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Species-specific performance and trade-off between growth and survival in the early-successional light-demanding group

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Abstract

We investigated if high irradiance imposes stress conditions and differently affects the performance of species from the early-successional light-demanding group and if the costs associated with plasticity underlie the trade-off between growth and survival. Survival, growth, chlorophyll *a* fluorescence, and carbon stable isotopic ratio ($\delta^{13}C$) were measured in seedlings of four tree species in a restoration area in the Atlantic Forest under full-sun exposure and partial shading treatments. The maximal quantum yield of PSII indicated stress conditions mainly in the full-sun exposure treatment (values from 0.72 to 0.81). The $\delta^{13}C$ ranged from –31.9 to –30.4‰, but did not differ between treatments for three species, suggesting that C assimilation in initial restoration conditions is stressful even in shade. The survival scaled negatively with growth and plasticity adjustments. We conclude that early-successional species do not form a homogenous species group because they differ in functional responses to stress, and phenotypic plasticity, with these variations showing a strong link with the trade-off between growth and survival. This information should be taken into account for species selection in restoration programs.

Keywords: biodiversity hotspots; chlorophyll *a* fluorescence; functional traits; leaf traits; photochemical parameters.

Introduction

Irradiance is well known for acting as a local environmental filter by restricting the establishment, growth, and reproduction of species depending on their photosynthetic light demands and the ability to adjust functional traits (Bazzaz and Pickett 1980, Silva *et al.* 2010, Lusk *et al.* 2011, Rabelo *et al.* 2013, Mediavilla *et al.* 2014, Teixeira

Highlights

- Early-successional species do not form a homogenous group in responses to stress
- Initial restoration conditions can be stressful even in partial shading conditions
- The differentiation in species' performances reveals a continuum of adaptive responses

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Abbreviations: C – elemental carbon; C_i – intercellular CO_2 concentration; D – diameter at soil level; F_v/F_m – maximal quantum yield of PSII; H – height; LA – leaf area; NL – number of leaves; NPQ – nonphotochemical quenching coefficient; PCA – principal component analysis; PC1 – first principal component; PC2 – second principal component; q_P – photochemical quenching coefficient; RCI – relative chlorophyll index; RDPI – relative distance plasticity index; RGR – relative growth rate; SLA – specific leaf area; $\delta^{13}C$ – C stable isotopic ratio.

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et al. 2015, 2018; Kardiman *et al.* 2019). Functional traits are defined as morpho-physio-phenological traits which impact fitness indirectly *via* their effects on growth, reproduction, and survival, the three components of individual performance (Violle *et al.* 2007). High irradiance often reduces the leaf's ability to properly maintain the photochemical apparatus, which in turn decreases the net photosynthesis, particularly during the seedling stage (Vitória *et al.* 2016, Paula *et al.* 2019).

Plant performance in stressful environments depends on both individual and coordinated adjustments in functional traits (Bongers *et al.* 2017, Delhaye *et al.* 2020). For example, high irradiance can improve the carbon gain and favor the plant growth, but it comes at the cost of adjusting several, if not all, leaf traits to avoid photoinhibition (Vieira *et al.* 2015, Vitória *et al.* 2016). In addition, high irradiance can increase the need for a high carotenoids (Car)/chlorophyll (Chl) ratio, high dissipation of excess excitation energy and high maximal quantum yield of PSII (F_v/F_m), low specific leaf area, and high discrimination against $^{13}CO_2$ that results in ^{13}C-enriched leaf tissues (Farquhar *et al.* 1989, Demmig-Adams and Adams 1992, Lage-Pinto *et al.* 2012, Goldstein *et al.* 2016, Paula *et al.* 2019). On the other hand, low irradiance can benefit species performance by reducing the costs associated with photoacclimation, although it leads to low growth rates (Vieira *et al.* 2015, Paula *et al.* 2019).

Early-successional species evolved to deal with high irradiance, not only due to a particular set of functional traits, such as high dark respiration rate, light-compensation point, light-saturated net photosynthetic rate, and dissipation of excess excitation energy, but also due to higher phenotypic plasticity compared to late successional species (Vitória *et al.* 2016, Calzavara *et al.* 2019). Phenotypic plasticity, defined as the ability of an organism to express different phenotypes triggered by environmental variations (Gratani 2014), is assumed to enable beneficial adjustments, particularly in open areas where high irradiance imposes restrictions against several species (Winn 1996, Kenzo *et al.* 2011). Phenotypic plasticity allows functional adjustments that may increase the species performance in photosynthesis, reproduction, survival, and growth (DeWitt *et al.* 1998, Valladares *et al.* 2000, Valladares and Niinemets 2008, Couso and Fernández 2012, dos Anjos *et al.* 2015, Cerqueira *et al.* 2018, Silva *et al.* 2020), although some plasticity adjustments are neutral or may not result in improved performance (van Kleunen and Fischer 2005, Sánchez-Gómez *et al.* 2006, Ghalambor *et al.* 2007, Liu *et al.* 2016). High phenotypic plasticity may also lack beneficial adjustments, and even compromise the survival and growth in stressful environments such as restoration areas (DeWitt *et al.* 1998, Alpert and Simms 2002, Gianoli and González-Teuber 2005, Valladares *et al.* 2007, Valladares and Niinemets 2008, Bongers *et al.* 2017).

In restoration programs around the world, the selection of species is a critical and challenging step that determines their success, particularly in degraded and open areas (Kardiman *et al.* 2019). This is especially relevant for the Atlantic Forest of South America, which is one of the three biodiversity hotspots most vulnerable to climate change (Myers *et al.* 2000, Bellard *et al.* 2014, Scarano *et al.* 2016), and one of the biomes with high conservation priority (Fontana *et al.* 2018). In practice, the selection of species is based on their successional status, with an emphasis on two large groups formed by early-successional light-demanding species and late-successional shade-tolerant species (Swaine and Whitmore 1988, Redondo-Brenes 2007, Rodrigues *et al.* 2009, 2011; Calzavara *et al.* 2019). Despite the long tradition of prioritizing the successional status (Bazzaz and Pickett 1980, Chazdon *et al.* 1996, Strauss-Deberiedetti and Bazzaz 1996), this type of selection ignores that species may differ within the groups and, in fact, the variation among species can be large enough to create a continuum of strategies rather than groups (Goldstein *et al.* 2016). It suggests that the flexibility in the demand for light is not necessarily related to the successional status (dos Anjos *et al.* 2015, Goldstein *et al.* 2016, Cerqueira *et al.* 2018, dos Santos *et al.* 2019, Kardiman *et al.* 2019). A continuum of strategies for the use of light has been observed in seedlings, with the typical pioneers at one end of the continuum and shade-tolerant ones at the opposing end (Calzavara *et al.* 2019). However, it is not entirely clear how photoacclimation and photoplasticity of functional traits may affect the survival and growth of seedlings of light-demanding species at the beginning of the restoration, known as the most susceptible phase of the restoration process (Ruiz-Jaen and Potvin 2011, Martínez-Garza *et al.* 2013, 2016; Paine *et al.* 2015).

Here, we carried out an experiment under natural rainfall, air temperature, and photosynthetically active radiation, under full-sun exposure and partial shading treatments, in a restoration area in the Atlantic Forest of South America. The survival and growth rates as well as morphological and physiological leaf traits of four early-successional native species were measured to answer the following questions: (*1*) Does the irradiance variation impose stress and differently affect the performance of species from the early-successional light-demanding group? (*2*) Do the costs of phenotypic plasticity underlie the trade-off between growth and survival?

Materials and methods

Study area, plant material, and experimental design: The study was carried out in a restoration area at the União Biological Reserve, Rio de Janeiro state, Brazil (22°27'30"N, 42°02'15"W). This Reserve consists of 7,500 ha of preserved Atlantic Forest, and 220 ha of restoration area, which replaced an old eucalyptus plantation (*Corymbia citriodora*) after forest management programs in 2013. The vegetation is classified as lowland wet forest (Braga *et al.* 2016). The climate is tropical humid with a dry winter (Aw; Alvares *et al.* 2013), a mean annual temperature of 25°C, and a mean annual precipitation of 1,900 mm, concentrated between October and April. The environmental data sets for the experimental period are presented in Fig. 1S (*supplement*). Air temperature was measured in the studied restoration area using a thermo-hygrometer (*910.15*, *CHH*, Alla, Brazil), and rainfall was measured by a manual pluviometer. The restoration area has a gently undulating topography, which varies from the sea level to 370 m a.s.l. The soil is dystrophic red-yellow podzolic with sandy clay texture (Lima *et al.* 2011).

Four tree species were selected based on their success to survive as shown in previous restoration programs. It included *Vitex polygama* Cham., Lamiaceae; *Cupania oblongifolia* Mart., Sapindaceae; *Cytharexylum myrianthum* Cham., Verbenaceae; and *Guarea guidonia* (L.) Sleumer, Meliaceae; all classified as early-successional light-demanding species (Swaine and Whitmore 1988). As the species belong to different genera, generic names were used hereafter to facilitate reading. Seedlings of these species aged between two and three months were purchased from a commercial nursery, which produces seedlings from seeds collected at the São João River hydrographic basin, where the Reserve is located.

Seedlings were planted in an area of 9.7 ha at 2.5 m apart from each other in December 2014 (rainy season), and then monitored during 210 d from February to September 2015. Twenty seedlings per species with similar height and number of leaves were randomly selected, marked, and equally divided in two groups to be exposed to full-sun treatment [around 2,000 μmol(photon) m^{-2} s^{-1}] and partial shading [around 950 μmol(photon) m^{-2} s^{-1}]. Partial shading was achieved by artificial structures made of wooden slats and polyethylene mesh, which were placed right over the seedlings to reduce incident irradiance to levels similar to intermediate canopy understory conditions. The PPFD was measured using a quantum sensor coupled with a light meter (*Li-190* and *Li-250A*, *Li-Cor Biosciences*, Lincoln, Nebraska, USA).

Survival, growth, and morphological traits: The counting of alive seedlings, analyses of growth and morphological traits were carried out eight times in intervals of 30 d from time zero to the end of the experiment (T_0, T_{30}, T_{60}, T_{90}, T_{120}, T_{150}, T_{180}, and T_{210}). For each interval, the growth was measured through the increment in height (H [cm]), diameter at soil level (D [cm]), and number of leaves (NL), and estimated by the slope of simple linear regressions between H, D, and NL as response variables, and the time as predictor. Relative growth rate (RGR) was calculated for H, D, and NL at each interval, as: $RGR = (\ln H_1 - \ln H_0)/(t_1 - t_0)$, where H_0 and H_1 were initial and final values, and t_0 and t_1 were initial and final measurement times.

Morphological traits included the total leaf area (LA [cm^2]), specific leaf area (SLA [cm^2 g^{-1}]), and the relative Chl index (RCI). They were measured in two healthy and fully expanded leaves of ten individuals per species and treatment. Leaves were scanned with a metric scale and had the area estimated by the software *Image J 1.46r* (https://imagej.nih.gov/ij/). Then, leaves were oven-dried at 60°C for 72 h to obtain the dry mass. Specific leaf area was obtained by the ratio between LA and dry mass (Pérez-Harguindeguy *et al.* 2013). Relative Chl index was taken using a portable chlorophyll meter (*SPAD-502*, *Minolta*, Japan).

Chl *a* fluorescence: Chl *a* fluorescence was measured at the beginning and end of the experiment in four individuals per species, and two healthy and fully expanded leaves per individual, always in the third pair (Vitória *et al.* 2016). The measurements were carried out at 7:00 h using a portable modulated light fluorometer (*FMS2*, *Hansatech*, UK). Leaves were dark-adapted for 30 min prior to the measurements using leaf clamps, and then exposed to weak, modulated beam of approximately 6 μmol(photon) m^{-2} s^{-1} at 660 nm, followed by highly-intense actinic white light [10,000 μmol(photon) m^{-2} s^{-1}] during 0.8 s (Genty *et al.* 1989). The physiological traits were maximal quantum yield of PSII (F_v/F_m), photochemical quenching (q_P), and nonphotochemical quenching (NPQ) coefficients.

Carbon stable isotopic analyses: At the end of the experiment, the carbon stable isotopic ratio ($\delta^{13}C$) was determined for two fully expanded leaves in the third pair, with little to no sign of damage, for four seedlings per species per treatment. Leaves were oven-dried at 60°C for at least two days and grounded to fine powder. The elemental carbon, and carbon isotopic composition in samples of approximately 1 mg were measured by a continuous flow elemental analyzer (*Flash 2000* Organic Elemental Analyzer, *Thermo Fisher Scientific*, Germany) coupled to a stable isotope ratio mass spectrometer (*IRMS Delta V Advantage*, *Thermo Fisher Scientific*, Germany). Pee Dee Belemnite (PDB) was used as a standard for carbon analyses. The analytical precision was ± 0.1‰ for $\delta^{13}C$, and the accuracy for elemental and isotopic compositions were determined by certified standard (*Protein OAS/Isotope Cert 114859*, *Elemental Microanalysis*).

Data analyses: All statistical analyses were carried out in the *R* software (R Core Team 2019). Phenotypic plasticity was analyzed individually for H, D, NL, SLA, RCI, F_v/F_m, q_P, NPQ, and $\delta^{13}C$ for each species using the relative distance plasticity index (RDPI), which varies from zero to one and allows the comparison of traits with distinct units (Valladares *et al.* 2006). It was calculated by the *rdpi* function of the 'Plasticity' package (Ameztegui 2017). To avoid biased interpretations from multiple comparisons, a general RDPI for each species was calculated as the sum of all RDPI values. Then, the general RDPI was standardized by the highest observed value to scale the variation from zero to one. Finally, the general RDPI was modeled as a function of time for each species using cubic and quartic polynomial fits, by the *lm* and *poly* functions of the 'base' package (R Core Team 2019). The adjusted multiple coefficient of determination, and the associated *p*-values were reported.

To evaluate how much species differed in survival, growth, morphological, and physiological traits when submitted to irradiance treatments (question one), several analyses of covariance (*ANCOVA*s) were performed using the general RDPI as predictor and time as the covariable. *ANCOVA*s were run by the *glm* function of the 'base' package (R Core Team 2019). Data were transformed using the maximum likelihood by the *boxcox* function of 'MASS' package (Venables and Ripley 2002) to meet assumptions of normality, linearity, and homoscedasticity of residuals. If no effect was observed for the covariable, then models were updated to test differences in survival, growth, or general RDPI over the time only. Multiple comparisons among species were performed using the *Tukey*'s correction by the *emmeans* function of the 'emmeans' package (Lenth 2020).

To evaluate the cost associated with plasticity and its impact on species performance (question two), the survival and growth ratios between the full-sun exposure and partial shading treatments were related to the general RDPI through a generalized linear model, using the *glm* function of the 'base' package. The explanatory power of models was obtained as the residual deviance divided by the null deviance minus one.

A principal component analysis (PCA) was run to confirm the clustering of species based on survival, growth, morphological, and physiological traits. Variables were *z*-scaled (*i.e.*, standard deviation of one and mean of zero) to avoid the influence of different units on the formation of clusters. The PCA was run using the *ggbiplot* function of the 'ggbiplot' package (Vu 2011). Ellipses were plotted in two PCA dimensions to group species, considering one standard deviation from ellipses centroid (68% confidence interval) (Vu 2011). The percentage of overlap among ellipses measured the differences between species, and it was calculated by the *maxLikOverlap* function of the 'SIBER' package (Jackson *et al.* 2011).

Results

Physiological traits: Despite the absence of statistical difference, the F_v/F_m values indicated stress conditions at T_0 and T_{210} for both treatments, although the majority of the lowest values were observed at T_{210} under full-sun exposure (Fig. 1, Table 1). For all species, the partial shading treatment showed the highest F_v/F_m values. The q_P values were higher than 0.91. All the NPQ values were below 0.18, with the highest values being recorded for *Vitex* at the partial shading treatment.

For all species, Chl was higher under partial shading (RCI values ranged from 34.23 to 45.95) than under full-sun exposure (from 26.54 to 35.18) (Table 1). The irradiance treatments did not change the $\delta^{13}C$ for *Vitex*, *Cupania*, and *Guarea* (values ranged from –30.40 to –31.93‰), but *Cytharexylum* had ^{13}C-enriched leaves under the full-sun exposure (Table 1).

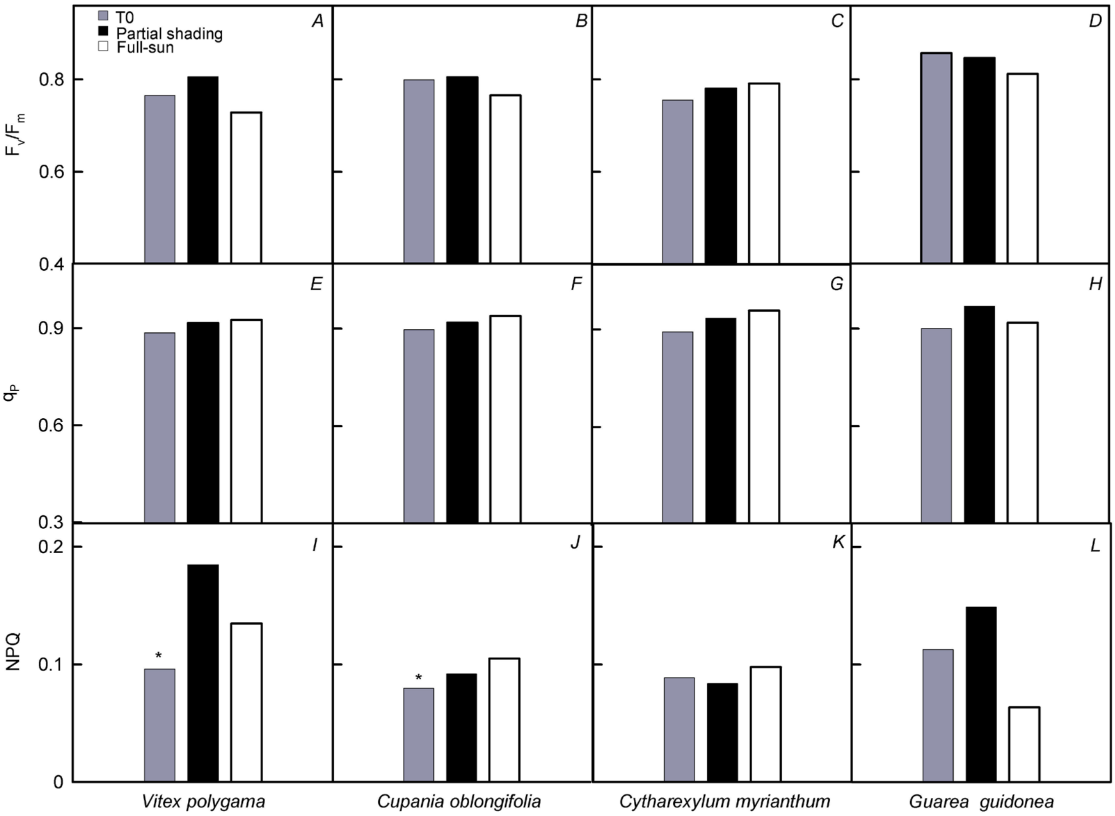

Fig. 1. Maximal quantum yield of PSII (F_v/F_m) (*A–D*), photochemical quenching (q_P) (*E–H*), and nonphotochemical quenching (NPQ) (*I–L*) measured at 7:00 h before establishing the experiment *in situ* (T_0) and at the end of the experiment (210 d) in full-sun exposure and partial shading treatments. *Vitex polygama* (*A,E,I*); *Cupania oblongifolia* (*B,F,J*); *Cytharexylum myrianthum* (*C,G,K*); *Guarea guidonia* (*D,H,L*) in the União Biological Reserve, Brazil. Values are means, $n = 4$. Statistical analyses in Table 1S (*supplement*). * Compare treatments ($p \leq 0.05$).

Table 1. Average relative growth rate (RGR) for growth traits (H – height; D – diameter at ground level; NL – number of leaves) for 210 d (February 2015 to September 2015), and for physiological traits (SLA – specific leaf area; $\delta^{13}C$ – carbon stable isotopic ratio; RCI – relative chlorophyll index; F_v/F_m – maximal quantum yield of PSII; q_P – photochemical quenching and NPQ – nonphotochemical quenching coefficients) at the end of the experiment (T_{210}) (September 2015). *Capital letters* compare irradiance treatments (full-sun exposure and partial shading) considering the same species ($p \leq 0.05$). RDPI – relative distance plasticity index.

Traits	*Vitex polygama*			*Cupania oblongifolia*			*Cytharexylum myrianthum*			*Guarea guidonea*		
	Full-sun exposure	Partial shading	RDPI	Full-sun exposure	Partial shading	RDPI	Full-sun exposure	Partial shading	RDPI	Full-sun exposure	Partial shading	RDPI
H [$m\ m^{-1}\ d^{-1}$]	0.0019^B	0.0046^A	0.23	0.0022^B	0.0043^B	0.19	0.0037^A	0.0054^A	0.17	0.0047^A	0.0036^B	0.11
D [$cm\ cm^{-1}\ d^{-1}$]	0.0068^B	0.0126^A	0.47	0.0070^A	0.0079^A	0.05	0.0086^A	0.0113^A	0.13	0.0103^A	0.0098^A	0.06
NL [no. $no.^{-1}\ d^{-1}$]	0.0061^B	0.0157^B	0.39	0.0084^A	0.0144^A	0.18	0.0090^A	0.0076^A	0.23	0.0100^A	0.0112^A	0.13
SLA [$cm^2\ g^{-1}$]	0.62^B	23.65^A	0.73	0.53^B	2.67^A	0.64	18.61^A	19.26^A	0.13	4.42^A	2.48^B	0.38
$\delta^{13}C$ [‰]	-31.92^A	-31.93^A	0.13	-31.22^A	-31.80^A	0.12	-31.18^A	-32.12^B	0.11	-30.77^A	-30.40^A	0.07
RCI	26.45^B	34.23^A	0.12	31.50^B	45.95^A	0.13	35.18^B	41.15^A	0.07	32.88^B	45.95^A	0.16
F_v/F_m	0.72^B	0.80^A	0.11	0.76^A	0.80^A	0.06	0.81^B	0.84^A	0.07	0.79^A	0.78^A	0.04
q_P	0.92^A	0.91^A	0.04	0.93^A	0.91^A	0.17	0.91^A	0.96^A	0.11	0.95^A	0.93^A	0.03
NPQ	0.13^B	0.18^A	0.21	0.10^A	0.09^A	0.14	0.09^A	0.08^A	0.17	0.06^B	0.14^A	0.22

Plant performance: In the PCA based on survival and growth rates over time, two principal components explained 91.4% of the total variance. The PC1 explained 72.7% of the total variation and was influenced by NL and the number of surviving seedlings, mostly because of the *Cytharexylum* performance. The PC2 explained 18.7% of the remaining variation, with this axis being associated with H and D (Fig. 2*A*), and more suitable to separate the species *Vitex*, *Guarea*, and *Cupania*. In the PCA based on morphological and physiological traits measured at the end of experiment (Fig. 2*B*), two principal components explained 57.8% of the total variance. The PC1 explained 35.1% and was directly influenced by morphological traits (*e.g.*, SLA) and the photosynthetic apparatus status (F_v/F_m and RCI). The PC2 explained 22.7% of the remaining variation and was associated with photochemical traits (q_P, NPQ, and $\delta^{13}C$) (Fig. 2*B*). The overlapping areas between ellipses distinguished the specific performances and traits and highlighted the particularities of *Cytharexylum* for both set of data (Fig. 2). *Cupania* and *Guarea* species had narrower ellipses than the two other species, which indicate greater constancy in traits variance (Fig. 2).

Survival and growth: Seedling survival decreased over time in a nonlinear decay for both full-sun exposure and partial shading treatments, but the magnitude of decrease was species-specific: *Cytharexylum* > *Guarea* > *Cupania* > *Vitex* (Fig. 3). The only exception was related to *Cytharexylum* in the partial shading treatment due to the survival of all seedlings (Fig. 3; Table 1S, *supplement*). However, seedling survival was from 6 to 23% higher under partial shading than under full-sun exposure. Pair-to-pair comparisons did not reveal differences in survival between species under the partial shading treatment, but differences were observed for *Vitex – Cytharexylum*, *Vitex – Guarea*, and *Cytharexylum – Cupania* under the full-sun exposure treatment (Table 2S, *supplement*).

The seedling growth in H, D, and NL increased over time in a nonlinear way for most species in both treatments, but the magnitude of increase was species-specific and tended to be higher under partial shading than that under full-sun exposure (Fig. 4, Table 1; Tables 1S, 3S, *supplement*). *Guarea* had the second highest growth rate among species under full-sun exposure, but it had one of the lowest growth rates under partial shading (Fig. 4, Tables 1S, 3S).

Photoplasticity: The investment in plastic adjustments over the time in H, D, NL, SLA, RCI, F_v/F_m, q_P, NPQ, and $\delta^{13}C$, measured through the individual RDPI (Table 4S, *supplement*) and general RDPI, was overall low among traits for *Cupania*, *Cytharexylum*, and *Guarea*, with values ranging from 0.2 to 0.4% (Fig. 5). However, *Vitex* showed a high general RDPI, which ranged from 0.2 to 0.8%. All models showed nonlinear significant fits.

The trait plasticity was negatively related to the seedling survival and growth for all species, showing a nonlinear decay over time (Fig. 6, Table 4S). *Vitex* was the species with the highest plasticity among the four species and able to maintain high survival for a longer period

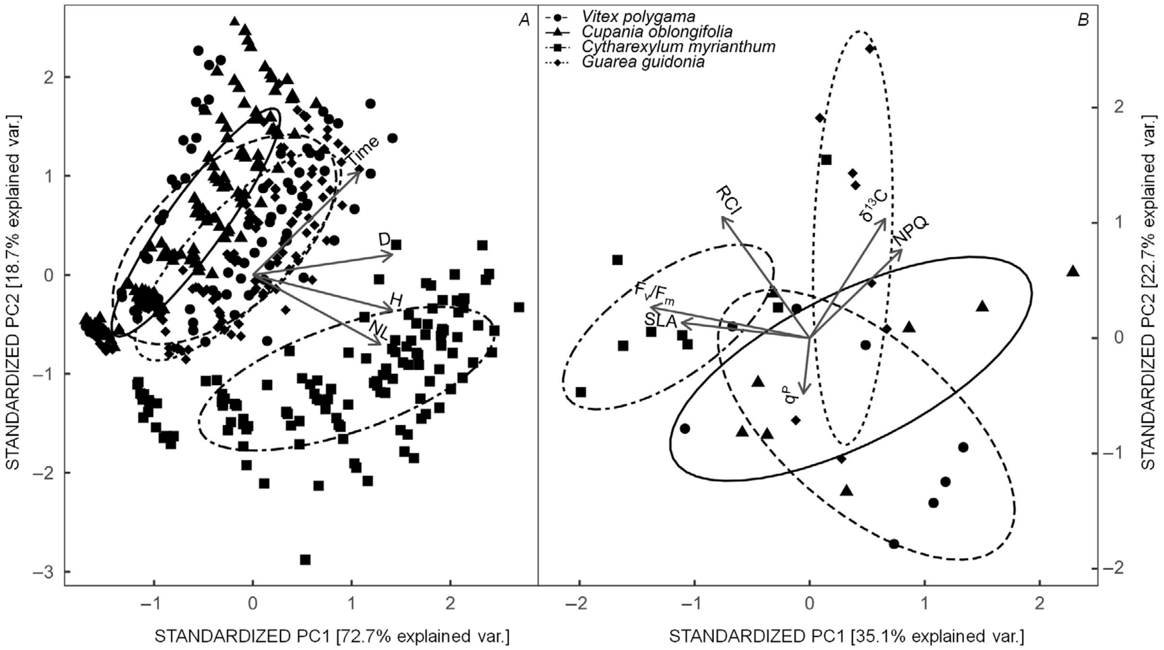

Fig. 2. Principal component analysis (PCA) considering: (*A*) the values of H – height; D – diameter at ground level; NL – number of leaves; and Time – eight intervals of 30 d for 210 d in full-sun exposure and partial shading treatments, and (*B*) the values of SLA – specific leaf area; RCI – relative chlorophyll index; F_v/F_m – maximal quantum yield of PSII; q_P – photochemical quenching and NPQ – nonphotochemical quenching coefficients; $\delta^{13}C$ – carbon stable isotopic ratio in full-sun exposure and partial shading treatments at the end of experiment (210 d). *Vitex polygama* (*dashed line*, *circle*), *Cupania oblongifolia* (*solid line*, *triangle*), *Cytharexylum myrianthum* (*dot-dashed line*, *square*), and *Guarea guidonia* (*dotted line*, *diamond*).

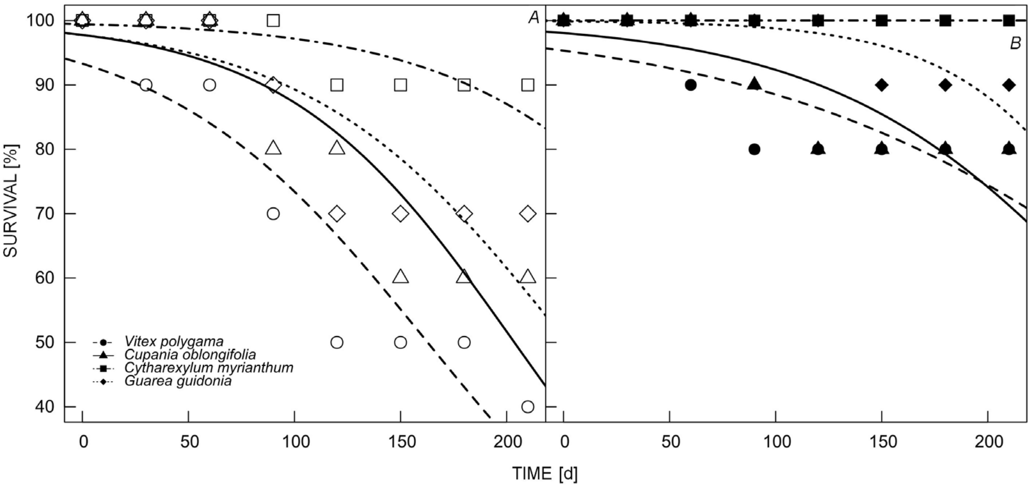

Fig. 3. Seedling survival under (*A*) full-sun exposure, and (*B*) partial shading over 210 d (from February to September 2015) in the União Biological Reserve, Brazil. *Vitex polygama* (*dashed line*, *circle*), *Cupania oblongifolia* (*solid line*, *triangle*), *Cytharexylum myrianthum* (*dot-dashed line*, *square*), and *Guarea guidonia* (*dotted line*, *diamond*). Values are means, $n = 10$.

when compared to *Guarea*. However, *Vitex* presented the lowest growth ratios (sun/shade) in a diameter and number of leaves (Fig. 6*C*,*D*).

Discussion

Our results suggest species-specific performance within the early-successional light-demanding group, with F_v/F_m values indicating stress conditions for some species, $\delta^{13}C$ variation suggesting that the initial restoration condition can be stressful even in partial shading conditions for water-use efficiency, as well as a trade-off between growth and survival. In addition, there were interspecific variations in seedling survival, growth, morphological, and physiological plasticity in response to irradiance for these species, which have been commonly used for

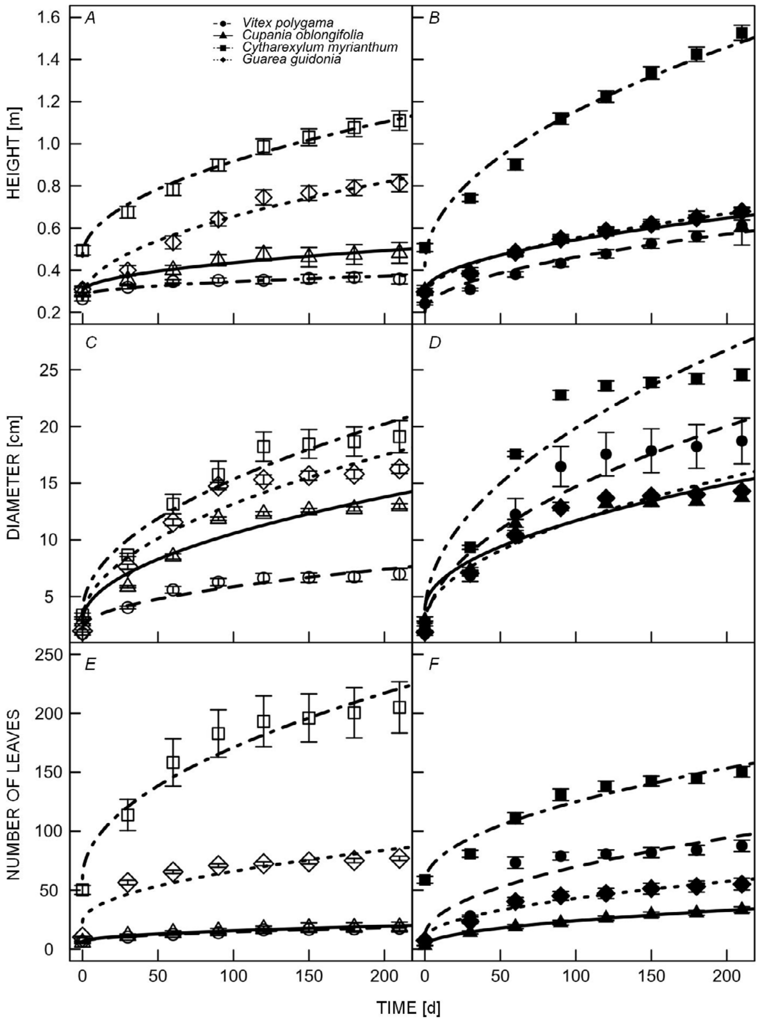

Fig. 4. Rate of growth in height (*A*,*B*), diameter (*C*,*D*), and number of leaves (*E*,*F*) in full-sun exposure (*A*,*C*,*E* – open symbols) and partial shading (*B*,*D*,*F* – closed symbols) over 210 d (from February to September 2015) in União Biological Reserve, Brazil. *Vitex polygama* (*dashed line*, *circle*), *Cupania oblongifolia* (*solid line*, *triangle*), *Cytharexylum myrianthum* (*dot-dashed line*, *square*), and *Guarea guidonia* (*dotted line*, *diamond*). Values are means ± SD, *n* = 10.

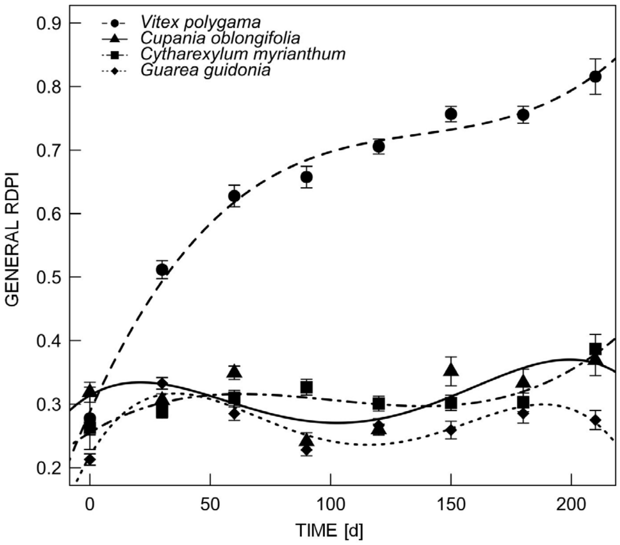

Fig. 5. General relative distance plasticity index (general RDPI) based on the values of RDPI for survival, H – height; D – diameter at ground level; NL – number of leaves; SLA – specific leaf area; RCI – relative chlorophyll index; F_v/F_m – maximal quantum yield of PSII; q_P – photochemical quenching and NPQ – nonphotochemical quenching coefficients; $\delta^{13}C$ – carbon stable isotopic ratio over 210 d (from February to September 2015) in the União Biological Reserve, Brazil. *Vitex polygama* (*dashed line*, *circle*), *Cupania oblongifolia* (*solid line*, *triangle*), *Cytharexylum myrianthum* (*dot-dashed line*, *square*), and *Guarea guidonia* (*dotted line*, *diamond*). Values are means ± SD, *n* = 4–10.

the restoration of the Atlantic Forest in South America. The differentiation in species' performances reveals a continuum of adaptive responses that change over the time (Ellis *et al.* 2000, Gilbert *et al.* 2006). In tropical forests, the continuum of strategies in the use of light often results from significant horizontal and vertical heterogeneity in light availability (Domingues *et al.* 2005, Vieira *et al.* 2015, Vitória *et al.* 2019). Even seedlings of neotropical

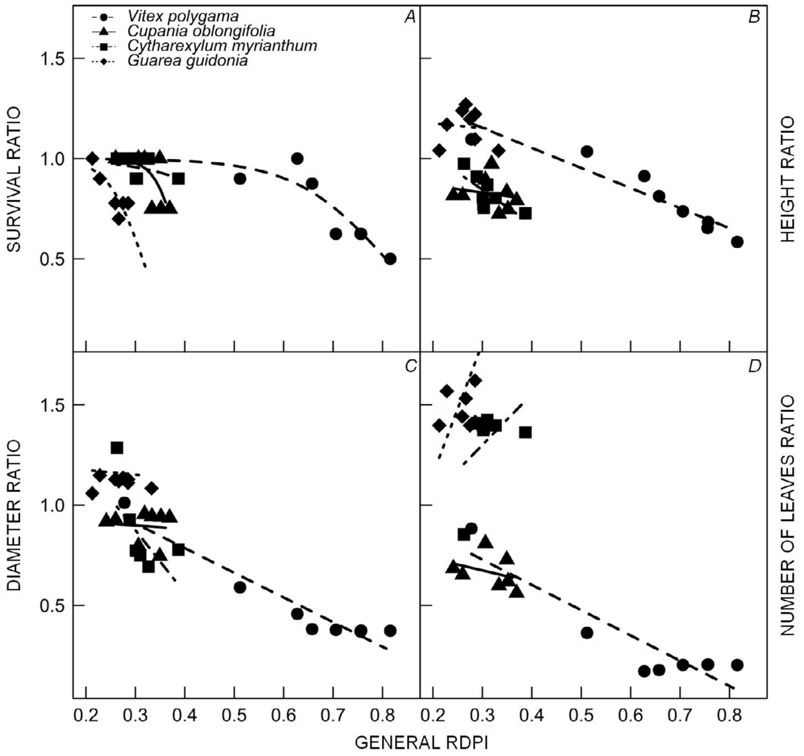

Fig. 6. Association between the capacity of species to have plastic adjustments, measured through the general relative distance plasticity index (general RDPI), and the sun/shade ratios of seedling survival and growth. *Vitex polygama* (*dashed line*, *circle*), *Cupania oblongifolia* (*solid line*, *triangle*), *Cytharexylum myrianthum* (*dot-dashed line*, *square*), and *Guarea guidonia* (*dotted line*, *diamond*).

tree species show a continuum of light requirements, although these differences are usually discussed in terms of the successional status (Calzavara *et al.* 2019).

The F_v/F_m of some species was negatively affected by high irradiance, suggesting the effectiveness of F_v/F_m for distinguishing species more vulnerable to full-sun exposure from those that can improve the photochemical conditions under partial shading. F_v/F_m has been used as an indicator of physiological efficiency (Bolhàr-Nordenkampf *et al.* 1989, Lüttge 2008, Vitória *et al.* 2016, Paula *et al.* 2019), with values above 0.8 reflecting optimal operation of the photosynthetic apparatus (Lüttge 2008). However, some authors are less restrictive on this regard, and consider photoinhibition when F_v/F_m is below 0.75 (Bolhàr-Nordenkampf *et al.* 1989). Photoinhibition occurs when the light intensity exceeds the leaf capacity to use it in photosynthesis and/or thermal dissipation (Takahashi and Murata 2008). Photoinhibition and stress conditions according to F_v/F_m were mostly observed in the full-sun exposure treatment. However, when we evaluated the RDPI for each parameter, it was low for q_P and F_v/F_m for all species, indicating that species were able to acclimate to both irradiance treatments. This capacity was possibly caused by the adjustments in energy dissipation as heat, as suggested by the RDPI for NPQ. NPQ is associated with heat energy dissipation and considered a protection mechanism against the excess of light in the photosynthetic apparatus, helping maintain the efficiency of photosynthetic functioning (Demmig-Adams and Adams 1992, Rabelo *et al.* 2013, Paula *et al.* 2019). Another mechanism to avoid light damage was the reduction of Chl content, a strategy observed in plants under high irradiance to avoid photooxidation (Zhang *et al.* 2018, Vitória *et al.* 2019).

In addition to F_v/F_m, the differentiation in species' performance can also be observed through the efficiency of water use, assessed by $\delta^{13}C$ (Farquhar and Richards 1984). Among all species, *Guarea* displayed the highest photosynthetic water-use efficiency. However, it did not reflect advantages for survival or growth, since *Cytharexylum* had the lowest $\delta^{13}C$ values and was the species with the highest survival rate. The $\delta^{13}C$ has been used to evaluate the acclimation to irradiance as a time-integrated response of photosynthesis in field conditions (Zimmerman and Ehleringer 1990, Dawson *et al.* 2002, Vitória *et al.* 2016). However, differently from photochemical evaluations, the irradiance treatments did not promote significant changes in the $\delta^{13}C$ values, except for *Cytharexylum*. It has been observed that shading conditions promote ^{13}C-impoverishment compared to full sun conditions (Vitória *et al.* 2016). This suggests restriction of stomatal opening regardless of irradiance treatments in the present study, possibly due to the studied period (dry season) and the restrictive conditions at the beginning of the restoration program. The supply of CO_2 at the site of Rubisco carboxylation determines discrimination against $^{13}CO_2$ relative to $^{12}CO_2$ during photosynthesis (Farquhar and Richards 1984). Under high irradiance conditions and water restriction, photosynthesis depends strongly on the intercellular CO_2 concentration (C_i), which releases the discrimination against $^{13}CO_2$ and results in ^{13}C-enriched tissue (Farquhar *et al.* 1989, Vitória *et al.* 2016, 2018).

Differences in survival between species were observed between the full-sun exposure and partial shading treatments, which demonstrate that even light-demanding species respond positively to a reduction of 60% in irradiance. Species performance showed that trait combinations can exhibit trade-offs of photosynthetic and ecological strategies that relate to growth in the restoration process (Ellis *et al*. 2000, Gilbert *et al*. 2006, Goldstein *et al*. 2016). In addition, results corroborate the light functional classification of species in the early-successional category (Björkman 1981, Kitajima 1994, 1996; Strauss-Deberiedetti and Bazzaz 1996, Valladares *et al*. 2000, Cai *et al*. 2005, Portes *et al.* 2010) but emphasize the vulnerability of species selection based only on functional classification, because it does not consider the interspecific variability within the functional group.

Plasticity adjustments are responsible for establishing limits between preferences and tolerances (Valladares and Niinemets 2008) and it was measured in this study by the RDPI. It was able to show distinct photoacclimation capacities between species. The greatest investments in plasticity were found for morphological traits in the construction of leaf tissue (LA and SLA), with plasticity being negatively related to survival and growth, mainly in the full-sun exposure treatment. It can be understood as a strategy to invest part of the resources in the construction of new structures to maintain and maximize the use of high irradiance (Violle *et al*. 2007, Rosado *et al*. 2013). The greater plasticity in morphological traits than that in physiological traits across the studied species is in contrast to to the results of Bongers *et al*. (2017), who pointed out that physiological traits are more plastic due to regulatory mechanisms that make them more easily adjustable to irradiance variation. However, it is important to highlight that our data were obtained for seedlings, a stage of development that under favorable conditions grows intensely and constantly. Thus, the new leaves produced in the partial shading treatment showed structural changes in order to deal with new environmental conditions since the beginning of its ontogeny, differing from the leaf structures produced in the full-sun exposure treatment.

One of the most notable results in this study was that plastic responses appear to have a cost for the species performances and paying this cost unfavored some of them. We constructed 'norm reaction-type' graphs to represent how phenotypes change in response to irradiance variation over the time, with slopes of the relationships representing the strength of phenotypic plasticity. The results revealed a negative relationship between plasticity and survival, indicating a cost for growth. In this regard, the general RDPI showed great differences between *Vitex* and all the other species, which supported the hypothesis of species-specific performance associated with functional amplitude and the cost for plasticity adjustments. Our results not only suggested that the high plasticity observed for the *Vitex* species in response to irradiance variation was passive, but also that it was maladaptive. Passive plasticity responses are not necessarily adaptive and can involve maladaptive responses, while active plasticity can enhance phenotype adjustments to increase the fitness (Smith-Gill 1983, Parsons *et al*. 2020). We assumed that phenotypic plasticity is an advantage for the species when it increases their fitness, and thereby considered as active (or adaptive) (Muth and Pigliucci 2007, Smith-Gill 1983, van Kleunen *et al*. 2011, Valladares *et al*. 2014). Although plastic adjustments have been verified, some plastic responses may not have a positive effect on the fitness or even reduce it, being considered as neutral and maladaptive responses, respectively (van Kleunen and Fischer 2005, Sánchez-Gómez *et al*. 2006, Ghalambor *et al*. 2007, Liu *et al*. 2016).

In contrast to *Vitex*, *Cytharexylum* exhibited a lower plasticity and more efficient performance in both irradiance treatments in comparison to all species. The observed performance corroborates the pattern revealed by the ellipses in the PCA analyses. The survival–growth trade-off found in our study is consistent with the leaf economic scheme based on allocation patterns, in which investments to enhance growth may come at the cost of restricting allocation to traits related to survival and plasticity (Kitajima 1994, 1996; Westoby *et al*. 2002, Wright *et al*. 2004, 2010; Reich *et al*. 2006, Sánchez-Gómez *et al*. 2006). This survival–growth trade-off characterizes the cost associated with plasticity adjustments based mainly on morphological traits, as observed elsewhere (Wright and Sutton-Grier 2012, Rosado *et al*. 2013, dos Anjos *et al*. 2015, Bongers *et al*. 2017). Contrary to the regeneration under an intact forest canopy, where growth and survival are often negatively correlated with irradiance (Kitajima and Poorter 2008, Silva *et al*. 2020), our data were collected above 40% of full irradiance, simulating open area conditions. Greater growth in shaded conditions is likely related to the stem elongation effect, where elongation occurs in response to low irradiance as a strategy to intercept more irradiance (Weinig and Delph 2001).

We expected changes in species plasticity over time, and it was possible to identify two groups, distinguished by extreme and intermediate performances. The first group was formed by *Vitex* and *Cytharexylum*, which showed extreme performances (low and high, respectively) that remained constant over the time. The cubic and polynomial fits on the data of *Vitex* and *Cytharexylum* suggest predictable performance along two response peaks (investment in plasticity adjustments) related to inflection points. These results indicate the competitive advantage of *Cytharexylum* and its ability to establish at the beginning of the restoration process (Stratton and Goldstein 2001, Ewe and Sternberg 2003, 2005). This species has a large functional niche amplitude, which corresponds to a more generalist performance. In contrast, *Vitex* showed a contrasting performance, with narrower niche and low restoration potential, although it presented a wider plasticity than the other species. In that sense, we suggest that *Vitex* should not be used at the beginning of plantings. These results reveal the two extremes in the continuum of responses within the group of light-demanding species and the high influence of plasticity to improve restoration success. The second group formed by *Guarea* and *Cupania* suggest an intermediate investment in plasticity related to short and long-term adjustability. The polynomial fit on the data of these species directly reflects their greater ability to adjust distinct responses to environmental variability over time. The quartic polynomial fit indicates four points of inflection. In this sense, *Guarea* and *Cupania* revealed niche amplitudes that corroborate their restoration potentials, as well as their persistence in the understory. We suggest that *Guarea* and *Cupania* could be used in initial plantings or different stages of the restoration process. The occurrence of two mathematical functions in the discretion of species performance highlights the heterogeneity of response within the functional group of early-successional light-demanding species.

We conclude that species from the same successional status and growing under similar irradiance conditions were able to differ in their responses to stress, performance, and phenotypic plasticity. It was more evident under high irradiance, which imposed stress condition for some species and required greater requirements in plasticity, whereas low irradiance conditions released species from phenotypic adjustments. In addition, we were able to demonstrate that the costs associated with phenotypic plasticity promoted a trade-off between growth and survival, particularly greater for morphological than physiological traits. In this sense, our results provide a baseline for justifying the close relationship between photosynthetic traits and seedling performance of the early-successional species, and their influences on the success of restoration programs. Our approach suggested that the success for restoration of tropical rain forests can be improved by the selection of species with a higher cost effectiveness in plasticity. We emphasize, however, that these recommendations are related to seedlings under natural conditions of establishment.

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