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ORIGINAL ARTICLE

Photosynthesis, growth, and biomass allocation responses of two *Inga* species to contrasting light

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Abstract

Inga marginata and *Inga subnuda* are evergreen N-fixing tree species that are frequently found in the initial stages of forest regeneration. *I. marginata* has a wide geographic distribution, encompassing the Brazilian Atlantic Rainforest and dry forests of central Brazil, whereas *I. subnuda* is endemic to the Brazilian Atlantic Rainforest. We conducted this study to compare the physiological, growth, and biomass allocation responses of *I. marginata* and *I. subnuda* to contrasting light environments. Considering that *I. marginata* and *I. subnuda* have a similar position in the forest succession and different geographic distributions, we tested a hypothesis that these two congeneric species have similar photosynthetic and growth responses to light availability but different biomass allocation. The plants were grown under three light conditions (36, 15, and 6 mol photons m^{-2} day^{-1}) for 105 days. Growth, biomass allocation, light–response curves, and leaf pigments were compared among the light conditions and between species by using two-way ANOVA. Our hypothesis was partially supported because the two species had similar photosynthetic responses to changes in light availability, but differences in growth and biomass allocation. The higher relative growth rate in mass of *I. subnuda* is associated with its higher allocation of biomass to light capture, as shown by the higher values of leaf mass fraction (LMF) and leaf area ratio (LAR). Conversely, the higher values of root mass fraction for *I. marginata* were in contrast to the higher values of LMF, LAR, and specific leaf area for *I. subnuda*; this indicates that *I. marginata* should be better adapted to environments where water could be a limiting factor, which is consistent with its wide geographic distribution.

Keywords Congeneric species · *Inga marginata* · *Inga subnuda* · N-fixing trees · Tropical trees

Abbreviations

Carot	Carotenoids
Chl *a*	Chlorophyll *a*
Chl *b*	Chlorophyll *b*
Chl *a* + *b*	Chlorophyll total
PAR	Photosynthetic active radiation
Pgmax	Maximum gross photosynthetic rate in saturating light
Pn	Net photosynthetic rate
LA	Leaf area
LAR	Leaf area ratio
LMF	Leaf mass fraction
LN	Leaf number
LCP	Light compensation point
LSP	Light saturation point
NAR	Net assimilation rate
Rd	Respiration rate in the dark
RGR_D	Relative growth rate in diameter
RGR_H	Relative growth rate in height
RGR_M	Relative growth rate in mass
RMF	Root mass fraction
SLA	Specific leaf area

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SMF	Stem mass fraction
α	Apparent quantum yield
$\phi(I_0)$	Quantum yield at $I = 0$ μmol (photon) $m^{-2}\ s^{-1}$

Introduction

Interspecific variations among congeneric species are directly related to their evolution and ability to occupy different habitats or ecological niches (Singhakumara et al. 2003; Rossatto et al. 2013). Studies with congeneric species minimized the effect of phylogenetic differences and make clearer the ecological filters that limit the distribution and occurrence of a plant species (Bevill and Louda 1999; Lloyd et al. 2002; Swenson et al. 2006; Zhang et al. 2010). The genus *Inga* has approximately 300 species and is one of the most abundant and diversified in the plant kingdom (Valencia et al. 1994; Steege et al. 2013; Nicholls et al. 2015; Wiggins et al. 2016). In Brazil, it is represented by about 144 species, of which 72% are restricted to the Brazilian Atlantic Rainforest (Mata 2009). Among *Inga* spp., two are noteworthy for the contrast of distribution on Brazilian territory. *Inga marginata* and *I. subnuda* are evergreen N-fixing tree species in initial stages of forest regeneration (Aidar et al. 2003; Simonelli et al. 2010; Marchiori et al. 2016), and they are very important for forest restoration (Ferreira et al. 2007; Ramos Silva and Corrêa 2008) and agroforestry systems (Souza et al. 2012). Both species are usually classified as pioneers or early successional (Ramos Silva and Corrêa 2008; Rolim et al. 2006; Guaratini et al. 2008). However, *I. marginata* has a wide geographic distribution and occurs in the Cerrado (Brazilian savanna), Amazonian Forest, Pantanal, and Brazilian Atlantic Rainforests (Teixeira et al. 2008; Siminski et al. 2011; Silva et al. 2016), whereas *I. subnuda* is endemic to the Brazilian Atlantic Forest (Peterle et al. 2015; Silva et al. 2015), with high occurrence in restinga areas (Zamith and Scarano 2004; Souza et al. 2008; Peterle et al. 2015; Silva et al. 2015) and lowland and montane rainforests (Peterle et al. 2015).

The light gradients inside forest ecosystems influence the colonization and spatial distribution of species and position occupied by each species in the ecological succession (Swaine and Whitmore 1988; Bazzaz and Pickett 1980; Valladares et al. 2000; Poorter et al. 2006; Valladares and Niinemets 2008). The pioneer or early successional trees usually have characteristics similar to those of sun plants, whereas trees that regenerate in the late successional stages, have the typical characteristics of shade plants in their initial growth phase (seedlings and saplings) (Bazzaz and Pickett 1980; Swaine and Whitmore 1988; Poorter et al. 2006). The adjustments to light changes during forest succession are related to changes in leaf and whole-plant carbon balance (Givnish 1988; Aleric and Kirkman 2005). Low light availability compromises the net carbon gain, and light levels above the processing capacity of plants can damage the photosynthetic apparatus (Lüttge 2008). In both situations, impairments to the growth (Kitajima 1994; Aleric and Kirkman 2005; Lusk and Jorgensen 2013) and survival (Kitajima 1994; Ashton et al. 1995; Goodale et al. 2014) of seedlings and saplings are observed. In addition, inside a forest, seedlings and saplings sometimes grow under the shade of larger trees and may be subjected to a high incidence of light in the gaps (Palow and Oberbauer 2009). The ability of seedlings and saplings of different tree species to tolerate low light levels inside a forest is a very important feature that drives forest dynamics and structure (Valladares and Niinemets 2008). However, the ability to tolerate high light is important for plants to colonize gaps or open areas (Davies 1998).

Plants are very plastic organisms, and several morphological, anatomical, and physiological characteristics contribute to the ability of plants to cope with multiple environmental factors (Chapin et al. 1987) and colonize different ecosystems. Plants adapted to the shade environments of forest understories have higher chlorophyll content and lower chlorophyll *a*/*b* ratio (Boardman 1977; Givnish 1988; Valladares and Niinemets 2008). In addition, shade plants have a higher apparent quantum yield (α), lower dark respiration rate (Rd), lower light compensation point (LCP), as well as lower maximum gross photosynthetic rate in saturating light (Pgmax) than sun plants (Givnish 1988; Lee 1996; Yano and Terashima 2004; Pearcy 2007; Hallik et al. 2012; Yang et al. 2013). Sun plants have thicker leaves, higher carotenoid content (Carot), and greater stomatal density when compared to shade plants (Strauss-Debenedetti and Bazzaz 1996). Plants adapted to dry environments exhibit some morphological and physiological characteristics similar to those of plants adapted to high light environments (Chaves et al. 2002; Lüttge 2008), such as mechanisms to dissipate the high excitation states of energy during the photochemistry of photosynthesis. Although analysis of physiological and anatomical changes may elucidate the adaptive strategies of plants in different ecosystems, biomass allocation can also be an excellent descriptor of the ability of plants to cope with multiple environmental limiting factors (Gleeson and Tilman 1992). For example, Markesteijn and Poorter (2009) compared the seedling root morphology and biomass allocation of 62 tropical tree species and reported that the average values of leaf area (LA), specific leaf area (SLA), leaf mass fraction (LMF), and leaf area ratio (LAR) were significant higher in the species of moist rather than dry forests; the average values of root mass fraction (RMF) were significantly higher in the seedlings of dry forest trees. Thus, congeneric species are expected occupy the same position in the ecological succession but have different geographical distributions (moist versus dry tropical forests), similar physiological characteristics in relation to shade tolerance, and different biomass allocation attributes related to the capacity to colonize drought-prone ecosystems.

We considered that *I. marginata* and *I. subnuda* have similar positions in the forest succession and different geographic distributions and conducted this study to compare their physiological growth and biomass allocation responses to contrasting light environments. We tested the hypothesis that these two congeneric species have similar photosynthetic and growth responses to contrasting light availability but different biomass allocations.

Materials and methods

Study site, plant materials, and experimental set-up

The experiment was performed at Universidade Estadual de Santa Cruz (UESC), located in Ilhéus, Bahia, Brazil (39°13′59″O; 14°45′15″S). The seedlings were produced in the Instituto Floresta Viva nursery, Serra Grande, Uruçuca, Bahia, Brazil (39°7′60″W, 14°31′0″S). At 120 days after germination, 64 plants of each species were transferred to UESC and transplanted in 1.5-L plastic bags containing the forest soil as the substrate. After 1 week of acclimatization, 54 plants of each species were placed in PVC tubes of 100 mm diameter and 250 mm height. A randomized block design was used, where a single repetition of each light environment was assigned to each block (a total of three treatments and three blocks). In each block, six plants of each species were placed, with a total of 18 plants per light environment. At 80 days after the beginning of the experiment, supplemental fertilization was performed, that is, 50 mL of the following solution was applied to each plant: 10 L of water, 26.34 g of urea, 40 g of monoammonium phosphate (MAP), and 10.68 g of potassium chloride (KCl) as a source of the basic nutrients nitrogen, phosphorus, and potassium, respectively. The experiment had a total duration of 105 days.

The plants were grown at three levels of light availability. The light environments were established using black screens arranged on wooden structures of 1 m width × 1 m length × 0.80 m height. Each light environment was repeated three times. The photosynthetic active radiation (PAR) was monitored in each treatment by using S-LIA-M003 light radiation sensors coupled to Hobo Micro Station Data Logger H21-000 (Onset, USA). Temperature (*T*) and relative air humidity (RH) were monitored throughout the experiment with an S-THB-M002 sensor coupled to the data logger. The air vapor pressure deficit (VPD) was calculated from the values of T and RH. The station was programmed to collect PAR data every second and store the average values every 10 min. The average daily PAR was calculated from the data stored every 10 min, after considering the time of sunrise and sunset. The mean PAR values throughout the experiment in the three light environments were approximately 36 (L1), 15 (L2), and 6 (L3) mol photons m^{-2} day^{-1}. During the experiment, the daily mean values of T and VPD were 24.5 °C and 0.63 kPa, and the maximum daily values were 37.6 °C and 3.2 kPa, respectively.

Plant growth and biomass allocation

At the beginning of the experiment, ten plants of each species were used to measure the height (*H*), stem diameter (*D*), number of leaves (LN), leaf area (LA), and dry mass of roots (RDM), stems (SDM), leaves (LDM), and their total (TDM). The LA was measured with an LI-3100 area meter (Li-Cor, Inc. Lincoln, Nebraska, USA). The biomass was measured after washing the plants, separating the roots, stems, and leaves and storing them in properly labeled paper bags, and drying all the plant tissues in a forced circulation oven at 50 °C to constant dry mass. At 105 days after the start of the experiment, evaluation of D, H, and LN as well as biomass and LA was performed in all plants of the experiment, followed by the same procedures performed at the beginning of the experiment. From the biomass values, we calculated the following variables: specific leaf area (SLA = LA/LDM), leaf area ratio (LAR = LA/TDM) and stem (SMF = SDM/TDM), leaf (LMF = LDM/TDM) and root (RMF = RDM/TDM) mass fraction. The mean relative growth rate in mass (RGR_M) and mean net assimilation rate (NAR) were calculated following Hunt (1990): $RGR_M = ([1nTDM_{105} - 1nTDM_0]/105)$ and $NAR = [(TDM_{105} - TDM_0)/(LA_{105} - LA_0)] \times [(lnLA_{105} - lnLA_0)/105]$; where 105 is the total time in days from the beginning to the end of the experiment. Based on the first and last measurements of *D* and *H* we calculated the relative growth rates in diameter (RGR_D) and height (RGR_H) following the same procedure described above for RGR_M.

Light–response curves

The light–response curves were created at the end of the experiment by analysis of leaf gas exchange with a portable LI6400 photosynthesis measurement system (Li-Cor, USA) equipped with a 6400-02B RedBlue light source. Measurements were always obtained between 08:00 and 11:00 a.m. from the third fully expanded leaf from the apex of three individuals of each species per block/light environment. The equipment was programmed to provide instantaneous PAR values of 1200, 1000, 800, 600, 400, 200, 100, 50, 25, 10, 5 and 0 µmol photons m^{-2} s^{-1} at a chamber temperature of 27 °C and CO_2 concentration (394.92 ± 2.69 µmol mol^{-1}). Then, six models were tested for curve fitting (de Lobo et al. 2013). From the lowest value of the sum of the squares and the highest value of R^2, we selected the model proposed by Jassby and Platt (1976):

$$\mathrm{Pn} = \mathrm{Pgmax} \times \tan h\ (\phi(I_0) \times \mathrm{PAR}/\mathrm{Pgmax}) - \mathrm{Rd}, \tag{1}$$

$$\mathrm{LCP} = \tan h\,(\mathrm{Rd}/\phi(I_0) \times \mathrm{Pgmax})/\phi(I_0), \tag{2}$$

$$\mathrm{LSP} = \tan h\ ((((\mathrm{Pgmax} - \mathrm{Rd}) \times 0.85) + \mathrm{Rd})/\mathrm{Pgmax}) \times \mathrm{Pgmax}/\phi(I_0). \tag{3}$$

On the basis of this model, the following parameters were obtained: maximum net photosynthetic rate (Pn), maximum gross photosynthetic rate (Pgmax), apparent quantum efficiency (α), dark respiration rate (Rd), light compensation point (LCP) and light saturation point (LSP).

Pigment content

The contents of chlorophyll *a* (Chl *a*), *b* (Chl *b*) and carotenoids (Carot) and chlorophyll *a*/*b* ratio (Chl *a*/*b*) were measured for comparing the acclimation capacity of the light-collecting systems of the two species in the three environments (Boardman 1977; Givnish 1988; Valladares and Niinemets 2008). The total chlorophyll content, in addition to indicating the acclimatization of leaves to light availability, is related to nitrogen and magnesium contents in the leaves and, consequently, to the acquisition of these mineral nutrients (Lambers et al. 2008). For chlorophyll extraction, the third fully expanded leaf of four seedlings per species/block/treatment was used. Chlorophyll measurements were obtained from the same leaves in which photosynthesis were measured. Five leaf discs, whose sum of areas is equal to 1 cm^2, were removed from the leaves and immersed in tubes containing 3 mL of dimethylsulfoxide (DMSO) and saturated with 5% $\mathrm{CaCO_3}$ (Hiscox and Israelstam 1979). The tubes containing the samples were wrapped in foil for protection from light and maintained for 24 h at room temperature (25 °C). Then, absorbance of the extracts was measured at wavelengths 480, 649, and 665 nm by using a dual beam spectrophotometer (Mesu Lab Enterprise Co, Ltda., China). The contents of chlorophylls and carotenoids were calculated on the basis of area by using the equations proposed by Wellburn (1994).

Statistical analysis

We performed analysis of variance (two-way ANOVA), followed by Tukey's mean comparison test at 5% level of significance by using statistical software R. A randomized block design was used in a 2 × 3 × 3 factorial scheme with two species, three light environments, three blocks, and six plants per species/block for growth and biomass allocation variables, three plants per species/block for light–response curves, and four plants per species/block for pigment contents.

Results

All the seedlings of the two species survived the different light levels, and no type of pathogen injury or insect attack was observed during the experiment. Independent of light conditions, significant differences between species were observed for $\mathrm{RGR_M}$, $\mathrm{RGR_D}$, RMF, SMF, LMF, LAR, LN, SLA, Chl*a* + *b*, Chl*a*/Chl*b* ratio, and Carot (Table 1). Non-significant differences were observed between species for all light-response curve parameters. Among variables with significant differences between species, the average values of $\mathrm{RGR_M}$, $\mathrm{RGR_D}$, LMF, LAR, SLA, and Chl*a* + *b* were higher for *I. subnuda* than for *I. marginata*. Conversely, the average values of RMF, SMF, LN, Chl*a*/Chl*b* ratio, and Carot were higher for *I. marginata* than for *I. subnuda*. Independent of the light environment, the average values of LMF, LAR, and SLA were about 16%, 36%, and 34%, respectively, higher for *I. subnuda* than for *I. marginata*.

The light environments significantly influenced NAR, $\mathrm{RGR_M}$, $\mathrm{RGR_H}$, $\mathrm{RGR_D}$, RMF, LMF, LAR, SLA, Rd, LCP, Chl*a*, and Chl*b* (Table 1). With the increments in light availability, and independent of the species, NAR, $\mathrm{RGR_M}$, $\mathrm{RGR_D}$, RMF, and Rd increased but $\mathrm{RGR_H}$, LMF, LAR, Chl*a*, and Chl*b* decreased (Table 2). From the highest (L1) to lowest (L3) light conditions, for both species, decreases in order of 27% and 51% were observed for $\mathrm{RGR_M}$ and NAR, respectively. Conversely, an increase in the order of 78% was observed from L1 to L3 for LAR (Table 2).

Interactions between species and light environments were observed only for LAR, SLA, and LCP (Table 1). The average values of LAR were higher for *I. subnuda* than for *I. marginata* in all the light environments. A proportional decrease was observed for *I. marginata* with increased light availability, but no significant difference for this variable between L2 and L3 was detected for *I. subnuda* (Table 3). From L1 to L3, increases in LAR in the order of 85% and 73% were observed for *I. marginata* and *I. subnuda*, respectively. A similar trend was observed for SLA. From L1 to L3, increases in SLA in the order of 82% and 73% were observed for *I. marginata* and *I. subnuda*, respectively. The average values of LCP increased proportionally to the light availability for *I. marginata*; however, after a significant increase in LCP was observed between L3 and L2, a significant decrease was observed from L2 to L1 for *I. subnuda*.

Table 1 Mean values (±se) and significance levels of two-way ANOVA for net assimilation rate (NAR, mg cm^2 day^{-1}), relative growth rate in mass (RGR_M, mg g^{-1} day^{-1}), height (RGR_H cm cm^1 day^{-1}), and diameter (RGR_D mm mm^{-1} day^{-1}), root mass fraction (RMF), stem mass fraction (SMF), leaf mass fraction (LMF), leaf area ratio (LAR cm^2 g^{-1}), number of leaves (LN), specific leaf area (SLA cm^2 g^{-1}), maximum gross photosynthetic rate (Pgmax, μmol CO_2 m^{-2} s^{-1}), dark respiration rate (Rd, μmol CO_2 m^{-2} s^{-1}), apparent quantum efficiency (α, μmol CO_2 μmol $photons^{-1}$), light compensation point (LCP, μmol photons m^{-2} s^{-1}), light saturation point (LSP, μmol photons m^{-2} s^{-1}), chlorophyll *a* (Chl*a*, mg m^{-2}), chlorophyll *b* (Chl*b*, mg m^{-2}), total (Chl*a*+*b*, mg m^{-2}), Chl*a*/Chl*b* ratio, carotenoids (Carot, mg m^{-2}) of young plants of *Inga* spp. subjected to contrasting light conditions for 105 days

Variable	Species		Anova		
	I. marginata	*I. subnuda*	Species (*S*)	Light (*L*)	$S \times L$
NAR	0.27±0.05	0.26±0.05	ns	***	ns
RGR_M	17.25±1.76	20.78±1.74	***	***	ns
RGR_H	0.009±0.001	0.009±0.001	ns	***	ns
RGR_D	0.006±0.0004	0.008±0.0004	***	***	ns
RMF	0.36±0.08	0.26±0.06	***	*	ns
SMF	0.23±0.02	0.14±0.02	*	ns	ns
LMF	0.41±0.02	0.60±0.03	***	***	ns
LAR	73.46±12.54	98.70±15.21	***	***	*
LN	21.52±2.15	10.98±1.2	**	ns	ns
SLA	73.46±7.10	98.70±10.27	***	***	*
Pgmax	10.60±1.42	11.65±0.97	ns	ns	ns
Rd	0.62±0.07	0.64±0.12	ns	***	ns
α	0.044±0.013	0.047±0.013	ns	ns	ns
LCP	14.32±1.82	13.49±1.99	ns	**	***
LSP	365.74±45.50	378.90±33.66	ns	ns	ns
Chla	56.09±2.75	64.13±3.68	ns	**	ns
Chlb	33.97±1.77	43.48±2.63	ns	***	ns
Chla+b	90.06±4.46	107.62±5.96	***	ns	ns
Chla/Chlb	1.65±0.02	1.48±0.06	***	ns	ns
Carot	7.24±0.51	6.78±0.40	***	ns	ns

ns, $p > 0.05$; *$p \le 0.05$; **$p \le 0.01$

Table 2 Mean values (±se) of for net assimilation rate (NAR, mg cm^2 day^{-1}), relative growth rate in mass (RGR_M, mg g^{-1} day^{-1}), height (RGR_H cm cm^1 day^{-1}) and diameter (RGR_D mm mm day^{-1}), leaf mass fraction (LMF), root mass fraction (RMF), dark respiration rate (Rd, μmol CO_2 m^{-2} s^{-1}), and contents of chlorophyll *a* (Chl*a*, mg m^{-2}) and chlorophyll *b* (Chl*b*, mg m^{-2}) of young plants of *Inga* spp. subjected to contrasting light conditions for 105 days

Variable	PAR (mol photons m^{-2} day^{-1})		
	L1 (36)	L2 (15)	L3 (6)
NAR	0.37±0.01a	0.26±0.01b	0.18±0.01c
RGR_M	21.57±0.40a	19.81±0.41b	15.67±0.44c
RGR_H	0.071±0.001b	0.0107±0.001^{a}	0.0103±0.001a
RGR_D	0.0082±0.0006a	0.0079±0.0005b	0.0067±0.0006c
RMF	0.63±0.03a	0.54±0.06^{a}	0.33±0.02b
LMF	0.50±0.01c	0.54±0.02b	0.61±0.01a
Rd	0.85±0.07a	0.77±0.08^{a}	0.26±0.04b
Chl*a*	58.58±2.84	60.45±1.85^{a}	61.52±2.04a
Chl*b*	36.99±1.84a	38.00±1.41^{a}	39.44±1.44a

Means followed by the same letters do not differ between light environments. All comparisons were made by the Tukey's test at the 5% probability level

Discussion

Morphological and physiological adjustments such as those that occur in *I. marginata* and *I. subnuda* are inherent to the process of acclimatization of plants to contrasting light environments (Valladares and Niinemets 2008). Among the changes, we highlighted the decrease in LAR and increase in NAR with an increase in light availability. The decrease in LAR promotes a decrease in the transpiration demand, whereas the increase in NAR reflects the changes in carbon balance at leaf and plant scales and contributes to higher RGR_M. However, the lower values of NAR and RGR_M in L2 and L3 indicate impairment of growth of the young plants of *I. marginata* and *I. subnuda* below 15 mol photons m^{-2} day^{-1}. The higher RGR_H and lower RGR_D under low light availability are recurrent in forest species as a shade escape strategy (Davidson et al. 2002; Yang et al. 2013; Amissah et al. 2015). Higher RGR_H, associated with the maintenance of positive photosynthetic rates, indicates that both species can respond to a gap-opening situation (Matsubara et al. 2008). However, the investment in height

Table 3 Mean values (±se) of specific leaf area (SLA $cm^2\ g^{-1}$), leaf area ratio (LAR, $cm^2\ g^{-1}$), and light compensation point (LCP, μmol photons $m^{-2}\ s^{-1}$) of young plants of *Inga* spp. subjected to contrasting light environments for 105 days

Variable	Species	PAR (mol photons m^{-2} day^{-1})		
		L1 (36)	L2 (15)	L3 (6)
LAR	*I. marginata*	52.76 ± 2.12Bc	71.50 ± 3.72Bb	96.11 ± 2.85Ba
	I. subnuda	69.10 ± 3.18Ab	107.40 ± 6.33Aa	119.61 ± 3.07Aa
SLA	*I. marginata*	52.77 ± 5.21Bc	71.51 ± 9.12Bb	96.11 ± 6.99Ba
	I. subnuda	69.10 ± 7.78Ab	107.40 ± 15.51Aa	119.62 ± 7.52Aa
LCP	*I. marginata*	22.19 ± 2.33Aa	14.10 ± 1.33Ab	6.67 ± 1.79Ac
	I. subnuda	17.54 ± 1.57Ab	18.20 ± 3.04Aa	4.72 ± 1.36Ac

Means followed by the same capital letter do not differ between species, and means followed by the same lowercase letters do not differ between light environments. All comparisons were performed using Tukey's test at 5% probability level

occurs at the expense of a smaller increment in diameter, as exhibited by the lower values of RGR_D in L2 and L3 for both species; this makes them more susceptible to mechanical damage.

With respect to biomass allocation, *I. marginata* allocated more carbon to roots than *I. subnuda* did, which may indicate a larger storage capacity that would allow seedlings to survive in limited light environments and have reserves to respond rapidly when light availability increases (DeLucia et al. 1998; Saldanã-Acosta et al. 2009; Yang et al. 2013). However, higher values of LMR can be considered a strategy of *I. subnuda* to increase the carbon gain (Souza and Válio 2003; Feijó et al. 2009), leading to the higher values of RGR_M observed for this species under all light conditions. Plants growing in environments with greater light availability usually have increased leaf temperature and are subjected to a higher evaporative demand of the atmosphere, which leads to higher transpiration rates (Lenhard et al. 2013). Higher values of RMF, and lower values of LAR, under high light availability, as found in *I. marginata*, can be considered a strategy to maintain higher water supply and hydration of plants (Poorter and Markesteijn 2008; Markesteijn and Poorter 2009; Cortina et al. 2013). However, the higher allocation of biomass to leaves (higher LAR values), associated with the increase in SLA, in environments with low light availability, as found in *I. subnuda*, indicates a greater investment of carbon to capture light (Santelices et al. 2014; Tang et al. 2015). Thus, the higher mean values of RMF and lower LAR and SLA verified for *I. marginata* indicate different strategies for occupancy of similar niches for the two species in different ecosystems. *I. subnuda* invests in light capture (higher LAR and SLA), and *I. marginata* invests in storage (higher RMF). In addition, the lower values of LAR and SLA and higher values of RMF in *I. marginata* than in *I. subnuda* indicate a greater capacity to cope with environments with limited water (Poorter and Markesteijn 2008; Markesteijn and Poorter 2009), which is consistent with its wide geographic distribution (Teixeira et al. 2008; Siminski et al. 2011; Silva et al. 2016).

Under low light availability, plants tend to produce leaves whose epidermis is thinner, with larger surface area per unit mass and more spongy structure (Givnish 1988; Gong et al. 2016). The inherent high values of leaf mass per area, the inverse of SLA, are related to the occurrence of a plant species in dry and nutrient-poor habitats (Wright et al. 2002). The significantly higher values of SLA in *I. subnuda* than in *I. marginata* in all the light environments indicate that this species is adapted to environments where water is not a limiting factor; in contrast, *I. marginata* has the leaf characteristics of environments prone to water deficit. The comparison of SLA between the species is related to the geographic distribution: *I. subnuda* occurs in the moist forests of the Brazilian Atlantic coast (Peterle et al. 2015; Silva et al. 2015), and *I. marginata* has a widespread distribution in the central Brazilian ecosystems (Teixeira et al. 2008; Siminski et al. 2011; Silva et al. 2016). The results of the congeneric species of *Inga*, that is, *I. marginata* exhibited higher RMF, lower LAR, and lower SLA than *I. subnuda*, are consistent with those of other studies that compared seedlings and adult trees from forest and savanna formations (Hoffmann and Franco 2003).

At the leaf scale, the carbon balance of both *I. marginata* and *I. subnuda* was minimally affected by the light levels because only LCP and Rd were altered by changes in light availability. The decrease in LCP may be related to a significant decrease in Rd when plants grow under limited light conditions. Plants acclimated to shade generally have a lower concentration of photosynthesis-related proteins and enzymes, which reduces their respiratory cost (Griffin et al. 2004). The decrease in metabolic rates, as exhibited by the low values of Rd, associated with the changes in SLA in low light environments, is a typical response of plants to low light availability (Boardman 1977; Givnish 1988; Valladares and Niinemets 2008). In addition, under low irradiance conditions, lower LCP values increase the photosynthetic performance, minimizing CO_2 loss by improving carbon gain potential (Walters and Reich 1999; Santos et al. 2012; Yang et al. 2013). However, the absence of significant differences between light environments for Pgmax and LSP indicates that both species were not able to reach the maximum potential photosynthesis values throughout the experiment under light conditions below 15 mol photons m^{-2} day^{-1}. Thus, based on the data for leaf gas exchange and growth, we can conclude that the responses of both species are typical of trees that cannot tolerate shade in the phase of seedlings and saplings and need a great amount of light to complete the life cycle (Poorter 1999; Davidson et al. 2002; Souza and Válio 2003; Singhakumara et al. 2003; Kelly 2009; Yang et al. 2013).

Changes in RGR_M in response to changes in light availability are directly related to both changes in NAR and LAR (Poorter and van der Werf 1998; Poorter 1999). In our study, the decreases in NAR in low light were associated with the limited capacity of both species to reach the maximum potential photosynthesis throughout the experiment under light conditions below 15 mol photons m^{-2} day^{-1} (as the mean values of Pgmax and LSP did not change with changes in light availability). However, both species showed increased LMF and LAR and decreased RMF and Rd from the highest (L1) to the lowest (L3) light conditions. A greater dependence of RGR_M to NAR at high light and to LAR at low light is well documented in the literature, and it is dependent on changes in the carbon balance at leaf and whole-plant scales (Poorter and van der Werf 1998). For both *I. marginata* and *I. subnuda*, the low values of Rd at leaf scale and changes in biomass allocation, i.e., greater LAR and lower RMF, at whole-plant scale may be the main mechanisms of adjustment to low light availability. As discussed above, it was not sufficient to maintain high values of RGR_M, and low growth rates below 15 mol photons m^{-2} day^{-1} clearly indicate that *I. marginata* and *I. subnuda* are typical light-demanding species.

At high light availability, usually, the leaves have a lower concentration of chlorophyll, which decreases their light absorption capacity (Valladares and Niinemets 2008). This pattern was not observed in our study, where, independent of the species, the contents of Chl*a* and Chl*b* remained constant between treatments. In this scenario, the dissipation of energy becomes extremely important, reducing the risk of photoinhibition. Although the contents of Chl*a* and Chl*b* were similar among treatments, Chl*a*/Chl*b* ratio was higher in *I. marginata* than in *I. subnuda* under all light conditions. Equivalent results were found in *Dalbergia miscolobium* (savanna species), whose leaves presented higher Chl*a*/Chl*b* ratio than *Dalbergia nigra* (Atlantic rain forest species) under full sunlight (Barros et al. 2012). This alteration in the proportion of chlorophyll contents has already been interpreted as an indication of higher proportion of reaction center to light-harvesting complex, which favors higher rates of photochemical work (Demmig-Adams 1998). However, the increase in Carot content in both species when exposed to the L1 environment indicates that, under this condition, the leaves have greater capacity to dissipate the excess energy of excitation. In this case, the increased Carot content protects the chloroplast membrane from photo-oxidation by eliminating singlet oxygen and extinguishing the triplet state of chlorophyll (Demmig-Adams 1990; Tang et al. 2015). In addition, the higher mean values of Carot in *I. marginata* than in *I. subnuda* indicate that this species has more effective mechanisms to dissipate the high excitation states of energy in photosynthesis, which can be an advantage under conditions in which plants need to cope with high light and water deficit (Chaves et al. 2002).

In conclusion, our hypothesis was partially supported because the two species had similar photosynthetic responses to changes in light availability, but differences in growth and biomass allocation. The absence of significant differences between the light environments with respect to Pgmax and LSP indicates that both species were not able to reach the maximum potential photosynthesis values at 15 and 6 mol photons m^{-2} day^{-1}, demonstrating that they are typical light-demanding species. The higher RGR_M of *I. subnuda* is associated with its higher allocation of biomass to light capture, as shown by the higher values of LMF and LAR. Conversely, the higher values of RMF for *I. marginata* in contrast to the higher values of LMF, LAR, and SLA for *I. subnuda* indicate that *I. marginata* should be better adapted to environments where water could be a limiting factor, which is consistent with its wide geographic distribution.

Author contribution statement HASP, ACD and MSM designed the experiment. HASP, GSC and ACD performed the experiment. HASP and ACS performed statistical analyses. HASP, ACD, MCS, and MSM wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Aidar MPM, Schmidt S, Moss G, Stewart GR, Joly CA (2003) Nitrogen use strategies of neotropical rainforest trees in threatened Atlantic Forest. Plant Cell Environ 26:389–399

Aleric KM, Kirkman LK (2005) Growth and photosynthetic responses of the federally endangered shrub *Lindera melissifolia* (Lauraceae) to varied light environments. Am J Bot 92:682–689

Amissah L, Godefridus MJM, Kyereh B, Poorter L (2015) The effects of drought and shade on the performance, morphology and physiology of *Ghanaian* tree species. PLoS One 10:1–22

Ashton PMS, Gunatilleke CVS, Gunatilleke IAUN (1995) Seedling survival and growth of four *Shorea* species in a Sri Lankan rain forest. J Trop Ecol 11:263–279

Barros FV, Goulart MF, Sá Telles SB, Lovato MB, Valladares F, Lemos-Filho JP (2012) Phenotypic plasticity to light of two congeneric trees from contrasting habitats: Brazilian Atlantic Forest *versus* cerrado (savanna). Plant Biol 14:208–215

Bazzaz EA, Pickett STA (1980) Physiological ecology of tropical succession: a comparative review. Annu Rev Ecol Syst 11:287–310

Bevill RL, Louda SM (1999) Comparisons of related rare and common species in the study of plant rarity. Conserv Biol 13:493–498

Boardman NK (1977) Comparative photosynthesis of sun and shade plants. Ann Rev Plant Physiol 28:355–377

Chapin FS III, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. Bioscience 37:49–57

Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho I, Faria T, Pinheiro C (2002) How plants cope with water stress in the field. Photosynthesis and growth. Ann Bot 89:907–916

Cortina J, Vilagrosa A, Trubat R (2013) The role of nutrients for improving seedling quality in drylands. New For 44:719–732

Davidson R, Mauffette Y, Gagnon D (2002) Light requirements of seedlings: a method for selecting tropical trees for plantation forestry. Basic Appl Ecol 3:209–220

Davies SJ (1998) Photosynthesis of nine pioneer Macaranga species from Borneo in relation to life history. Ecology 79:2292–2308

de Lobo FA, Barros MP, Dalmagro HJ, Dalmolin AC, Pereira WE, Souza EC, Vourlitis GL, Rodriguez-Ortiz CE (2013) Fitting net photosynthetic light-response curves with Microsoft Excel a critical look at the models. Photosynthetica 51:445–456

DeLucia EH, Sipe TW, Herrick J, Maherali H (1998) Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. Am J Bot 85:955–963

Demmig-Adams B (1990) Carotenoids and photoprotection in plants: a role for the xanthophyll zeaxanthin. Biochim Biophys Acta 1020:1–24

Demmig-Adams B (1998) Survey of thermal energy dissipation and pigment composition in sun and shade leaves. Plant Cell Physiol 39:474–482

Feijó NSA, Mielke MS, Gomes FP, França S, Lavinsky A (2009) Growth and photosynthetic responses of *Gallesia integrifolia* (Spreng.) Harms and *Schinus terebinthifolius* Raddi seedlings in dense shade. Agrofor Syst 77:49–58

Ferreira WC, Botelho AS, Davide AC, Faria JMR (2007) Avaliação do crescimento do estrato arbóreo de área degradada revegetada à margem do rio Grande, na usina hidroelétrica de Camargos, MG. Rev Árvore 31:177–185

Givnish TJ (1988) Adaptations to sun and shade: a whole plant perspective. Aust J Plant Physiol 15:63–92

Gleeson SK, Tilman D (1992) Plant allocation and the multiple limitation hypothesis. Am Nat 139:1322–1343

Gong HD, Wang H, Jiao DY, Cai ZQ (2016) Phenotypic plasticity of seedlings of five tropical tree species in response to different light and nutrient availability. Trop Ecol 57:727–737

Goodale UM, Berlyn GP, Gregoire TG, Tennakoon KU, Ashton MS (2014) Differences in survival and growth among tropical rain forest pioneer tree seedlings in relation to canopy openness and herbivory. Biotropica 46:183–193

Griffin JJ, Ranney TG, Pharr DM (2004) Photosynthesis, chlorophyll fluorescence and carbohydrate content of Illicium taxa grown under varied irradiance. J Am Soc Hort Sci 129:46–53

Guaratini MTG, Gomes EPC, Tamashiro JY, Rodrigues RR (2008) Composição florística da Reserva Municipal de Santa Genebra, Campinas, SP. Rev Bras Bot 31:323–337

Hallik L, Niinemets U, Kull O (2012) Photosynthetic acclimation to light in woody and herbaceous species: a comparison of leaf structure, pigment content and chlorophyll fluorescence characteristics measured in the field. Plant Biol 14:88–99

Hiscox JD, Israelstam GE (1979) A method for the extraction of chlorophyll from leaf tissue without maceration. Can J Bot 57:1332–1334

Hoffmann WA, Franco AC (2003) Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. J Ecol 91:475–484

Hunt T (1990) Basic growth analysis: plant growth analysis for beginners. Unwin Hyman, London

Jassby AD, Platt T (1976) Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol Oceanogr 21:540–547

Kelly J (2009) Growth and physiological response of six Australian rainforest tree species to a light gradient. For Ecol Manage 257:287–293

Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. Oecologia 98:419–428

Lambers H, Chapin STIII, Pons TJ (2008) Plant physiological ecology. Springer, New York

Lee WD (1996) Irradiance and spectral quality affect asian tropical rain forest tree seedling development. Ecology 77:568–580

Lenhard NR, Paiva Neto VB, Scalon Sde PQ, Alvarenga AA (2013) Crescimento de mudas de pau-ferro sob diferentes níveis de sombreamento. Pesqu Agropecu Trop 43:178–186

Lloyd KM, Lee WG, Wilson JB (2002) Competitive abilities of rare and common plants: comparisons using *Acaena* (Rosaceae) and *Chionochloa* (Poaceae) from New Zealand. Conserv Biol 16:975–985

Lusk CH, Jorgensen MA (2013) The whole-plant compensation points as a measure of juvenile tree light requirements. Funct Ecol 27:1286–1294

Lüttge U (2008) Physiological ecology of tropical plants. Springer, Berlin

Marchiori NM, Rocha HR, Tamashiro JY, Aidar MPM (2016) Tree community composition and aboveground biomass in a secondary Atlantic forest, Serra do Mar State Park, São Paulo, Brazil. Cerne 22:501–514

Markesteijn L, Poorter L (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J Ecol 97:311–325

Mata MF (2009) O Gênero *Inga* (Leguminosae, Mimosoideae) no Nordeste do Brasil: Citogenética, Taxonomia e Tecnologia de Semente. Tese de Doutorado, Programa de Pós-Graduação em Agronomia. Universidade Federal da Paraíba, Areia, PA. p 229

Matsubara S, Krause GH, Seltmann M, Virgo A, Kursar TA, Jahns P, Winter K (2008) Lutein epoxide cycle, light harvesting and photoprotection in species of the tropical tree genus *Inga*. Plant Cell Environ 31:548–561

Nicholls JA, Pennington RT, Koenen EJM, Hughes CE, Hearnl J, Bunnefeld L, Dexer KG, Stonel GN, Kidner CA (2015) Using targeted enrichment of nuclear genes to increase phylogenetic resolution in the neotropical rain forest genus *Inga* (Leguminosae: Mimosoideae). Front Plant Sci 6:1–20

Palow DT, Oberbauer SF (2009) Soil type affects seedling shade response at low light for two Inga species from Costa Rica. Plant Soil 319:25–35

Pearcy RW (2007) Responses of plants to heterogeneous light environments. In: Pugnaire FI, Valladares F (eds) Handbook of functional plant ecology. CRC Press, Boca Raton, pp 213–257

Peterle PL, Chagas AP, Thomaz LD, Dutral VF, Valadares RT (2015) Mimosoideae (Leguminosae) do Parque Estadual Paulo César Vinha, Espírito Santo, Brasil. Rodriguesia 66:245–257

Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morfological and physiological traits. Func Ecol 13:396–410

Poorter L, Markesteijn L (2008) Seedling traits determine drought tolerance of tropical tree species. Biotropica 40:321–331

Poorter H, van der Werf A (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Backhuys Publishers, Leiden, pp 309–336

Poorter L, Bongers L, Bongers F (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology 87:1289–1301

Ramos Silva LC, Corrêa RS (2008) Sobrevivência e crescimento de seis espécies arbóreas submetidas a quatro tratamentos em área minerada no Cerrado. Rev Árvore 32:731–740

Rolim SG, Ivanauskas NM, Rodrigues RR, Nascimento MT, Gomes JML, Folli DA, Couto HTZ (2006) Composição florística do estrato arbóreo da Floresta Estacional Semidecidual na planície aluvial do rio Doce, Linhares, ES, Brasil. Acta Bot Bras 20:549–561

Rossatto DR, Hoffmann WA, Ramos Silva LC, Haridasan M, Sternberg LSL, Franco AC (2013) Seasonal variation in leaf traits between congeneric savanna and forest trees in Central Brazil: implications for forest expansion into savana. Trees 27:1139–1150

Saldanã-Acosta A, Meave JA, Sanchez-Velasquez LR (2009) Seedling biomass allocation and vital rates of cloud forest tree species: responses to light in shade house conditions. For Ecol Manage 258:1650–1659

Santelices R, Espinoza S, Cabrera AM (2014) Effect of four levels of shade on survival, morphology and chlorophyll fluorescence of *Nothofagus alessandrii* container-grown seedlings. iForest 8:638–641

Santos TA, Mielke MS, Peireira HAS, Gomes FP, da Silva DC (2012) Leaf gas exchange and growth of *Protium heptaphyllum* March (Burseraceae) seedlings subjected to soil flooding under two light environments. Sci For 40:047–056

Silva ED, de Tozzi AMGA, Meireles LD (2015) Distribution of Leguminosae tree species in different altitudinal levels along the Atlantic Rain Forest in the Brazilian coast. J Syst Evol 53:266–279

Silva ED, de Tozzi AMGA, Meireles LD (2016) Leguminosae in an altitudinal gradient in the Atlantic Forest of Serra do Mar State Park, São Paulo, Brazil. Biota Neotrop 16:1–15

Siminski A, Fantini AC, Guries RP, Ruschel AR, Reis MS (2011) Secondary forest succession in the Mata Atlantica, Brazil: floristic and phytosociological trends. ISRN Ecol 11:1–19

Simonelli M, Magnago LFS, Martins SV, Matos FAR, Demuner VG (2010) Composição de espécies arbóreas em três estádios sucessionais de floresta ciliar na Lagoa Jacunem, Espírito Santo, Brasil. Bol Mus Biol Mello Leitão 28:5–19

Singhakumara BMP, Gamage HK, Ashton MS (2003) Comparative growth of four *Syzygium* species within simulated shade environments of a Sri Lankan rain forest. For Ecol Manage 174:511–520

Souza RP, Válio IFM (2003) Seedling growth of fifteen Brazilian tropical tree species differing in successional status. Rev Bras Bot 26:35–47

Souza RD, Correia MEF, Pereira MG, Silva EMR, Paula RR, Menezes LFT (2008) Estrutura da comunidade da fauna edáfica em fragmentos florestais na Restinga da Marambaia, RJ. Ver Bras de Ciências Agrárias 3:49–57

Souza HN, Goede RGM, Brussaard L, Cardoso IM, Duarte EMG, Fernandes RBA, Gomes LC, Pulleman MM (2012) Protective shade, tree diversity and soil properties in coffee agroforestry systems in the Atlantic Rainforest biome. Agric Ecosyst Environ 146:179–196

Steege H, Pitman N, Sabatier D, Baraloto C, Salomão JE, Guevara JE et al (2013) Hyperdominance in Amazonian tree the flora. Science. https://doi.org/10.1126/science.1243092

Strauss-Debenedetti S, Bazzaz F (1996) Photosynthetic characteristics of tropical trees along successional gradients. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 162–186

Swaine MD, Whitmore TC (1988) On the definition of ecological species groups in tropical rainforest. Veget 75:81–96

Swenson NG, Enquist BJ, Pither J, Thompson J, Zimmerman J (2006) The problem and promise of scale dependency in community phylogenetics. Ecology 87:2418–2424

Tang H, Hu YY, Yu -Y, Song LL, Wu JS (2015) Photosynthetic and physiological responses of *Torreya grandis* seedlings to varied light environments. Trees 29:1011–1022

Teixeira AP, Assis MA, Siqueira FR, Casagrande JC (2008) Tree species composition and environmental relationships in a Neotropical swamp forest in Southeastern Brazil. Wetlands Ecol Manage 16:451–461

Valencia R, Balslev H, Miño GP (1994) High tree alpha diversity in Amazonian Ecuador. Biodivers Conserv 3:21–28

Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. Annu Rev Ecol Evol Syst 39:237–257

Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81:1925–1936

Walters MB, Reich PB (1999) Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? New Phytol 143:143–154

Wellburn AR (1994) The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids using various solvents with spectrophotometers of different resolution. J Plant Physiol 144:307–313

Wiggins NL, Forrister DL, Endara MJ, Coley PD, Kursar TA (2016) Quantitative and qualitative shifts in defensive metabolites define chemical defense investment during leaf development in Inga, a genus of tropical trees. Ecol Evol 6:478–492

Wright IJ, Westoby M, Reich PB (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. J Ecol 90:534–543

Yang W, Liu F, Zhou L, Zhang S, An L (2013) Growth and photosynthetic responses of *Canarium pimela* and *Nephelium topengii* seedlings to a light gradient. Agrofor Syst 87:505–516

Yano S, Terashima I (2004) Developmental process of sun and shade leaves in *Chenopodium album* L. Plant Cell Environ 27:781–793

Zamith LR, Scarano FR (2004) Produção de mudas de espécies das Restingas do município do Rio de Janeiro, RJ, Brasil. Acta Bot Bras 18:161–176

Zhang J, Song B, Li B, Ye J, Wang X, Hao Z (2010) Spatial patterns and associations of six congeneric species in an old-growth temperate forest. Acta Oecol 36:29–38