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BRIEF COMMUNICATION

Photosynthetic light-response curves of light-demanding and shade-tolerant seedlings of neotropical tree species

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Abstract

Light-response curves of seedlings of five light-demanding (LD) and four shade-tolerant (ST) neotropical tree species, native to the Brazilian Atlantic biome, were analyzed, aiming to verify differences between these functional groups regarding the light use. We hypothesized that variations in the light requirement of seedlings would occur not only between LD and ST species, but also within these functional groups. The apparent quantum yield of CO_2 assimilation, dark respiration rate (R_D), photorespiration rate (R_P), light-compensation point (I_{comp}), light-saturation point (I_{max}), and light-saturated photosynthetic rate (P_{Nmax}) were estimated from fitted light-responses curves and using equations available in the literature. The results revealed great differences between the functional groups. R_D, R_P, I_{comp}, I_{max}, and P_{Nmax} were effectively higher in the LD than those in the ST species. Furthermore, a continuum of strategies regarding the light use was observed, matching with some ecological characteristics of the species studied here.

Additional key words: early-successional species; gas exchange; late-successional species; photosynthetic photon flux density.

The understory of a tropical rainforest is characterized by low light availability, with a vertical gradient of increasing irradiance towards the canopy (Houter and Pons 2012). Most late-successional tree species are shade-tolerant (ST), but can be exposed to full sunlight as they grow and reach the canopy, experiencing a broad range of light conditions during their development (Kitajima 1994). On the other hand, typical early-successional trees are light-demanding (LD) and depend on the formation of canopy gaps (Kitajima 1994). Due to the significant horizontal and vertical heterogeneity in light availability in tropical forests, the demand for light of each species varies according to the niches occupied by them, so that a broad range of responses regarding the light use can be observed among species that co-occur in the forest (Clark and Clark 1992, Davies *et al*. 1998).

Under high light, photon absorption is not a limiting factor. In LD species, adapted to high irradiance, the investment in leaf traits that maximize the photosynthetic rate and photoprotective mechanisms is generally high, relative to those associated with light absorption (Valladares and Niinemets 2008, Dusenge *et al*. 2015). In low light environments, photon absorption limits photosynthetic rates, as in a tropical forest understory. Therefore, ST species invest proportionally more in structural components and pigments, resulting in greater light absorption, compared to LD species (Feng *et al*. 2004, Valladares and Niinemets 2008, Dusenge *et al*. 2015). Shade tolerance is characterized by low dark respiration rate (R_D), cell maintenance cost, light-compensation point (I_{comp}), light-saturation point, net photosynthetic rate (P_N), and electron transport rate, due to the low concentration of photosynthetic enzymes in the leaves (Raaimakers *et al*. 1995, Craine and Reich 2005, Valladares and Niinemets 2008).

Seedlings of neotropical tree species show different light requirements. Long-term exposure to excess light can severely limit the survival of seedlings of some species (Gómez-Aparicio *et al*. 2006). Under such conditions, photorespiration may be essential for plants to withstand light stress (Osmond and Grace 1995, Kozaki and Takeba 1996). Short-term supersaturating quantum fluxes can also generate photoinhibitory effects, decreasing the electron transport rate (Brodribb and Hill 1997) and P_N (Ye 2007), which occurs at lower light intensities in species with low light requirement, compared to LD species. In this study, light-response curves of seedlings of LD and ST neotropical tree species were analyzed, aiming to verify differences between these functional groups, regarding the light use, according to the parameters estimated with the fitted curves. It is expected that LD species present lower apparent quantum yield of CO_2 assimilation (Φ), but higher R_D, photorespiration rate (R_P), I_{comp}, light-saturation point (I_{max}), and light-saturated photosynthetic rate (P_{Nmax}) than ST species. We hypothesized that variations in the light

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Abbreviations: I_{comp} – light-compensation point; I_{max} – light-saturation point beyond which there is no significant change in P_N; LD – light-demanding; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate; R_P – photorespiration rate; ST – shade-tolerant; Φ – apparent quantum yield of CO_2 assimilation.

requirement of seedlings would occur not only between LD and ST species, but also within these functional groups.

Five light-demanding, *Cecropia pachystachya* Trécul (Urticaceae), *Croton floribundus* Spreng. (Euphorbiaceae), *Trema micrantha* (L.) Blume (Cannabaceae), *Lonchocarpus muehlbergianus* Hassl. (Fabaceae), and *Heliocarpus popayanensis* Kunth (Malvaceae) and four shade-tolerant, *Cabralea canjerana* (Vell.) Mart. (Meliaceae), *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae), *Pouteria* sp. (Sapotaceae), and *Trichilia elegans* A. Juss. (Meliaceae), tree species, native to the Brazilian Atlantic biome, were chosen.

The species were grouped in LD or ST primarily according to the nursery's specialists (Cavalheiro *et al.* 2002), and also based on research performed in the same phytophysiognomy and region where the seeds were collected and the seedlings were grown (Metzger *et al.* 1997, Pillar and Quadros 1997, Silva and Soares-Silva 2000, Zangaro *et al.* 2003, Abreu *et al.* 2014), in addition to other studies (Kammesheidt 2000, Morellato 2004). It is a consensus that *C. pahystachya*, *T. micrantha*, and *C. urucurana* are typical light-demanding pioneers. *H. popayanensis* (syn. *H. americanus*) is a pioneer, or early secondary, fast-growing species, occurring exclusively in light-exposed areas (Kammesheidt 2000, Silva and Soares-Silva 2000, Cavalheiro *et al.* 2002, Zangaro *et al.* 2003). We consider *L. muehlbergianus* an early secondary, light-demanding species (Silva and Soares-Silva 2000, Cavalheiro *et al.* 2002, Abreu *et al.* 2014), although the literature is divergent and this species may be classified as late secondary (Zangaro *et al.* 2003). Among the ST species, *C. canjerana* and *C. estrellensis* are represented by tall trees whose crowns can exceed the average level of the canopy (Pillar and Quadros 1997, Silva and Soares-Silva 2000), unlike *Pouteria* sp. and *T. elegans*, which inhabits only the forest understory (Silva and Soares-Silva 2000, Morellato 2004).

The seedlings were grown in the growth sector of an outdoor nursery of the Laboratory of Biodiversity and Ecosystem Restoration from the State University of Londrina, Brazil, under the PPFD routinely adopted by the nursery for the initial development of neotropical seedings (40% of total environmental PPFD). This PPFD is considered adequate for seedlings of both LD and ST species, since chronic photoinhibition have not yet been detected in plants grown under the light conditions of the growth sector (Mazzanatti *et al.* 2016, Calzavara *et al.* 2017). The maximum PPFD on sunny days at the nursery was around 700 μmol(photon) m^{-2} s^{-1}. The seedlings were irrigated four times a day for 30-min periods and subjected to natural temperature conditions. The youngest fully expanded leaf of five seedlings per species was used for gas-exchange analyses.

The leaf gas-exchange parameters were measured using a portable photosynthesis system (*LI-6400XT*; *LI-COR Biosciences*, Lincoln, USA) with an infrared gas analyzer (IRGA) connected to a *6400-02B* measuring chamber with a LED light source. The responses of P_N to PPFD were determined on sunny days (between 08:00 and 11:00 h). The leaves were supplied with ambient CO_2 concentration and saturating PPFD [1,900 μmol(photon) m^{-2} s^{-1}], until both P_N and intercellular CO_2 concentration had stabilized (1–2 min, on average). After this, PPFD was reduced in a step-wise fashion [1,900; 1,500; 1,000; 600, 300, 200, 100, 75, 50, 20, and 0 μmol(photon) m^{-2} s^{-1}]. At each PPFD, P_N was recorded once the leaves had reached steady-state values, as described above. Leaf temperature at the time of all measurements varied from 27 to 33°C. Φ, R_D, I_{comp}, and P_{Nmax} were determined through P_N/PPFD curves, fitted using *Sigma Plot 10.0* software (*Systat Software Inc.*, San Jose, USA) in accordance with Avola *et al.* (2008). R_P was calculated according to Sharkey (1988): $R_P = (P_N + R_D)/(1/\Theta - 0.5)$, where Θ is the ratio between carboxylation and oxygenation rates of Rubisco according to Farquhar and von Caemmerer (1982). The light-saturation point beyond which there is no significant change in P_N (I_{max}) was estimated using the *Excel* (*Microsoft*, Washington, USA) tool made available by Lobo *et al.* (2013), following the model described by Ye (2007).

The normality and homogeneity of variances of data were checked. When necessary, data were log transformed for statistical analyses. Comparisons of Φ, R_D, R_P, I_{comp}, I_{max}, and P_{Nmax} between the functional groups (LD and ST) were performed using one-way *ANOVA* (*F*-test; $p<0.05$) in the *Statistica 10.0* software (*Statsoft Inc.*, Tulsa, USA).

To check the fitted curves of the LD and ST species, *see* Fig. 1S (*supplement*). Comparisons between the functional groups showed that LD species had higher R_D, R_P, I_{comp}, I_{max}, and P_{Nmax} than ST species, while Φ did not differ (Table 1). According to Bazzaz and Pickett (1980) and Valladares and Niinemets (2008), early-successional species usually show high R_D, I_{comp}, I_{max}, and P_N, but higher Φ than the late-successional ones. Although a pattern is consistently observed for I_{comp} and I_{max} (lower in ST compared to LD species), the expectations for Φ are challenged (Valladares and Niinemets 2008). For instance, Dusenge *et al.* (2015) reported lower Φ in late-successional, compared to pioneer species, suggesting that late-successional species over-invest in light-harvesting complexes in relation to photosynthesis, since their higher leaf chlorophyll content did not translate into higher light-use efficiency. Our results for I_{comp}, I_{max}, and P_{Nmax} corroborate those pointed out in the mentioned reviews (Bazzaz and Pickett 1980, Valladares and Niinemets 2008) and by Givnish *et al.* (2004), whereas Φ showed no differences between the functional groups. The higher P_{Nmax} of LD species may result from a higher proportion of chlorophyll parenchyma in the leaves, in relation to other tissues (Terashima *et al.* 2006), leading to an increased photosynthetic proteins content compared to ST species (Houter and Pons 2012). This increases cell maintenance costs, increasing R_D and I_{comp} (Craine and Reich 2005), variables that showed a strong increase (>350%) in the LD species in this study.

A marked difference in R_P between LD and ST species was verified in the present study. The results for photorespiration (R_P) in the literature do not clearly distinguish patterns for LD and ST species (Souza *et al.* 2008, Oliveira *et al.* 2012, Slot *et al.* 2016). Using the same equations adopted here to calculate R_P, Oliveira *et al.* (2012) found no difference between a pioneer (*Croton urucurana*) and

Table 1. Apparent quantum yield of CO_2 assimilation (Φ), dark respiration rate (R_D), photorespiration (R_P), light-compensation point (I_{comp}), light-saturation point of CO_2 assimilation (I_{max}), and light-saturated net photosynthetic rate (P_{Nmax}) of leaves from seedlings of neotropical light-demanding and shade-tolerant tree species. The data are the means ± SE. *Asterisks* indicate significant differences between the functional groups (F-test, *ANOVA* at $p<0.05$; *Degrees of freedom* = 1).

Variable	Light-demanding	Shade-tolerant	F
Φ [mol mol^{-1}]	0.054 ± 0.003	0.046 ± 0.004	2.3
R_D [μmol(CO_2) m^{-2} s^{-1}]	0.731 ± 0.072	0.148 ± 0.045	40.9*
R_P [μmol(CO_2) m^{-2} s^{-1}]	2.601 ± 0.189	1.19 ± 0.136	43.5*
I_{comp} [μmol(photon) m^{-2} s^{-1}]	13.84 ± 1.14	3.036 ± 0.886	51.5*
I_{max} [μmol(photon) m^{-2} s^{-1}]	919.9 ± 62.3	419.6 ± 64.3	30.6*
P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	10.18 ± 1.07	5.327 ± 0.486	14.2*

a late-successional species (*Cariniana legalis*). Souza *et al.* (2008) obtained results similar to those reported here (higher R_P in LD species than that in late-successional ones), but under a condition of high light intensity. Since photorespiration can serve as an alternative electron sink, dissipating excessive photochemical energy (Kozaki and Takeba 1996), the results highlight the greater capacity of the LD species to tolerate the damaging effects of high irradiances, compared to the ST species.

The I_{max} verified for ST and LD species were quite different. The highest I_{max} mean was observed in the LD species *C. pachystachya* [1,086 μmol(photon) m^{-2} s^{-1}]. Among the ST species, the highest I_{max} was verified in *C. canjerana* [559 μmol(photon) m^{-2} s^{-1}]. Studies have shown that in non-pioneer understory species, P_N saturates at an PPFD range of 300–600 μmol(photon) m^{-2} s^{-1}, but in pioneer species these values exceed 800 and can reach 1,200 μmol(photon) m^{-2} s^{-1} (Lugo 1970, Stephens and Waggoner 1970, Thompson *et al.* 1992). Considering the higher I_{max} observed among the LD species and the variation of I_{max} within the group, we suggest that PPFD above 1,300 μmol(photon) m^{-2} s^{-1} should be adopted to estimate the P_{Nmax} of LD neotropical seedlings, since under irradiances below I_{max}, P_N is limited by electron transport rate, Rubisco activity is downregulated (Salvucci 1989, Ögren and Evans 1993), and P_{Nmax} is not reached. Following the same criteria, for ST species, minimum values of 750 μmol(photon) m^{-2} s^{-1} of PPFD are recommended, but the use of extremely high irradiances [above 1,000 μmol(photon) m^{-2} s^{-1}] is not required and not advised, since undesirable photoinhibitory effects can occur (Ye 2007), especially in these species sensitive to photoinhibition (Valladares and Niinemets 2008). The approach described by Lobo *et al.* (2013) to calculate I_{max} (the point beyond which there is no significant change in P_N), applied here, was appropriate for verifying the PPFD that the P_{Nmax} is actually achieved, unlike many approaches that adopt a value of PPFD in which P_N reaches a percentage of P_{Nmax} (*e.g.*, 50 or 90%) to express the light-saturation point.

A continuum of strategies regarding the light use was observed (Table 2), with the typical pioneers at one extreme (*C. pachystachya*, *T. micrantha*, and *C. urucurana*), presenting the highest R_D, R_P, I_{comp}, I_{max}, and P_{Nmax}. On the other extreme of shade tolerance, the understory ST species had the lowest values of the analyzed parameters (*Pouteria* sp. and especially *T. elegans*). These variations are probably related to the light conditions of the habitats where these species are found. *T. elegans* is a shade-tolerant species, represented by small trees (up to 3.2 m) found in the understory of semi-deciduous forests (Morellato 2004), where the incident PPFD is very low. On the other hand, *C. canjerana* and *C. estrellensis* are classified as emergent trees (Pillar and Quadros 1997, Silva and Soares-Silva 2000) whose crowns experience a wide range of light conditions during their ontogeny, from the ground level to above the canopy. According to Clark and Clark (1992), emergent species might share important physiological characteristics and constitute one well-defined functional group among the non-pioneer species. Due to the adaptation to the different strata that *C. canjerana* and *C. estrellensis* explore throughout the life cycle, exposing their leaves to high irradiances at some point, it is reasonable that the photosynthetic characteristics of their seedlings resemble those of some LD species. Consistent with this hypothesis, our group have already demonstrated that *C. estrellensis* seedlings have nitrogen-use strategies intermediary to LD and understory ST species (Oliveira *et al.* 2017). In this previous study, we have also detected variations in nitrogen-use strategies among LD species, according to their specific ecological characteristics (Oliveira *et al.* 2017). Here, *L. muehlbergianus* and *H. popayanensis* differed from *C. pachystachya* in some parameters (I_{max} and P_{Nmax} for *L. muehlbergianus*; Φ, R_D, R_P, I_{max}, and P_{Nmax} for *H. popayanensis*), indicating different light requirements among the LD species, despite their need for a high-light environment for establishment. It is noteworthy that the authors and most of the literature consulted consider *L. muehlbergianus* an early secondary species, but classifications of this species as late-successional can also be found (as in Zangaro *et al.* 2003).

The parameters estimated from the fitted light-curves revealed great differences between the functional groups, regarding the light use. R_D, R_P, I_{comp}, I_{max}, and P_{Nmax} were effectively higher in the LD than that in the ST species. A continuum of strategies regarding the light use was also verified, matching with some ecological characteristics of the species studied here. One extreme is represented by the typical pioneers that exhibited high R_D, R_P, I_{comp}, I_{max}, and P_{Nmax}, contrasting with the late successional understory

Table 2. Apparent quantum yield of CO_2 assimilation (Φ), dark respiration rate (R_D), photorespiration rate (R_P), light-compensation point (I_{comp}), light-saturation point of CO_2 assimilation (I_{max}), and light-saturated net photosynthetic rate (P_{Nmax}) of leaves from seedlings of neotropical light-demanding (LD) and shade-tolerant (ST) tree species. The data are the means ± SE ($n = 5$). *Different letters* indicate significant differences between the species in the column (*ANOVA* followed by *Tukey*'s *HSD* test at $p<0.05$).

	Species	Φ [mol mol^{-1}]	R_D [μmol(CO_2) m^{-2} s^{-1}]	R_P [μmol(CO_2) m^{-2} s^{-1}]	I_{comp} [μmol(photon) m^{-2} s^{-1}]	I_{max} [μmol(photon) m^{-2} s^{-1}]	P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]
LD	*Cecropia pachystachya*	0.065 ± 0.003^{a}	0.880 ± 0.107^{a}	3.23 ± 0.377^{a}	13.6 ± 1.76^{a}	1086 ± 111^{a}	13.7 ± 1.8^{a}
	Trema micrantha	0.049 ± 0.005^{abc}	0.863 ± 0.074^{a}	2.46 ± 0.113^{ab}	17.7 ± 1.02^{a}	1010 ± 72.7^{ab}	9.77 ± 0.51^{ab}
	Croton urucurana	0.053 ± 0.002^{ab}	0.622 ± 0.075^{ab}	2.79 ± 0.252^{ab}	11.8 ± 1.65^{a}	948 ± 54.1^{ab}	11.3 ± 0.8^{ab}
	Heliocarpus popayanensis	0.046 ± 0.002^{bc}	0.506 ± 0.044^{c}	2.13 ± 0.106^{bc}	11.4 ± 1.58^{a}	760 ± 60.1^{bc}	7.74 ± 0.26^{bcd}
	Lonchocarpus muehlbergianus	0.055 ± 0.005^{ab}	0.786 ± 0.126^{ab}	2.40 ± 0.247^{ab}	14.7 ± 2.92^{a}	795 ± 66.4^{bc}	8.39 ± 0.60^{bc}
ST	*Cabralea canjerana*	0.047 ± 0.002^{bc}	0.235 ± 0.033^{d}	1.40 ± 0.053^{cd}	4.97 ± 0.682^{b}	559 ± 18.1^{cd}	6.43 ± 0.18^{cde}
	Cariniana estrellensis	0.049 ± 0.003^{abc}	0.177 ± 0.034^{d}	1.44 ± 0.131^{cd}	3.55 ± 0.560^{b}	476 ± 54.7^{de}	5.69 ± 0.56^{def}
	Pouteria sp.	0.053 ± 0.003^{ab}	0.157 ± 0.032^{d}	1.04 ± 0.135^{e}	2.91 ± 0.499^{bc}	385 ± 26.0^{de}	5.05 ± 0.54^{ef}
	Trichilia elegans	0.035 ± 0.005^{c}	0.022 ± 0.012^{e}	0.89 ± 0.056^{e}	0.713 ± 0.421^{c}	259 ± 22.9^{e}	4.14 ± 0.37^{f}

species at the other extreme. The early secondary (LD) and the ST emergent species showed intermediate characteristics of light requirement, with similarities in some of the analyzed variables (such as in R_P, I_{max}, and P_{Nmax}), but also with very contrasting differences (R_D and I_{comp}) that make them closer to their respective functional groups (LD and ST) regarding the photosynthetic responses to light. The variations observed within the functional groups show different adaptations to the niches occupied by each species in the forest. Overall, the results will support further studies with information about stressful and nonstressful light conditions for neotropical tree seedlings.

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