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Photochemical responses by seedlings of two mangrove species grown under different light levels

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Abstract. Chlorophyll *a* (chl *a*) fluorescence transients and leaf photosynthetic pigment contents were analyzed to investigate the responses by seedlings of *Avicennia germinans* (L.) L. and *Rhizophora mangle* L. to three controlled light conditions: high light (HL, full lighting), medium light (ML, 50% shading) and low light (LL, 80% shading). For the seedlings grown under HL, the fluorescence transient analysis showed the occurrence of a K-band and a decreased maximal fluorescence (F_M), maximum quantum yield of primary photochemistry ($\varphi_{Po} = F_V/F_M$, where F_V is the maximal variable fluorescence) and performance index (PI_{ABS}, with ABS indicating an absorption basis). Both species showed a similar capacity to acclimate to full light, exhibiting protective mechanisms against damage to the photosynthetic apparatus, such as decreased chl a and chlorophyll *b* (chl *b*) contents and chl (*a*+*b*)/carotenoid ratio and increased energy dissipation shown by the following indicators: DI_O/ABS (maximum quantum yield of nonphotochemical de-excitation), DI_O/RC (dissipation of an active reaction center (RC)) and DI_O/CS (energy dissipation per cross section (CS)). However, *A. germinans* presented overall higher resistance, manifesting lower deviations in difference kinetics and variation in the JIP-test parameters among the various light levels when compared to the *R. mangle*, that presented higher physiological plasticity.

Keywords: *Avicennia germinans*, chlorophyll *a* fluorescence, K-band, photosynthetic pigments, *Rhizophora mangle*.

Resumo: Respostas fotoquímicas de plântulas de duas espécies de mangue cultivadas sob diferentes níveis de luminosidade. Os transientes da fluorescência da clorofila *a* (clo *a*) e o conteúdo de pigmentos fotossintéticos foram analisados para investigar as respostas de plântulas de *Avicennia germinans* (L.) L. e *Rhizophora mangle* L. a três condições controladas de luminosidade: alta luminosidade (AL, luz plena), média luminosidade (ML, 50% de sombreamento) e baixa luminosidade (BL, 80% de sombreamento). Nas plântulas do tratamento AL, a análise do transiente da fluorescência mostrou a ocorrência de uma banda-K e um decréscimo da fluorescência máxima (F_M), rendimento quântico máximo ($\varphi_{Po} = F_V/F_M$, onde F_V é a fluorescência máxima variável) e índice de desempenho (PI_{ABS}, com ABS indicando uma base de absorção). Ambas as espécies mostraram similar capacidade de aclimatação à alta luminosidade, exibindo mecanismos protetores contra danos ao aparato fotossintético, tais como redução nos conteúdos de clo *a* e clorofila b (clo *b*) e razão clo (*a*+*b*)/carotenoides e incremento na dissipação de energia mostrado pelos seguintes indicadores: DI_O/ABS (Rendimento quântico fotoquímico para dissipação de calor), DI_O/RC (Dissipação de calor por centro de reação) e DI_O/CS (dissipação de energia por seção transversal). Entretanto, *A. germinans* apresentou maior resistência de forma geral, demonstrando menores desvios nas diferenças cinéticas e

menor variação nos parâmetros do teste-JIP entre os vários níveis de luz quando comparada com *R. mangle*, que exibiu maior plasticidade fisiológica.

Palavras-chave: *Avicennia germinans*, fluorescência da clorofila *a*, banda-K, pigmentos fotossintéticos, *Rhizophora mangle.*

Introduction

Mangroves occur at tropical and subtropical latitudes where solar irradiance is high. Small gaps caused by lightning and trees death are common in mangrove forests (Smith 1992). When a gap is young, considerable extra light enters the gap and seedlings in the seedling bank are exposed to full sunlight, at least for part of the day, mostly around midday (Duke 2001). Excess light may result in photoinhibition, which is characterized by a loss of photosystem II (PSII) activity and light-dependent reduction in the fundamental quantum yield of photosynthesis (Osmond 1994), requiring the dissipation of excess excitation energy (Lovelock & Clough 1992, Demmig-Adams *et al*. 1995, 1996, Portela *et al*. 2019). Plants exposed to strong light also present decreases or adjustments in their leaf photosynthetic pigment contents, providing an important photoprotective mechanism (Burritt & Mackenzie 2003, Krause *et al*. 2012; Ulqodry *et al*. 2014, Souza *et al*. 2017).

Chlorophyll *a* (chl *a*) fluorescence transient (OJIP) analysis has been used to investigate the effects of increasing light levels on the photosynthetic apparatus (Gonçalves *et al*. 2007, Gonçalves *et al*. 2010, Portela *et al*. 2019). This method is highly sensitive, nondestructive and provides detailed information on photosynthetic efficiency (Krause & Weis 1991, Govindjee 1995, Strasser *et al*. 1995, Stirbet & Govindjee 2011). Fluorescence transient measurements can be analyzed using the JIP-test, which involves the calculation of different biophysical and phenomenological parameters that quantify PSII function and structure (Strasser *et al*. 1995, 2004). The JIP-test has been widely used to evaluate plant responses to different types of stress, such as salinity (Gonzalez-Mendoza *et al*. 2011, Falqueto *et al*. 2012a), temperature (Martinazzo *et al*. 2012), flooding (Santos Junior *et al*. 2015), heavy metals (Huang *et al*. 2017), hydrocarbons (Reinert *et al*. 2016), mealybug infestation (Falqueto *et al*. 2012b) and chlorosis (Chen & Cheng 2010).

Ecophysiological responses to excess sunlight vary between different species, or even during the plant life cycle (López-Hoffman *et al*. 2007), and may significantly affect the survival rate and spatial distribution of mangrove plants (Smith 1987).

Avicennia germinans (L.) L. (Acanthaceae) is a mangrove tree (or bush) widely distributed along tropical and subtropical sheltered coastal regions on the west coast of Africa and America as well as the east coast of America; this plant may occur together with other species or form monospecific mangroves (Jiménez & Lugo 1985, Tomlinson 1986). According to the classification by Bazzaz (1979), *A. germinans* may be considered a pioneer (light-demanding) plant. *Rhizophora mangle* L. (Rhizophoraceae) may present a tree or bush habit, shows a distribution similar to that of *A. germinans* (Jiménez 1985, Tomlinson 1986) and is commonly associated with other true mangrove species but may also form monospecific mangroves. Seedlings of *R. mangle* grow slowly beneath the canopy of mangrove forests and rapidly in forest gaps (Ellison & Farnsworth 1993), therefore exhibiting characteristics of both pioneer (light-demanding) and shade-tolerant species (Tomlinson 1986). However, López-Hoffman *et al.* (2007) indicated that *R. mangle* is gap dependent (light demanding), whereas *A. germinans* is shade promoted, considering the whole plant life cycle.

Most studies analyze the response of different ecophysiological parameters to salinity, flooding and nutrient availability under field conditions to explain the development and distribution of mangrove species (Ball 1988, Pascoalini 2014, Lovelock *et al*. 2014). Mangrove species development and dynamics in response to different light conditions have been evaluated in the field (Ellison & Farnsworth 1993, 1996, McKee 1995), but few studies have described their ecophysiological responses under controlled light conditions (Ulqodry *et al*. 2014).

In the present study, we analyzed chl *a* fluorescence transients and leaf photosynthetic pigment contents in seedlings of *A. germinans* and *R. mangle* grown under controlled light conditions. Previous studies have shown that seedlings and young individuals of both species can survive under all light levels (Sousa *et al*. 2003, Whelan 2005, López-Hoffman *et al*. 2007). Therefore, we formulated the following hypotheses: (1) *A.*

germinans and *R. mangle* can acclimate to intense light conditions, and (2) *R. mangle* has higher physiological plasticity compared with *A. germinans* because *R. mangle* presents characteristics of both pioneer and shade-tolerant species.

Material and Methods

Plant material and experimental design: Avicennia germinans and *R. mangle* propagules were collected from mangroves located in the estuary of the Mamanguape River, State of Paraíba, Brazil (06°46'35"S and 34°55'45"W), during March 2016. The propagules were planted in polystyrene containers and kept under dim light (25 µmol m^{-2} s^{-1}) for 20 days. The seedlings were then placed in nurseries installed in an open area (06°49'09"S and 35°06'91"W). During the experiment (March–May 2016), the average monthly temperature was 27.1°C, and the accumulated rainfall was 590 mm (National Institute of Meteorology).

A completely randomized design was used, with a 2 x 3 factorial scheme (two species and three light levels) and three replicates per treatment. Each replicate consisted of five seedlings of each species (n =5). The following light levels were tested: high light (HL, full light at 1,834±78 µmol m^{-2} s^{-1}), medium light (ML, 50% shading at 875±52 µmol m^{-2} s^{-1}) and low light (LL, 80% shading at 330±27 µmol m^{-2} s^{-1}). The maximum average temperatures were 30.3±1.4, 29.3±1.3 and 27.5±1.2 °C and the minimum average temperatures were 22.0±0.8; 22.7±0.8 and 22.4±0.8 °C, for the HL, ML and LL treatments, respectively. The shading screens were installed on wooden structures in dimensions of 1.2 x 1.5 x 1.5 m (height, width and length).

Mangrove seedlings grown in nurseries can be watered with brackish or fresh water (Saenger 1997, Ulqodry *et al*. 2014). Because the aim of the present study was to test the effect of different light levels, the seedlings were watered with fresh water during the whole experiment. The seedlings remained in the nurseries for 60 days, until the ecophysiological measurements were performed. This time interval was chosen because in degraded-area recovery projects, seedlings produced in nurseries are transferred to the field at approximately three month of age, when they present two to three leaf pairs (Snedaker & Biber 1997, Hong 1997).

Chlorophyll a fluorescence: Two seedlings were selected from each species and each treatment replicate, for a total of six samples per treatment. The chl *a* fluorescence measurements were performed with a portable modulated fluorometer (OS5p+, Opti-Sciences, Hudson, NH, USA), between 11:00 and 12:00 h (on a clear day, without clouds). Fully expanded and healthy leaves from the second leaf pair were dark adapted for 30 min by the use of leaf clips. Following the dark adaptation, the central region of the adaxial leaf surface was subjected to a saturating light pulse of 3,500 µmol m^{-2} s^{-1} (690 nm); and chl *a* fluorescence transients were recorded for 1 s, starting from 20 µs after the onset of illumination (for a total of 120 fluorescence data points).

The OJIP fluorescence transients were normalized based on several points, to calculate the relative kinetics (Oukarroum *et al*. 2009, Strasser *et al*. 2004, Yusuf *et al*. 2010). The LL treatment was used as the control. The relative variable fluorescence between steps O (20 µs) and P (300 ms) was calculated as $V_t = (F_t - F_O)/(F_M - F_O)$ [$= V_{OP}$] (see the glossary of terms in Table I), and the difference kinetics at time t was calculated as $\Delta V_{OP} = V_{OP}$ (treatment) − V_{OP} (control). The difference kinetics between steps O (20 µs) and K (0.3 ms), which reveals the L-band, was calculated by subtracting the treatment from the control: $\Delta V_{OK} = V_{OK}$ (control) − V_{OK}(treatment), where $V_{OK} = (F_t - F_O)/(F_K - F_O)$, and $\Delta V_{OK} = 0$ (control). The difference kinetics between steps O (20 µs) and J (2 ms), revealing the K-band, was calculated by subtracting the treatment from the control: $\Delta V_{OJ} = V_{OJ}$ (control) − V_{OJ} (treatment), where $V_{OJ} = (F_t - F_O)/(F_J - F_O)$ and $\Delta V_{OJ} = 0$ (control). The I-P phase (30 to 300 ms) was analyzed by calculating the difference kinetics as follows: $\Delta V_{IP} = V_{IP}$ (control) − V_{IP} (treatment), where $V_{IP} = (F_t - F_I)/(F_M - F_I)$ and $\Delta V_{IP} = 0$ (control).

The photosynthetic activity was analyzed using the JIP-test, which consists of the calculation of different parameters that give information regarding the structure, function and performance of the photosynthetic apparatus (Strasser *et al*. 2004, Tsimilli-Michael & Strasser 2008). The JIP-test data were plotted on a radar graph, with the LL treatment as the control. The JIP-test parameters used in the present study are described in Table I.

Photosynthetic pigments: The photosynthetic pigment contents were determined in disks cut from the same leaves used to measure the chl *a* fluorescence (n = 6). The disks (0.6 cm^2) were placed in Falcon tubes (15 mL) wrapped in aluminum foil. The pigments were extracted with dimethyl sulfoxide (DMSO) and measured at 480, 649 and 665 nm in a spectrophotometer (SP220, Biospectro). The following photosynthetic pigments were quantified according to Wellburn (1994): chl *a*,

Table I. Formulas and glossary of terms used by the JIP-test for the analysis of the OJIP fluorescence transient, modified after Strasser *et al*. (2004) and Santos Junior *et al*. (2015).

Data extracted from the recorded OJIP fluorescence transient	
$F_{20\mu s}$ (= F_O)	Minimal reliable recorded fluorescence
$F_{300\mu s}$	Fluorescence at 300 µs
$F_J = F_{2ms}$	Fluorescence at the J step (2 ms) of OJIP
$F_I = F_{30ms}$	Fluorescence at the I step (30 ms) of OJIP
F_P (= F_M)	Maximal recorded fluorescence at the P peak of OJIP
Fluorescence parameters derived from the extracted data	
$F_V = F_M - F_O$	Maximal variable fluorescence
$V_K = (F_{300\mu s} - F_{20\mu s})/(F_M - F_{20\mu s})$	Relative variable fluorescence at 300 µs
$V_J = (F_{2ms} - F_{20\mu s})/(F_M - F_{20\mu s})$	Relative variable fluorescence at 2 ms
$V_I = (F_{30ms} - F_{20\mu s})/(F_M - F_{20\mu s})$	Relative variable fluorescence at 30 ms
$OEC = 1 - (V_K/V_J)$	Oxygen-evolving complex
$M_O = [4(F_{300\mu s} - F_{20\mu s})/(F_M - F_{20\mu s})]$	Net rate of PSII closure
Yield or flux ratios	
φ_{Po} (TR_O/ABS) = $F_V/F_M = 1 - (F_{20\mu s}/F_M)$	Maximum quantum yield of primary photochemistry
ψ_O (ET_O/TR_O) = $1 - V_J$	Probability that a trapped exciton moves an electron further than Q_A^-
φ_{Eo} (ET_O/ABS) = φ_{Po} ($3\psi_O$) = $[1 - (F_{20\mu s}/F_M)]$ $(1 - V_J)$	Probability that an absorbed photon moves an electron further than Q_A^-
φ_{Do} (DI_O/ABS) = $DI_O/ABS = 1 - \varphi_{Po} = (F_{20\mu s}/F_M)$	Maximum quantum yield of nonphotochemical de-excitation
Specific energy fluxes (per Q_A- reducing PSII reaction center (RC))	
$ABS/RC = [(TR_O/RC)/(TR_O/ABS)]$	Effective antenna size of an active RC
$TR_O/RC = (M_O/V_J)$	Maximum trapping rate per RC
$ET_O/RC = [(TR_O/RC)$ $(ET_O/TR_O)]$	Electron transport of an active RC
$DI_O/RC = [(ABS/RC) - (TR_O/RC)]$	Dissipation of an active RC
Phenomenological energy fluxes (per excited cross section (CS))	
$TR_O/CS = (ABS/CS)$ (TR_O/ABS)	Energy flux for trapping per CS
$ET_O/CS = (ET_O/RC)$ (RC/CS)	Electron transport per CS
$DI_O/CS = (ABS/CS) - (TR_O/CS)$	Energy dissipation per CS
Performance index	
$PI_{ABS} = (RC/ABS)$ $[\varphi_{Po}/(1 - \varphi_{Po})]$ $[\psi_O/(1 - \psi_O)]$	Performance index on absorption basis

chlorophyll *b* (chl *b*), carotenoids (*carots*) and total chlorophylls (chl (*a*+*b*)). The chl *a*/chl *b* (chl *a*/*b*) and chl (*a*+*b*)/*carots* ratios were also calculated.

Statistical analysis: The data were subjected to a two-way ANOVA, considering the species and light level (HL, ML and LL) as factors. Means were compared using the Tukey test. When parametric assumptions were not met, a PERMANOVA and subsequent Dunn test were performed.

Results

Both species presented typical OJIP transients (Fig. 1a–b), with fluorescence rising from minimal (F_O) to maximal fluorescence (F_M). However, the transient height between the O and P steps decreased with increasing light, resulting in a decreased area above the fluorescence transient. This decrease was most pronounced for the HL treatment. Both species presented decreased J-I and I-P phases for the HL and ML treatments. The J and I steps were better defined for the LL treatment than for the remaining treatments (Fig. 1a–b). The analysis of the relative variable fluorescence between the O and P steps (Fig. 1c–d) showed a higher J step for *R. mangle* grown under HL and ML compared with the LL treatment.

The difference kinetics between O-P phases for the HL and ML treatments revealed negative and positive deviations from the control curve (Fig. 1e–f). Normalizing the fluorescence transient for the different transient steps showed these deviations in more detail (Fig. 2). Deviations in the L-band, which did not present a hyperbolic shape, were observed for both species (Fig. 2a–b). The difference kinetics for the O-J phase (Fig. 2c–d) revealed a positive K-band, which was more pronounced for the HL than for the ML treatment in both species and more pronounced for *R. mangle* than for *A. germinans*. The analysis of the I-P phase revealed negative deviations with increasing light levels for both species (Fig. 2e–f), with the deviations less pronounced for *A. germinans* under ML.

Functional and structural parameters derived by the JIP-test are shown in Figure 3. Regarding the extracted parameters, no significant differences in F_O were observed between the various light levels and species, but F_M decreased with increasing light. The highest values of F_M were observed for the LL treatment and the lowest values for the HL

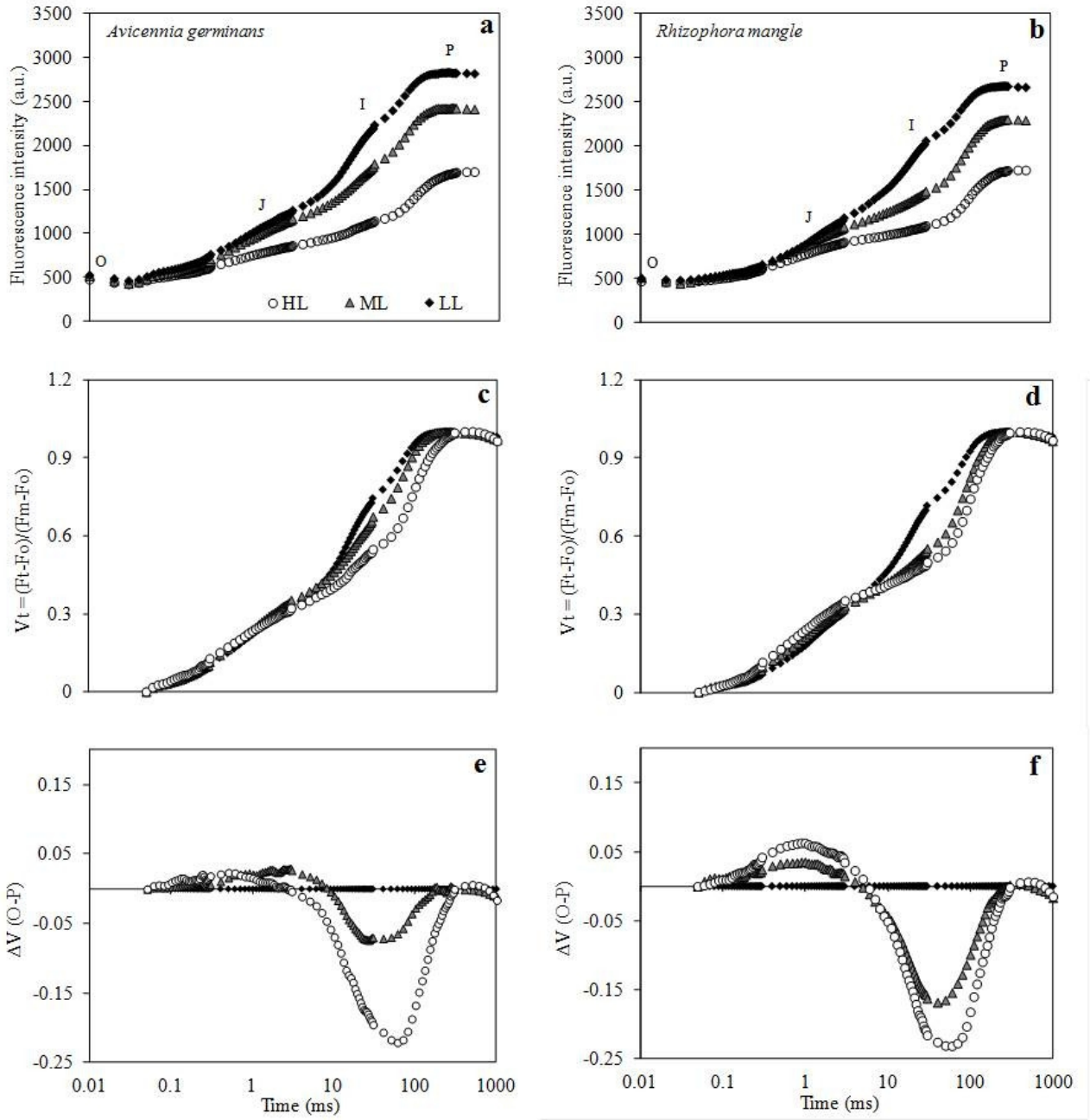

Figure 1. Chlorophyll *a* fluorescence transients (a and b), relative variable fluorescence (c and d) and difference kinetics for O-P phases (e and f) in seedlings of *Avicennia germinans* (left) and *Rhizophora mangle* (right) grown under three light levels: full light (HL), 50% shading (ML) and 80% shading (LL).

treatment. Regarding the calculated parameters, average F_V and V_I in *A. germinans* and *R. mangle* as well as the oxygen-evolving complex (OEC) in *R. mangle* decreased with increasing light, whereas V_K and the net rate of PSII closure (M_O) increased in *R. mangle*. The maximum quantum yield of primary photochemistry (φ_{Po}) decreased with increasing light, but the maximum quantum yield of nonphotochemical de-excitation' (φ_{Do}) increased.

Regarding the specific energy fluxes (per reaction center (RC)) observed in the HL and ML treatments, *R. mangle* showed relatively high means for the effective antenna size of an active RC (ABS/RC) and for the maximum trapping rate per RC (TR_O/RC), and both species presented relatively high values for the dissipation of an active RC (DI_O/RC). The phenomenological energy fluxes were also affected by increasing light: decreases occurred in the energy flux for trapping per cross

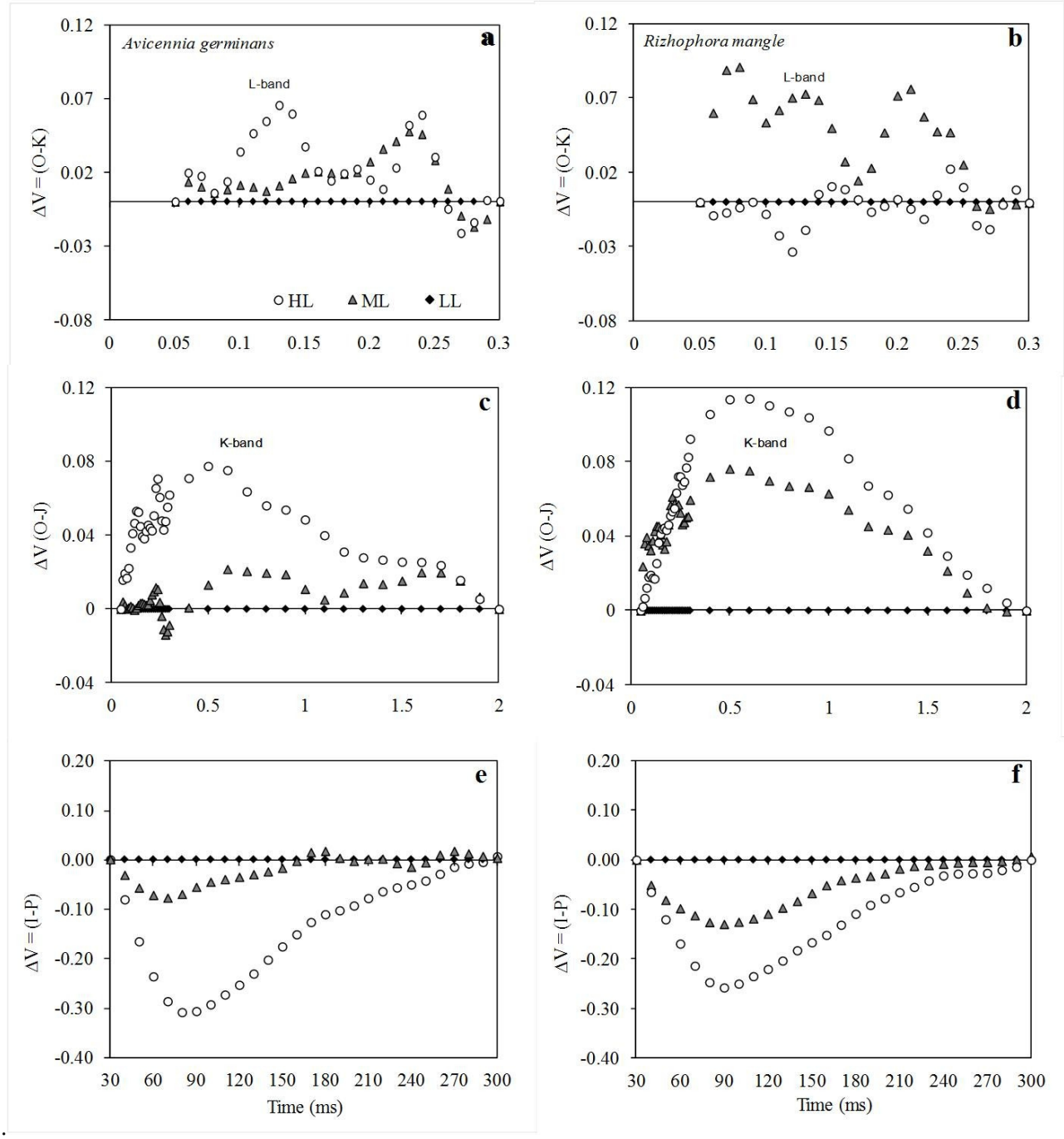

Figure 2. Difference kinetics for O-K (a and b), O-J (c and d) and I-P phases (e and f) in seedlings of *Avicennia germinans* (left) and *Rhizophora mangle* (right) grown under three light levels: full light (HL), 50% shading (ML) and 80% shading (LL)

section (TR_O/CS, *R. mangle*) and electron transport per CS (ET_O/CS, *A. germinans* and *R. mangle*), whereas the energy dissipation per CS (DI_O/CS, *A. germinans* and *R. mangle*) increased. Both species presented significantly lower performance index (PI_{ABS}, on an absorption basis) values for HL and ML compared with the LL treatment (Fig. 3). Significant differences between the species were only observed for PI_{ABS}, which was highest for *R. mangle* grown under LL ($p \leq 0.05$).

Both species presented relatively low chl *a* and chl *b* contents and chl (*a*+*b*)/*carots* ratio when grown under HL (Table II). No significant

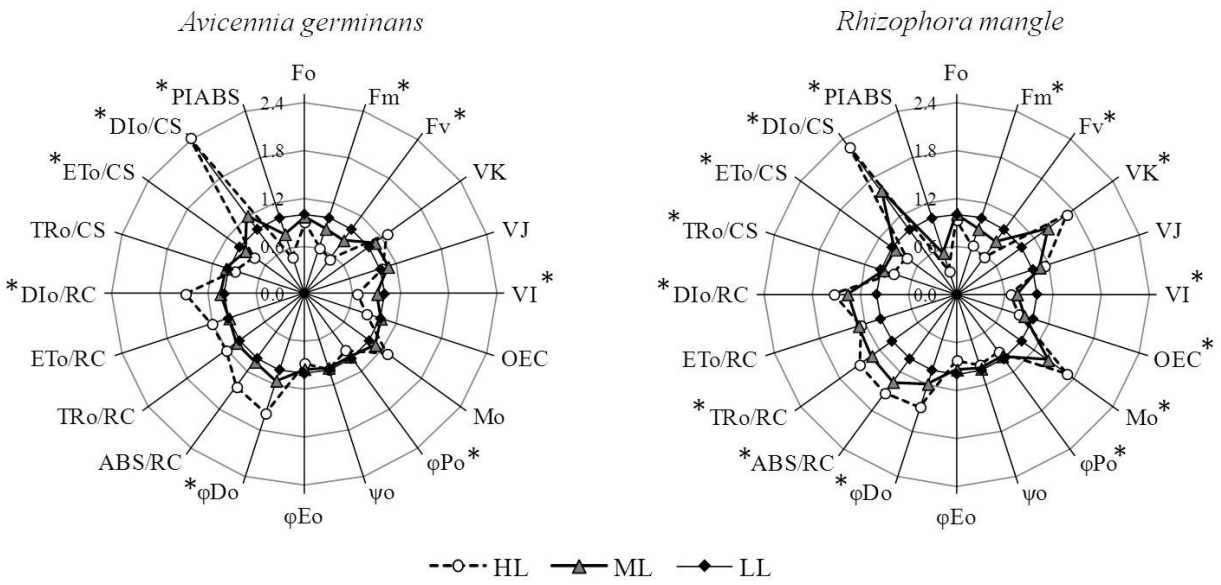

Figure 3. Functional and structural parameters derived by the JIP-test for *Avicennia germinans* (left) and *Rhizophora mangle* (right) seedlings grown under three light levels: full light (HL), 50% shading (ML). The derivation of each parameter is presented in Table 1. Asterisks indicate significant differences among treatments ($p \leq 0.05$).

Table II. Chlorophyll (chl) and carotenoid (*carot*) photosynthetic pigment measures in mangrove species grown at three light levels: full light (HL), 50% shading (ML) and 80% shading (LL). Values are means ± standard deviations (n = 6). Superscript capital letters compare the means between the species within measures and light levels, whereas superscript lower case letters compare the means among the light levels within species and measures. Different letters indicate a significant difference ($p \leq 0.05$).

Measure	Light level	*Avicennia germinans*	*Rhizophora mangle*
Chl *a* (nmol.cm^{-2})	HL	41.5 ± 4.4 ^{Ab}	40.5 ± 5.7 ^{Ab}
	ML	49.0 ± 4.5 ^{Aab}	49.5 ± 5.3 ^{Aab}
	LL	54.2 ± 5.5 ^{Aa}	51.0 ± 6.7 ^{Aa}
Chl *b* (nmol.cm^{-2})	HL	12.3 ± 1.1 ^{Ab}	11.3 ± 1.7 ^{Ab}
	ML	14.2 ± 1.0 ^{Aab}	13.9 ± 2.0 ^{Aab}
	LL	16.5 ± 2.1 ^{Aa}	15.1 ± 2.3 ^{Aa}
Carots (nmol.cm^{-2})	HL	19.1 ± 1.1 ^{Aa}	19.6 ± 2.7 ^{Aa}
	ML	18.2 ± 1.4 ^{Aa}	19.3 ± 1.8 ^{Aa}
	LL	18.4 ± 1.8 ^{Aa}	16.6 ± 1.8 ^{Aa}
Chl *a/b*	HL	3.4 ± 0.2 ^{Aa}	3.6 ± 0.3 ^{Aa}
	ML	3.5 ± 0.2 ^{Aa}	3.6 ± 0.2 ^{Aa}
	LL	3.3 ± 0.1 ^{Aa}	3.4 ± 0.1 ^{Aa}
Chl (*a*+*b*)/*carots*	HL	2.8 ± 0.3 ^{Aa}	2.7 ± 0.2 ^{Ab}
	ML	3.5 ± 0.1 ^{Aa}	3.3 ± 0.1 ^{Aab}
	LL	3.8 ± 0.1 ^{Aa}	4.0 ± 0.1 ^{Aa}
Chl (*a*+*b*)	HL	53.8 ± 5.4 ^{Ab}	52.0 ± 7.1 ^{Ab}
	ML	63.2 ± 5.4 ^{Aab}	63.4 ± 7.3 ^{Aa}
	LL	70.7 ± 7.5 ^{Aa}	66.1 ± 9.0 ^{Aa}

differences in photosynthetic pigment contents were observed between the species.

Discussion

Both species presented typical OJIP polyphasic transient rises (Strasser *et al*. 1995), showing that all the samples were photosynthetically active (Yusuf *et al*. 2010). The J and I steps were best defined for the LL treatment, indicating that photosynthesis was more efficient under comparatively shady light conditions.

The area above the fluorescence curve between F_O and F_M measures the size of the electron acceptor pool of PS II, the plastoquinone (PQ) pool

size (Govindjee 1995). In the present study, changes to the OJIP transient resulted in a decreased area above the fluorescence curve with increasing light. This effect was most pronounced for the HL treatment. This pattern indicates that the electron transfer from the RC to the quinone pool was compromised (Mehta *et al*. 2010). Similar results were observed for other tropical species grown under intense light (Gonçalves *et al*. 2010; Pinheiro 2012) and other stress conditions, such as flooding (tropical plants; Santos Junior *et al*. 2015), oil contamination (*Laguncularia racemosa* (L.) C. F. Gaertn; Reinert *et al*. 2016) and salinity (*L. racemosa* and *R. mangle*; Lopes 2014) (*Spartina patens* (Aiton) Muhl. and *Cyperus longus* L.; Duarte *et al*. 2015).

The O-J phase (the fastest and most light-dependent OJIP phase) relates to primary photochemical events on the acceptor side of PSII, leading to a reduction of the primary electron acceptor (Q_A); the J-I phase (thermal phase) relates to kinetic properties for the reduction/oxidation of the plastoquinone pool; and the I-P phase (thermal phase) involves the re-reduction of plastocyanin and $P700^+$ on PSI (Schreiber & Neubaeuer 1987, Pietrini *et al*. 2005, Schansker *et al*. 2005, Tóth *et al*. 2007). The relative variable fluorescence and difference kinetics showed that both the photochemical and thermal fluorescence phases were affected by increasing light, with an overall more pronounced effect for the HL treatment.

An analysis of the L-band provides information regarding the connectivity energy between PSII units (Strasser & Stirbet 1998). Positive deviations of the L-band indicate losses in the use of excitation energy and may be related to thylakoid stacking (Oukarroum *et al*. 2009). The fact that these deviations were not hyperbola shaped indicates that light had little effect on the L-band (Oukarroum *et al*. 2009).

Increasing light affected the donor side more than the acceptor side of PSII. This conclusion followed from the absence of significant differences between treatments for V_J and ψ_O, showing that the reoxidation and electron transport capacities on the acceptor side of PSII and beyond Q_A^- were not compromised (Mehta *et al*. 2010). However, a K-band occurred, the formation of which can be explained by an imbalance between the electron flow leaving the RC to the acceptor side and the electron flow coming to the RC from the donor side (Strasser 1997). The positive K-bands observed for both species indicated that the higher light levels caused OEC inhibition and are associated with limitations on the donor side of PSII (Strasser 1997, Tomek *et al*. 2001, Oukarroum *et al*. 2009, Chen & Cheng 2010). Similar results have been observed for seedlings (Gonçalves *et al*. 2007) and young individuals of tropical species (Gonçalves *et al*. 2010) subjected to intense light. The more pronounced K-band in *R. mangle* than in *A. germinans* may be attributed to variations in the protection mechanisms that stabilize the OEC, such as the compatible solutes proline and glycine betaine, which protect the OEC under stress conditions (Papageorgiou & Murata 1995, De Ronde *et al*. 2004). The genus *Avicennia* presents higher glycine betaine concentrations compared with those of *Rhizophora* (Popp *et al*. 1984, Medina & Francisco 1997), explaining the less pronounced K-band observed for *A. germinans*.

The I-P phase relates to the final electron acceptor pool on the acceptor side of PSI (Yusuf *et al*. 2010). The negative deviations in the I-P phase observed in the difference kinetics for both species indicate that the electron transference on the PSI acceptor side was unaffected by increasing light (Tsimilli-Michael & Strasser 2008; Yusuf *et al*. 2010).

The analysis of the parameters derived by the JIP-test showed similar response patterns for both species (Fig. 3). However, greater and more significant differences between the treatments were observed for *R. mangle* than for *A. germinans*. The photoaclimation of the species provided greater use of light resource in the different treatments. However, the results showed that *R. mangle* exhibited higher plasticity, indicating that this species may be more successful in recently opened gaps.

The respective values of φ_{Po} (= F_V/F_M) under HL, ML and LL growing conditions were 0.71, 0.79 and 0.81 for *A. germinans* and 0.72, 0.78 and 0.81 for *R. mangle*. F_V/F_M varies between 0.78 and 0.84 in healthy plants (Genty *et al*. 1989, Govindjee 1995). A decreased φ_{Po} value in response to increasing light has also been observed in *Rhizophora mucronata* Lam. (Ulquodry *et al*. 2014) and other tropical species (Dias & Marenco 2006, Mielke & Schaffer 2010, Vieira *et al*. 2011, Lage-Pinto *et al*. 2012, Portela *et al*. 2019).

The relatively low F_V/F_M and PI_{ABS} values observed for *A. germinans* and *R. mangle* grown under HL indicate photoinhibition, which results from the excessive excitation of the photosynthetic apparatus (Osmond 1981). Photoinhibitory damage

may inactivate the OEC, as indicated by positive K-bands. Lowered F_V/F_M ratios can result from increases in F_O or decreases in F_M (Dias & Marenco 2006). In the present study, F_M was significantly lower for the HL than for the ML or LL treatment. A lower F_M reflects a lower capacity for the reduction in Q_A by PSII (Falqueto *et al*. 2012b) and may be related to the photoprotective interconversion of violaxanthin to zeaxanthin (xanthine cycle), leading to nonphotochemical quenching (Demmig-Adams *et al*. 1995). A decrease in F_V/F_M may also be attributed to the conversion of active RCs into silent RCs (non-Q_A-reducing heat sinks) (Hermans *et al*. 2003, Strasser *et al*. 2004, Yusuf *et al*. 2010).

A heightened loss of absorbed light energy through heat dissipation by the antenna system and energy dissipation through electron transport are important to mitigate photoinhibition under intense light conditions (Demmig-Adams *et al*. 1996, Baroli & Melis 1998). The fact that electron transport of an active RC (ET_O/RC) remained stable and ET_O/CS decreased indicates that *A. germinans* and *R. mangle* were unable to regulate electron transport when exposed to strong light. This inference confirms that the photoprotective mechanism is related to a heightened dissipation of accumulated energy in the form of heat (Strasser *et al*. 2004), as indicated by the increases in φ_{Do}, DI_O/RC and DI_O/CS.

Rhizophora mangle presented significantly higher ABS/RCs with higher light levels, which may be explained by an increase in the size of the functional antenna (which supplies excitation energy to active RCs) and/or the conversion of active RCs to silent RCs (Strasser *et al*. 2004, Yusuf *et al*. 2010). The significant increase in M_O observed for the HL and ML treatments indicates diminished electron transport, most likely due to an increased number of silent RCs (Falqueto *et al*. 2012b). In the present study, the increase in ABS/RC was accompanied by an increase in TR_O/RC, indicating that both changes were caused by an increase in the number of silent RCs and in the size of the functional PSII antenna (Yusuf *et al*. 2010).

An effect of excess light was also evident from the lowered chl *a* and chl *b* contents, indicating stress due to oxidative processes in chloroplasts that results in an imbalance between the synthesis and degradation of chloroplastidial pigments (Smirnoff 1993, Krause *et al*. 2012). The lowered chl *a* and chl *b* contents observed under strong light are in accordance with reports for other tropical species (Morais *et al*. 2007, Mielke & Schaffer 2010, Lage-Pinto *et al*. 2012, Souza *et al*. 2017). Shaded leaves present characteristics that increase energy capture, such as an elevated photosynthetic pigment content (Boardman 1977, Souza *et al*. 2017), as observed in the present study.

Carots serve as accessory pigments and act as photoprotectors (dissipating excess energy) and antioxidant agents, minimizing the effect of reactive oxygen species (ROSs), such as the superoxide anion (O_2^-), hydrogen peroxide (H_2O_2) and the hydroxyl radical (OH^-) (Demmig-Adams *et al*. 1996, Muller *et al*. 2001). The lower chl (*a*+*b*)/*carots* ratio observed for seedlings grown under HL indicates an adjusted *carot* content in response to increasing light levels, resulting in a heightened efficiency of energy dissipation, which protects against photooxidative damage from intense light (Demmig-Adams *et al*. 1989). This adjustment reveals physiological plasticity, indicating that the seedlings can acclimatize at different luminosity intensities. The results suggest that the photoacclimation potential of the two species provided greater adjustment ensuring greater use of the light resource in the different treatments (Chazdon *et al*. 1996).

When grown under higher shading, *A. germinans* seedlings presented higher F_V/F_M and PI_{ABS} values compared with those presented by the remaining treatments. López-Hoffman *et al*. (2007) observed that although the seedling to juvenile progression rate of *A. germinans* increased with canopy openness, shaded patches were demographically more important to its population growth, indicating that this species is shade promoted.

The only significant differences between species were observed for PI_{ABS}, which was higher for *R. mangle* than for *A. germinans* grown under LL. This result shows that *R. mangle* was the more efficient of the two species in capturing and transporting energy under conditions of higher shading. This again demonstrates the greater physiological plasticity of *R. mangle*, which would also benefit beneath the canopy of mangrove forests. Although *R. mangle* exhibited higher physiological plasticity, it should be noted that the success of the species does not depend only on the light conditions. Other factors and their interaction, such as salinity and flood frequency are also important and influence the abundance of mangrove species.

Rhizophora mangle showed tolerance to heightened light levels but presented decreased maximum PSII quantum yield (F_V/F_M) and PI_{ABS} values. Similar results have been reported for shade-

tolerant (Barros *et al*. 2012, Portela *et al*. 2019) and pioneer species (Valladares *et al*. 2005). *Rhizophora mangle* may establish and survive in shaded environments (Ball 1980) but can establish at all light levels, presenting a relatively high density of young seedlings in wide gaps (Sousa *et al*. 2003, Whelan 2005). Our results showed that this species tolerates strong light, which is in accordance with López-Hoffman *et al*. (2007), who suggested that *R. mangle* is gap dependent (pioneer) when its whole life cycle is considered.

The hypotheses of the present study were confirmed. Both species showed similar capacities for acclimating to intense light, exhibiting protective mechanisms to avoid damage to the photosynthetic apparatus. However, *A. germinans* presented overall higher resistance, manifesting lower deviations in difference kinetics and variation in the JIP-test parameters among the various light levels when compared with *R. mangle*, which showed higher physiological plasticity.

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