetic effective quantum yield of PSII ($\Delta F/F_m'$) (*A*,*B*), electron transport rate (ETR) (*C*,*D*), and nonphotochemical quenching (NPQ) (*E*,*F*) in seedlings of *Cuspidaria sceptrum* and *Fridericia florida* permanently under full sunlight (*open square*), transferred from shade to full sunlight (*open circle*), and permanently under shade (*filled triangle square*). Data represent the mean ± SE in five leaves from different individuals. The values followed by *the same letters* do not differ statistically according to *Tukey*'s test ($P \leq 0.05$)

Table 1. Height, leaf number, stem diameter, total leaf area, dry mass of stem, leaves and roots, and total biomass of *Cuspidaria sceptrum* and *Fridericia florida*. The data represent mean ± SE. In each line, values followed by *the same letters* do not differ according to *Tukey*'s test ($P \leq 0.05$). F*(p)* = F values and their probabilities (*p*) are results from *ANOVA*.

	Cuspidaria spectrum				*Fridericia florida*			
Growth parameters	Full sunlight	Shade-full sunlight	Shade	F (*p*)	Full sunlight	Shade-full sunlight	Shade	F (*p*)
Height [cm]	17.35 ± 0.69^{a}	12.40 ± 0.82^{b}	11.95 ± 1.01^{b}	12.42 (0.0003)	6.73 ± 0.38^{a}	5.65 ± 0.35^{ab}	5.50 ± 0.20^{b}	4.15 (0.002)
Total leaf numbers	34.50 ± 2.93^{a}	19.2 ± 1.37^{b}	6.30 ± 0.54^{c}	55.69 (<0.0001)	11.4 ± 0.62^{a}	10.0 ± 1.01^{a}	9.10 ± 0.74^{a}	2.07 (0.144)
Total leaf area [cm^2]	97.86 ± 10.63^{a}	33.02 ± 8.04^{b}	11.35 ± 1.55^{c}	33.79 (< 0.0001)	55.69 ± 6.21^{a}	35.48 ± 6.56^{b}	16.81 ± 1.34^{c}	13.61 (0.0002)
Stem diameter [m]	2.55 ± 0.19^{a}	1.80 ± 0.08^{b}	1.51 ± 0.05^{b}	18.39 (<0.0001)	2.22 ± 0.13^{a}	1.76 ± 0.07^{b}	1.32 ± 0.08^{c}	21.44 (<0.0001)
Stem dry mass [g]	0.63 ± 0.10^{a}	0.13 ± 0.02^{b}	0.06 ± 0.004^{c}	80.44 (<0.0001)	0.16 ± 0.02^{a}	0.05 ± 0.006^{b}	0.03 ± 0.003^{b}	25.65 (<0.0001)
Leaf dry mass [g]	0.62 ± 0.10^{a}	0.20 ± 0.04^{b}	0.02 ± 0.003^{c}	56.78 (<0.0001)	0.44 ± 0.004^{a}	0.22 ± 0.03^{b}	0.06 ± 0.005^{c}	41.25 (<0.0001)
Root dry mass [g]	2.61 ± 0.30^{a}	0.32 ± 0.06^{b}	0.10 ± 0.001^{c}	115.89 (<0.0001)	0.76 ± 0.007^{a}	0.14 ± 0.03^{b}	0.05 ± 0.006^{c}	92.28 (<0.0001)
Total dry mass [g]	3.88 ± 0.38^{a}	0.65 ± 0.12^{b}	0.22 ± 0.03^{c}	116.53 (<0.0001)	1.37 ± 0.10^{a}	0.42 ± 0.05^{b}	0.15 ± 0.01^{c}	98.47 (<0.0001)

Table 2. ETR integrated over time [ETR$_{int}$], $\overline{\text{NPQ}}$ over the experiment time after transfer, and total dry mass [TDM] in seedlings of *Cuspidaria sceptrum* and *Fridericia florida* under full sunlight, under shade, and transferred from shade to full sunlight.

	Cuspidaria sceptrum			*Fridericia florida*		
	Full sunlight	Shade–full sunlight	Shade	Full sunlight	Shade–full sunlight	Shade
ETR$_{int}$ [mol m^{-2}]	321 ± 43	110 ± 18	17 ± 4	323 ± 37	215 ± 25	31 ± 9
$\overline{\text{NPQ}}$	3.15 ± 0.53	1.86 ± 0.28	1.05 ± 0.14	2.84 ± 0.46	3.84 ± 0.56	1.07 ± 0.11
TDM [g]	3.88 ± 0.38	0.65 ± 0.12	0.22 ± 0.03	1.37 ± 0.10	0.42 ± 0.05	0.15 ± 0.01

Increases in SLA were found for both species under SH conditions (Fig. 5*D*). When transferred from shade to full sunlight, both species were capable to produce leaves with lower SLA compared to SH plants, with similar values of FSU plants (F = 81.75, *p* = 0.0001 and F = 57.6, *p*<0.0001 for *C. sceptrum* and *F. florida,* respectively) (Fig. 5*D*). LAR values were twice as high for *F. florida* under SH in comparison to FSU plants (F = 25.36, *p*<0.0001) (Fig. 5*E*). After transfer, *F. florida* presented reductions in LAR, with intermediate values compared to FSU and SH plants (Fig. 5*E*). *C. sceptrum* did not show significant differences for LAR between SH and SH-FSU plants, but for FSU, LAR was significantly lower (F = 6.13, *p* = 0.006) (Fig. 5*E*). The RGR was higher under FSU and lower under SH for both species (Fig. 5*F*). In addition, both species exhibited increases in RGR when transferred from shade to full sunlight, but these values were lower than that for FSU plants (F= 136.9, *p*< 0.0001, F = 106.8, *p*<0.0001 for *C. sceptrum* and *F. florida,* respectively) (Fig. 5*F*).

Discussion

Both lianas of the present study are frequently found in edge forests, where conditions of high light intensity prevail. Even so, our data showed that these lianas underwent photoinhibition under full sunlight, since predawn and midday values of F_v/F_m were below 0.8 (Lüttge 2008). These values of F_v/F_m were significantly lower than those for shade plants during the day in April. During the second daily course in August, both species presented reductions on F_v/F_m close to midday and in the afternoon with a recovery during predawn and sunset, which suggests dynamic photoinhibition (Zhou *et al*. 2016). These results pointed to leaf adjustments to full sunlight over time, since photoinhibition was less severe for both species in August. It is probable that some protective mechanisms to deal with high light intensity were operating in these leaves (Franco and Lüttge 2002). The reductions in effective quantum yield ($\Delta F/F_m'$), 0.16 for *C. sceptrum* and 0.29 for *F. florida* (Fig. 2*C,D*) FSU plants, indicate that only a low fraction of light absorbed by Chl associated with

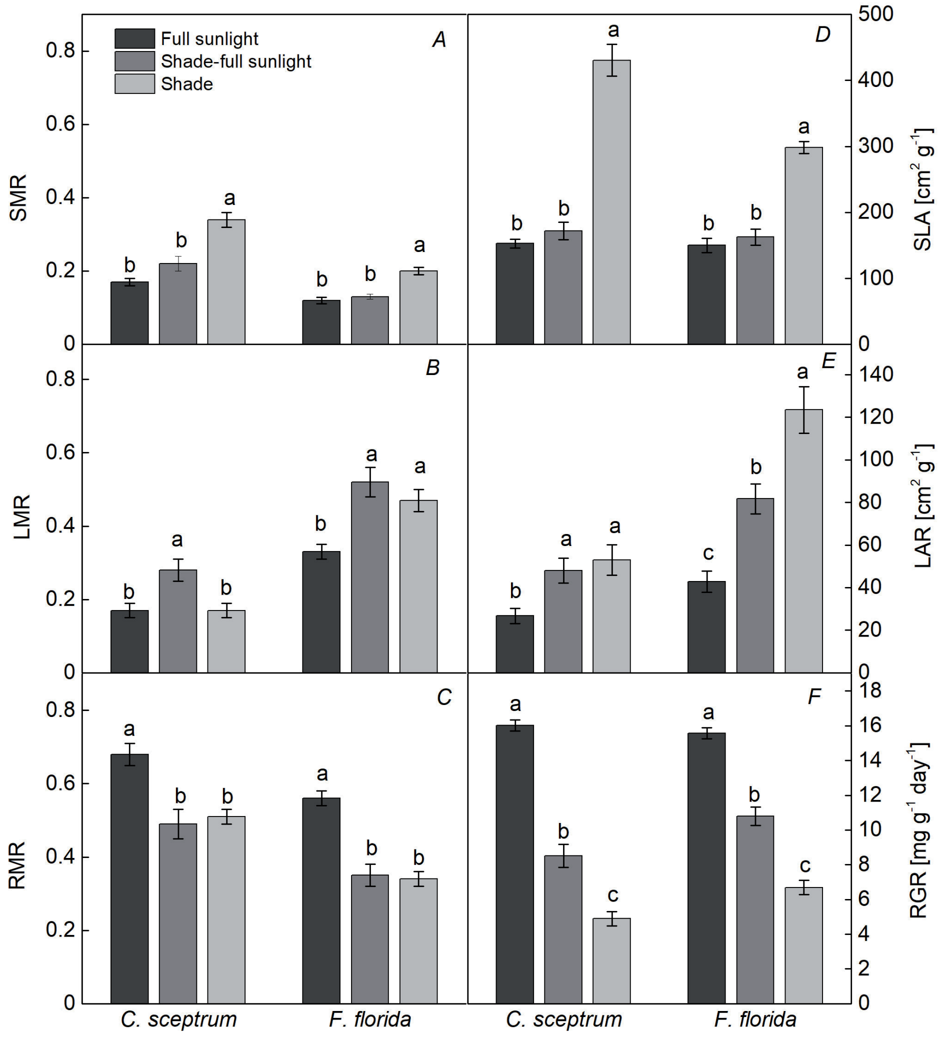

Fig. 5. Mean values of stem mass ratio (SMR) (*A*), leaf mass ratio (LMR) (*B*), root mass ratio (RMR) (*C*), specific leaf area (SLA) (*D*), leaf area ratio (LAR) (*E*), and relative growth rate (RGR) (*F*) in seedlings of *Cuspidaria sceptrum* and *Fridericia florida* permanently under full sunlight (*dark gray*), transferred from shade to full sunlight (*gray*), and permanently under shade (*light gray*). Data represent the mean ± SE in ten plants of different light treatments. The values followed by *the same letters* do not differ statistically according to *Tukey*'s test ($P \leq 0.05$).

PSII was used for photochemistry (Maxwell and Johnson 2000). Simultaneously, ETR maintained high values, over 100 µmol m^{-2} s^{-1} in both species between 10:00 and 15:00 h (Fig. 2*G*,*H*). These ETR values are within those found in *Canavalia parviflora*, a liana from semideciduous tropical forests of Brazil, and *Bridelia stipularis*, a liana from the savanna vegetation of Southwest China (Sanches and Válio 2008, Zhang *et al*. 2016), and may reflect a shift of electron flow to another process not directly involved in carbon assimilation, such as photorespiration (Franco and Lüttge 2002, Zhang *et al*. 2016).

Photoinhibition occurs when the light intensity, which reaches the leaf surface, greatly exceeds leaf capacity to use it in photosynthesis and/or in thermal dissipation (Takahashi and Murata 2008). This disbalance may be intensified mainly when shade plants are transferred to full sunlight, a common condition found when a gap is created within the forest (Valladares *et al*. 2002, Azevedo and Marenco 2012). Both liana species showed reductions in F_v/F_m on the first days of transfer from shade to full sunlight, especially *C. sceptrum*. This species exhibited strong photoinhibition at 5 DAT, with a sharp decline in F_v/F_m compared to SH and FSU plants. This abrupt drop in F_v/F_m led to the formation of necrosis in leaves developed under shade conditions. Between 6 and 8 DAT, all individuals of *C. sceptrum*, which had been transferred from shade to full sunlight, lost their leaves. This result indicates that, at least in the first days, the sudden exposure of shade leaves to full sunlight with concomitant increases in air temperature contributed to the occurrence of photodamage (Lüttge 2008). Furthermore, the higher values of SLA, *i.e.*, the production of thinner leaves, as found in *C. sceptrum* under shade, probably had an influence on the marked reduction of F_v/F_m on the first days of transfer. Higher SLA values can lead to higher absorption efficiency under shade (Sanches and Válio 2006), but when these thinner leaves are suddenly exposed to full sunlight, photoinhibition could be exacerbated. Similar findings were found by Tobita *et al*. (2010), where the leaves of *Sasa senanensis* with higher LMA (the opposite of SLA) were less susceptible to photoinhibition after increases in irradiance than that of *Quercus mongolica* and *Acer mono*. Although *C. sceptrum* lost its leaves shortly after its transfer, new leaves were produced under full sunlight. The formation of leaf primordia was already observed at 10 DAT. After 60 DAT, these leaves had completed their expansion. These newly formed leaves showed full recovery of photoinhibition, since F_v/F_m was close the values found in SH and FSU plants.

In *F. florida*, the drop of 47% of F_v/F_m, measured at 3 DAT, was not so sharp when compared to *C. sceptrum* indicating that photoinhibition was less severe in this species. The F_v/F_m values of 0.42 to 0.59 at predawn at 3 and 5 DAT, pointed to chronic photoinhibition in *F. florida* due to the absence of recovery in F_v/F_m overnight (Lüttge 2008, Azevedo and Marenco 2012). Hence, both species showed a dysfunction of PSII that led to reductions in F_v/F_m when transferred from shade to full sunlight. Also, in both species, the ratio F_0/F_m increased markedly just after the first days after transfer, indicating that they underwent stress when transferred from shade to full sunlight (Roháček 2002). In *F. florida*, the increases in F_0/F_m occurred due to lowering F_m, which is often related to non-radiative energy dissipation (Dias and Marenco 2006). Likewise, in *C. sceptrum,* the rise in F_0/F_m was due to reductions of F_m. However, this species exhibited necrosis in their leaves after sudden exposition to full sunlight, suggesting that energy dissipation was not efficient enough to protect PSII reaction centres. During midday, the increase in F_0/F_m was caused by the increase in F_0, which could explain the occurrence of photodamage in this species (Krause 1988).

The drop of $\Delta F/F_m$' as well as ETR values on the first days of transfer reinforces the occurrence of photoinhibition in both liana species (Kitao *et al*. 2006). However, *F. florida* was able to gradually increase F_v/F_m over time, with a complete recovery of the potential quantum yield of PSII at 82 DAT. It is important to emphasize that, contrary to *C. sceptrum*, the response of *F. florida* to increases in light intensity was achieved by adjustments in leaves previously developed under shade conditions, which suggests that mechanisms of nonphotochemical quenching were possibly operating in this species under full sunlight conditions (Guo *et al*. 2006). Indeed, transferred plants of *F. florida* were able to maintain the NPQ values close to those of FSU plants, whereas for *C. sceptrum,* the NPQ values were significantly lower at 5 DAT (Fig. 4*E*,*F*).

Considering the whole-plant acclimation, both species presented increases in leaf area and reductions in SLA and in SMR when they were transferred from shade to full sunlight. *C. sceptrum* produced higher leaf numbers, whereas in *F. florida*, leaf production was kept constant. This result points out to a more conservative response in *F. florida* compared to that of *C. sceptrum*. Although the leaf number was not changed among light treatments in *F. florida*, the total leaf area was larger at full sunlight than that at SH-FSU and the lowest at SH. These results mean that the leaf area of each leaf enlarged as the light intensity increased. Moreover, increases in stem, leaf, and root DM were achieved when these plants were exposed to full sunlight. It is important to mention that the increase in root DM in *C. sceptrum* and *F. florida* was about 69 and 64%, respectively, when compared to SH plants. This could explain the full physiological recovery found at the leaf level, as indicated by high values of F_v/F_m and ETR at the end of the experiment. Increases in root growth were able to meet the higher water demand as the alterations in growth conditions were followed by rises in air temperature and decreases in relative humidity. In *C. sceptrum*, the RMR was close to 0.50, as found in SH-FSU plants, which could contribute to the production of new leaves under full sunlight, since the roots may function as carbohydrate storage for the period of absence of leaves.

Although both species increased their growth when exposed to higher levels of light, the full acclimation at whole-plant level was only partially reached, as the total dry mass and RGR was lower in SH-FSU plants than that in FSU plants. The integration of ETR over time shows that although *F. florida* had higher values of ETR compared to *C. sceptrum*, the light available for photochemical reactions was not so efficiently converted into biomass at the end of the experiment compared to FSU plants (Table 2). This can be found from the NPQ values (Fig. 4). In the first days after the transfer, when both species experienced more severe photoinhibition, *F. florida* was able to maintain NPQ values similar to those of FSU plants, whereas in transferred plants of *C. sceptrum*, NPQ values were lower. NPQ is associated with energy dissipation as heat and is considered a protection mechanism against excess light (Guo *et al*. 2006, Rabelo *et al*. 2013). Hence, it is probable that the energy used to recover from initial photoinhibition and resume PSII activity was higher than the energy used to promote growth, especially in *F. florida.* In *C. sceptrum*, the lower values of NPQ may be an indicative of insufficient protection of PSII after the sudden increase in light intensity after transfer (Table 2). As a consequence, the leaves fell. In addition, the reduced growth in shade probably had a role in whole-plant acclimation. As pointed by Avalos and Mulkey (2014), a small seedling with little leaf area and root dry mass, as found in *C. sceptrum* and *F. florida* under shade, could limit the capacity of these species to increase resource acquisition under new light conditions. This pattern was not found in *Cedrela fissilis*, a tree species that showed complete recovery of total biomass when transferred from shade to full sunlight (Sanches *et al*. 2017). Although it is often assumed that lianas are light-demanding species (Dewalt *et al*. 2010), at least in the initial life stage, the relative growth and total biomass accumulation values are close to those found in late-successional tree species and lower than those found for pioneer tree species (Souza and Válio 2003, Feijó *et al*. 2009). These results show that lianas may share some life traits that are common with shade-tolerant tree species, while both groups are in the juvenile stage and lianas are still self-supporting plants, as in our experiment.

Finally, both liana species presented some traits that allow them to cope with contrasting light conditions. Under low light, increases of SLA and LAR, which favour light interception and carbon gain, were found. Whereas under full sunlight, opposite responses were observed, with reductions of SLA and LAR, and increases in RMR, that contribute to avoid light and water stress (Souza and Válio 2003, Paulilo *et al*. 2007, Feijó *et al*. 2009). However, when alterations in light conditions were imposed, distinct responses emerged. As a whole, the potential acclimation found in *F. florida* was achieved by physiological adjustments at leaf level, while *C. sceptrum* exhibited a morphological response, changing all older leaves for new ones under the new light conditions. The initial photoinhibition found during increases in light conditions impacted the growth of these two liana species, although they are frequently found in forest edges and have a heliophyte character when adult plants.

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