DOI: 10.1007/s11099-015-0085-6 PHOTOSYNTHETICA 53 (1): 118-127, 2015

The effect of irradiance and water restriction on photosynthesis in young jatobá-do-cerrado (*Hymenaea stigonocarpa*) plants

A.C. COSTA[*,+], S.L. REZENDE-SILVA[*], C.A. MEGGUER[*], L.M.F. MOURA[*], M. ROSA[*],
and A.A. SILVA[**]

Laboratório de Ecofisiologia e Produtividade Vegetal, Instituto Federal de Educação, Ciência e Tecnologia Goiano – Campus Rio Verde, Caixa Postal 66, 75901-970 Rio Verde, GO, Brazil[*]
Departamento de Biologia Vegetal, Ed. CCBII, Av. P. H. Rolfs s/n, Universidade Federal de Viçosa, Campus Universitário, 36570-900 Viçosa, MG, Brazil[**]

Abstract

High irradiance promotes decreases in the quantum yield in plants, which reduce the photosynthetic rate. The excess of light in combination with water deficit can intensify the response of plants to stress, especially in species susceptible to those factors. The aim of the present study was to characterize the photosynthetic activity of young jatobá-do-cerrado (*Hymenaea stigonocarpa* Mart. ex Hayne) trees under different irradiance conditions, both alone and/or in combination with water deficit. Four irradiances [45, 230, 510, and 1,700 µmol(photon) m^{-2} s^{-1}] and two levels of water in soil (90% and 50% of field capacity) were used. Gas exchange, water potential, and chlorophyll *a* fluorescence were measured. The highest rates of photosynthesis were observed under irradiances of 230 and 510 µmol(photon) m^{-2} s^{-1}. Irradiance of 1,700 µmol(photon) m^{-2} s^{-1} led to the photoinhibition of photosynthesis, as indicated by a reduced maximum quantum yield of PSII, effective quantum yield ratio, and electron transport rate, as well as higher nonphotochemical quenching. The most stressful to young *H. stigonocarpa* plants was high irradiance, while water deficit did not intensify the response to light stress.

Additional key words: Brazil savanna; luminosity; photoinhibition; water potential.

Introduction

Jatobá-do-cerrado (*Hymenaea stigonocarpa* Mart. ex Hayne) is an arboreous species belonging to the Fabaceae family. It is distributed in the Brazilian Cerrado, mainly in open Cerrado and Cerrado field formations; it grows slowly with low water and nutritional requirements (Carvalho 2007). The slow growth characterizes this species as late secondary (Pereira *et al.* 2011). *Hymenaea stigonocarpa* is the species with a great potential for recovering damaged areas due to its size and the richness of its roots (Lorenzi 2000). However, only few studies are available that explore this species for its photosynthetic capacity in contrasting environments of irradiance and water avail-ability. High light intensity and water restriction, which are frequent environmental conditions in a tropical climate, may be among the most significant factors that prevent plant growth.

The Cerrado, located in the central region of Brazil, is characterized by vegetation that range from grasslands, savanna, and forest formations (Kanegae *et al.* 2000, Capuzzo *et al.* 2012). It is also considered as a big biodiversity center and one of the world hotspots (Myers *et al.* 2000). Plants that occur in savannic formations, such as Cerrado *sensu stricto* and Cerrado field, are frequently exposed to stress, especially during the dry period.

Received 27 September 2013, *accepted* 30 June 2014.

[+]Corresponding author; phone: (55) (64) 3620 5636, fax: (55) (64) 3620 5640, e-mail: alcarcos@pq.cnpq.br

Abbreviations: C_i/C_a – ratio of intercellular and ambient concentration of CO_2; Chl – chlorophyll; *E* – transpiration rate; ETR – electron transport rate; F_m – maximal fluorescence yield of the dark-adapted state; F_0 – minimal fluorescence yield of the dark-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; FC – field capacity; g_s – stomatal conductance; LF – full sun [1,700 µmol(photon) m^{-2} s^{-1}]; L45, L230, and L510 – irradiances of 45, 230, and 510 µmol(photon) m^{-2} s^{-1}, respectively; P_N – net photosynthetic rate; NPQ – nonphotochemical quenching; q_P – photochemical quenching coefficient; VPD – vapor pressure deficient; $\Delta F/F_m'$ – effective quantum yield of PSII photochemistry; Ψ_w – water potential.

Acknowledgements: We thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), FINEP (Financiadora de Estudos e Projetos) and the Instituto Federal Goiano – Campus Rio Verde for their financial support.

This period is characterized by combined conditions of high light intensity, water deficit, high temperatures, low humidity, and high evaporative demand of the atmosphere (Franco *et al*. 2007). In regions of the Brazilian Cerrado, long periods of drought are common; it becomes a limiting factor to the establishment and growth of young plants (Kanegae *et al*. 2000).

Studies with the *Hymenaea* genus indicate that these plants possess reduced capacity to acclimatize to high irradiance and show a higher susceptibility to photoinhibition (Favaretto *et al.* 2011, Dos Anjos *et al.* 2012), which is a typical response of shade-tolerant plants. The capacity to acclimatize to different light intensities depends on characteristics intrinsic to the species (Wong *et al*. 2012), such as its ontogeny, age, and successional group, as well as the influence of environmental variations in its habitat (Bauer and Thöni 1988). The ability of adult plants to tolerate environmental stress increases during its ontogeny as a result of higher nonstructural carbohydrate reserves, when compared to juvenile plants that immediately require the carbohydrates from photosynthesis for their growth (Niinemets 2010). In adult plants, morphological development, greater lignification of tissues, greater root development, and hydraulic conductivity of the xylem confer tolerance to stressful conditions, especially drought (Poorter and Markesteijn 2008).

In tropical regions, the irradiance levels normally exceed those that plants actually use in photosynthesis. Under such circumstances, it becomes essential that plants regulate the light-collecting apparatus to avoid damage to the photosystems; they also need to dissipate excessive absorbed energy by means of nonphotochemical processes, minimizing photoxidative damage (Müller *et al.* 2001). Under high irradiance, PSII is the first protein complex to be affected, because the damage rate is higher than that of repair (Melis 1999, Murata *et al*. 2007). The processes of nonphotochemical quenching (NPQ) work as photoprotective mechanisms for PSII because they are associated to energy dissipation as heat by the xanthophyll cycle (Müller *et al*. 2001, Takahashi and Badger 2011). Thus, measuring chlorophyll (Chl) *a* fluorescence (Valladares and Pearcy 1997) provides information on the state of photosynthesis in plants under conditions of high luminosity (Gonçalves and Santos Jr. 2005).

The present study investigated the hypothesis that *H. stigonocarpa* seedlings are sensitive to high irradiance, suffer from photoinhibition, and that water deficit may intensify such a response. We aimed to characterize the photosynthetic capacity of young plants of *H. stigonocarpa* under contrasting irradiance conditions and the combination of irradiance and water deficit.

Materials and methods

Locality and climate: The experiment was conducted at the Laboratory of Ecophysiology and Plant Productivity at the Instituto Federal Goiano, Campus Rio Verde, Goiás, Brazil, located at the following coordinates: latitude 17º48'07"S and longitude 50°54'21"W. Second to the Köppen climate classification, the climate is type Aw (rainy tropical savanna), characterized by a dry period during the winter and a rainy period during the summer. Instantaneous data on maximum and minimum temperatures and relative humidity were collected at the meteorological station of University of Rio Verde during the period from July to September 2011, when the experiments were realized. The vapor pressure deficit (VPD) was calculated according to the equation used in Jones (1992).

Plants: To obtain *H. stigonocarpa* seedlings, fruits were collected from a single individual in an area of the Cerrado that showed the appropriate *sensu stricto* plant physiognomy. This tree was located at the Fontes do Saber farm near the city of Rio Verde in southwestern Goiás at the following coordinates: latitude 17º47'24"S and longitude 50°56'31"W. The mother plant was identified and a voucher specimen was deposited in the herbarium of the IF Goiano-Rio Verde Campus (IFRV), Goiás, Brazil, registered under the number IFRV41. Fruits were cut open and the pulp covering the seeds was properly washed under running water. Seeds were dried in a covered, well-ventilated area. Germination was carried out using the method of mechanical scarification described by De-Carvalho (2005). The prior-germinated seeds were transferred to 5-l pots containing soil from the area where the original plant was found. The soil used in this study was identified as Oxisol typical (EMBRAPA, 1999), which, according to the physicochemical analysis, has the following characteristics: pH in water 5.4, 1.8 mg(P) dm^{-3}; 0.1 cmol$_c$(K) dm^{-3}, 1.1 cmol$_c$(Ca) dm^{-3}; 0.6 cmol$_c$(Mg) dm^{-3}; 7.2 cmol$_c$ dm^{-3} of H and Al; 2% of organic matter, and 20.8% of base saturation; texture with 46.8% clay, 15.5% silt, and 37.6% sand. The pots were kept under natural shade provided by the canopy of trees and promoted for 70 d until two pairs of fully expanded leaves were observed on the emerged plants.

Different light intensities: Variations in this factor were chosen to try to reproduce the natural conditions found in the Cerrado. Thus, three shelters were assembled, each one with a total area of 3.36 m^2 (2.10 m long and 1.60 m wide), and entirely covered with multiple layers of shade cloth to obtain different irradiance levels. A shelter without shade cloth was used to expose the plants to natural irradiance or full sun.

Four growth environments regarding incident irradiances [μmol(photon) m^{-2} s^{-1}] were tested: (*a*) 45 (L45), (*b*) 230 (L230), (*c*) 510 (L510), and (*d*) 1,700 (LF, full sun) (Table 1). The values were obtained by evaluation

Table 1. Environments with different irradiance intensities.

Environment	Irradiance [μmol m^{-2} s^{-1}]	Covering
L45	45	Shade cloth
L230	230	Shade cloth
L510	510	Shade cloth
LF	1,700	Without shade cloth

of PAR at noon (12:00). Radiation was assessed using a PAR sensor (*QSO-S*; *Decagon Devices*, Pullman, WA, USA). In environments *a*, *b*, and *c*, the internal variations of humidity and temperature were not measured. In environment *d*, these characteristics were the same as those collected at the meteorological station previously mentioned.

Ten pots containing plants of the same height were transferred to each of the different irradiance environments. The plants remained under these conditions for 54 d. The soil moisture in the pots was maintained at field capacity (FC).

To evaluate the interference of light intensity upon the physiology, seven physiological examinations of gas exchange and Chl *a* fluorescence were performed. At the beginning of the experiment, the plants were already 71 d after germination. The evaluations started 12 d after the plant transfer to the environments with different irradiances, with weekly observations. All evaluations used only full expanded leaves from the middle third of the plants that displayed good physical and sanitary conditions. The results presented here included the data from the first (12 d) and the last evaluation (54 d).

The study was conducted in randomized blocks with a 4 × 7 factorial design, including four different irradiances in the growth environment and seven time points. Ten repetitions were performed for each treatment. The resulting data were used for an analysis of variance (*ANOVA*), and the averages were compared with *Tukey*'s test ($p<0.05$) using the *SAEG* ("Sistema de Análises Estatísticas Gerais") *version 9.0* software package. Plots were made in *SigmaPlot V.10* (*Systat Software Inc.*, San Jose, CA, USA).

Different light intensities combined with water regime changes: After 54 d under the light conditions described above, the same plants were exposed to an additional changes in the water regime. Half of the pots in each of the growth environments were maintained at 50% field capacity (FC50), while the other half was maintained as control at 90% FC (FC90). The water tension in the soil was controlled by weighing and applying enough water for the daily maintenance of the desired field capacity. The plants remained under these experimental conditions for 14 d. Three assessments were performed to measure gas exchange and Chl *a* fluorescence. Evaluations were performed weekly on sunny days.

After 14 d of treatment, two more measurements of Chl *a* fluorescence were taken to evaluate the dynamics of photoinhibition in the plants. The first measurement was performed at noon (12:00 h), and the second one was performed on the following day at 8:00 h. An effort was made to use the same leaf from each plant. Leaf water potential was measured at the end of the experiment.

The study was conducted in randomized blocks with a 4 × 2 × 3 factorial design with four irradiance conditions in the growth environment, two water tensions in the soil (90% and 50% FC), and three time points. Five repetitions were performed for each treatment. The data were used for an analysis of variance (*ANOVA*) and the averages were compared by using *Tukey*'s test ($p<0.05$) in *SAEG version 9.0*. Graphs were made using *SigmaPlot V.10* (*Systat Software Inc.*, San Jose, CA, USA).

Gas exchange and water status: The gas-exchange characteristics of the *H. stigonocarpa* plants were measured to estimate photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and the ratio between internal and external CO_2 (C_i/C_a). Measurements were performed with a portable photosynthesis system (*LCi Light Systems*, *ADC Bioscientific*, Herts, England). This system is equipped with a light source, which consisted of a support with an opening containing a 20 W dichroic halogen lamp that created a photon flux density of 1,000 μmol m^{-2} s^{-1}. Measurements were performed using CO_2 and temperature under environment conditions.

Leaf water potential (Ψ_w) was measured with a Scholander pressure chamber (*Model 3005-1412*, *Soilmoisture Equipment Corp.*, Goleta, CA, USA). The same completely expanded leaves as those used for the gas exchange and Chl *a* fluorescence studies were used to measure Ψ_w. To avoid water loss by transpiration, the leaves were cut at the petiole insertion point, wrapped in a plastic sac and stored in a styrofoam box. Assessments were performed before dawn between 4:00–6:00 h to avoid turgor pressure loss.

Chl *a* fluorescence was measured in parallel with the gas exchange from the same leaf using a *MINI-PAM* (*Walz,* Effeltrich, Germany) modulated fluorometer. Analyses were performed by using the methods of Bilger *et al.* (1995) and Rascher *et al.* (2000). First, the leaves were acclimated to the dark for 30 min; then, they were exposed to a weak pulse of red light (0.03 μmol m^{-2} s^{-1}) and the initial fluorescence (F_0) was measured. Next, the leaves were exposed to 0.8 s of saturating actinic light (>6,000 μmol m^{-2} s^{-1}) and the maximum fluorescence was measured (F_m). Using this data, the effective quantum yield of PSII (Genty *et al.* 1989) was determined by superimposing a saturating pulse of leaves that was previously acclimated to ambient light and calculating $\Delta F/F_m' = (F_m' - F)/F_m'$, where F is the maximum fluorescence during the saturating pulse. The $\Delta F/F_m'$ was then used to estimate the apparent electron transport rate (ETR) as performed in Bilger *et al.* (1995) *via* the equation

ETR = $\Delta F/F_m'$ × PFD × 0.5 × 0.84, where PFD is the photon flux density incident to the leaf, 0.5 is the value of the fraction of the excitation energy that is distributed to PSII (Laisk and Loreto 1996), and 0.84 is the value of the fraction of incident light that is absorbed by the leaves (Ehleringer 1981). The Stern-Volmer NPQ coefficient was calculated as NPQ = $(F_m - F_m')/F_m'$ (Bilger and Björkman 1990).

Results

Climatic conditions: Air temperature during the experiment period ranged from 18ºC (minimum) to 33ºC (maximum). Maximum relative humidity was 56%, while minimum was 43% and the VPD varied between 1.2 and 1.7 kPa.

Physiological characteristics of plants under different light intensities

Gas exchange analysis showed a significant interaction between irradiance and the number of days under different growth environments. There was an increase in P_N during exposure to different irradiances, with the highest rates being observed at 54 d, except plants under the highest irradiance, which showed a significant reduction. Higher P_N [approximately 10 μmol(CO_2) m^{-2} s^{-1}] was observed in plants grown at intermediate irradiances, *i.e.*, L230 and L510 (Table 2). The different levels of irradiance did not influence the g_s and C_i/C_a (Table 2) in any of the evaluated periods. Otherwise, an increase in *E* at 54 d occurred independently of irradiance. When young plants of *H. stigonocarpa* were exposed only to different light intensities, the g_s remained stable. However, under the same condition, a reduction of P_N occurred in plants grown under LF.

Chl *a* fluorescence: Changing characteristics of Chl *a* fluorescence were a function of the interaction between irradiance and the number of days in the growth environment. At 12 d after treatment, the values for maximum quantum yield of PSII (F_v/F_m) remained high with an average of 0.82. However, plants under the highest irradiance (LF) showed a reduced F_v/F_m value (0.64) at the end of treatment (Table 2), indicating the occurrence of photoinhibition.

The effective quantum yield of PSII ($\Delta F/F_m'$) was higher in plants grown at irradiances of L230 and L510 after 12 d of treatment. At 54 d, there was a decrease in the yield for plants grown at the extreme irradiances (L45 and LF) (Table 2).

There was no interaction between the irradiance level during growth and the time of treatment in the electron transport rate (ETR) pattern that was similar to the $\Delta F/F_m'$ (Table 2). The level of irradiance during growth led to a significant increase in ETR, with the highest rate being measured in plants grown at L510 (Fig. 1). NPQ was significantly higher at 54 d of treatment in plants grown at the irradiance of LF (Table 2).

Physiological characteristics under different light intensities combined with water regime changes

Gas exchange and water potential: Gas exchange in young *H. stigonocarpa* plants revealed only an interaction between irradiance and days of treatment under different light growth environments (Fig. 2). The P_N, g_s, *E*, and C_i/C_a did not change significantly in plants grown at irradiances of L45 and L230 (Fig. 2*A*–*D*). However, with the exception of the C_i/C_a (Fig. 2*C*), under irradiances of L510 and LF, a reduction of P_N, g_s, and *E* occurred as a function of the prolonged treatments. Independent of irradiance, water deficit significantly reduced P_N, g_s, C_i/C_a, and *E* in young plants of *H. stigonocarpa* in comparison with the control plants (Fig. 3).

The water potential (Ψ_w) of young *H. stigonocarpa* plants was influenced by the growth irradiance and the water regime, but in an independent fashion. The Ψ_w was lower in plants under water deficit (Fig. 4) and in plants grown under an irradiance of LF (Fig. 5), representing *ca.* 60% reduction in plants grown at L45.

Chl *a* fluorescence parameters were not significantly affected by the water regime. However, there was an interaction between irradiance level and treatment time. The F_v/F_m decreased significantly over time in plants grown under LF, reaching approximately 0.59 at the end of the exposure period. At irradiances of L45, L230, and L510, the F_v/F_m values remained near 0.8 during the experiment (Fig. 6*A*). The $\Delta F/F_m'$ in plants under LF decreased over time (Fig. 6*B*). However, more pronounced decreases were observed under the extreme irradiances (*i.e.*, L45 and LF) during the experiment (Fig. 6*B*).

The ETR at 14 d of treatment was approximately 2.5 times lower in the plants receiving L45 and LF compared to those grown under intermediate irradiances (Fig. 6*C*). Unlike the ETR, the NPQ increased from 0.9 to 1.5 over the course of the treatment in the plants receiving LF irradiance. The values represented a greater than 65% increase compared to plants grown under lower irradiances (Fig. 6*D*).

Additional testing of photoinhibition dynamics (Table 3) did not show recovery of F_v/F_m values in the plants grown under LF. The F_v/F_m values were 0.59 at noon and 0.69 at 8:00 h the next day.

Discussion

The ability of young plants to adjust physiologically and morphologically according to changes in irradiance can be decisive for their survival in new environments (Yamashita *et al*. 2002). In this study, plants of *H. stigonocarpa* demonstrated a high capacity for photosynthetic acclimation, even at high irradiance, although it was reduced by prolonging the time of exposure to such conditions. This response was observed during the initial period (12 d) of exposure to increasing light intensities, where no changes in the characteristics of gas exchange and Chl *a* fluorescence (with the exception of $\Delta F/F_m'$) were observed, demonstrating that this species has efficient mechanisms to tolerate the excess of incident energy. However, when conditions of excessive irradiance were extended, these mechanisms did not prevent a damage of the photosynthetic apparatus, as we observed after 54 d. The decrease in P_N during this period under LF environment suggests that in the juvenile stage, the plants of this species are sensitive to excessive light and are shade-tolerant. The stressful effects of irradiance in this case were not associated with stomatal limitation in view of its stability, but to the low efficiency of the photochemical dissipation processes as demonstrated by the presented fluorescence parameters.

At 12 d, the values of F_v/F_m remained about 0.80; at 54 d, these values were lower than 0.6 in the plants grown at LF, indicating the occurrence of photoinhibition. The plants grown at L510 showed a slight reduction in the F_v/F_m ratio but they showed values still within a range that does not characterize photoinhibition. Decreased photosynthesis caused by photoinhibition is a condition that generally occurs in plants that are exposed to excessive light (Maxwell and Johnson 2000). Thus, it is essential that plants frequently exposed to high irradiance, high temperature, and low humidity maintain a balance between the light absorbed by photosynthesis and the dissipation of energy (Franco 2007).

Previous studies with another species of jatobá (*H. courbaril*) have shown that the species is notably sensitive to high irradiance, which results in decreased F_v/F_m values (Silvestrini *et al*. 2007, Silva 2010, Favaretto *et al*. 2011). Because the *H. stigonocarpa* is a shade-tolerant species, a decreased F_v/F_m ratio under high irradiance and rapid acclimatization to intermediate irradiances is consistent with what is expected for a species at this succession level. According to Dos Anjos *et al*. (2012), photoinhibition susceptibility and the ability to adjust to different light regimes are directly correlated with this successional group.

Low photosynthetic rates of plants growing under high irradiance are related to inefficient use of energy, which can result in dissipation mechanisms such as heat or fluorescence, and generally leads to a reduction in the incorporation of CO_2 (Thach *et al*. 2007, Gonçalves *et al*. 2010). Plants grown at irradiances of L230 and L510

Table 2. Net photosynthetic rate (P_N), stomatal conductance (g_s), ratio of internal and external concentration of CO_2 (C_i/C_a), transpiration rate (*E*), maximal quantum yield of PSII photochemistry (F_v/F_m), effective quantum yield of photosystem II ($\Delta F/F_m'$), electron transport rate (ETR), and nonphotochemical quenching (NPQ) in young *Hymenaea stigonocarpa* plants as a function of irradiance during growth and time of treatment. Averages followed by the same *uppercase letters* for the days and *lowercase letters* for the irradiances are not significantly different according to *Tukey*'s test ($P<0.05$). Values are the means ± SE ($n = 10$).

Irradiance [μmol m^{-2} s^{-1}]	P_N [μmol(CO_2) m^{-2} s^{-1}]	g_s [mol(H_2O) m^{-2} s^{-1}]	C_i/C_a	*E* [mmol(H_2O) m^{-2} s^{-1}]	F_v/F_m	$\Delta F/F_m'$	ETR [mmol m^{-2} s^{-1}]	NPQ
	12 days of treatment							
45	6.69 ± 0.40^{Bb}	0.16 ± 0.02	0.88 ± 0.02^{Aa}	1.29 ± 0.09^{Bab}	0.81 ± 0.00^{Aa}	0.24 ± 0.02^{Ab}	82 ± 2.57	0.39 ± 0.09^{Ab}
230	9.30 ± 0.43^{Ba}	0.23 ± 0.05	0.79 ± 0.02^{Aa}	1.53 ± 0.11^{Bab}	0.81 ± 0.01^{Aa}	0.40 ± 0.02^{Aa}	147 ± 7.65	0.79 ± 0.07^{Aa}
510	6.75 ± 0.63^{Bb}	0.15 ± 0.03	0.77 ± 0.02^{Aa}	1.15 ± 0.14^{Bb}	0.83 ± 0.00^{Aa}	0.39 ± 0.03^{Aa}	158 ± 8.09	0.78 ± 0.07^{Aa}
1,700	7.65 ± 0.50^{Ab}	0.20 ± 0.03	0.82 ± 0.02^{Aa}	1.61 ± 0.12^{Bab}	0.80 ± 0.01^{Aa}	0.28 ± 0.02^{Ab}	118 ± 5.18	0.81 ± 0.06^{Ba}
	54 days of treatment							
45	9.16 ± 0.33^{Ab}	0.13 ± 0.02	0.71 ± 0.02^{Aa}	2.03 ± 0.11^{Aab}	0.83 ± 0.00^{Aa}	0.19 ± 0.01^{Bc}	71 ± 3.72	0.71 ± 0.06^{Ab}
230	10.76 ± 0.32^{Aab}	0.20 ± 0.02	0.75 ± 0.02^{Aa}	2.30 ± 0.16^{Aab}	0.81 ± 0.00^{Aa}	0.34 ± 0.02^{Bb}	129 ± 7.48	0.95 ± 0.12^{Aa}
510	10.01 ± 0.32^{Aab}	0.19 ± 0.02	0.75 ± 0.01^{Aa}	2.25 ± 0.13^{Aab}	0.78 ± 0.01^{Bb}	0.42 ± 0.02^{Aa}	155 ± 10.88	0.68 ± 0.05^{Aa}
1,700	6.31 ± 0.25^{Bc}	0.13 ± 0.01	0.74 ± 0.02^{Aa}	1.79 ± 0.09^{Abc}	0.64 ± 0.03^{Bc}	0.31 ± 0.01^{Ab}	128 ± 7.43	1.11 ± 0.08^{Ba}

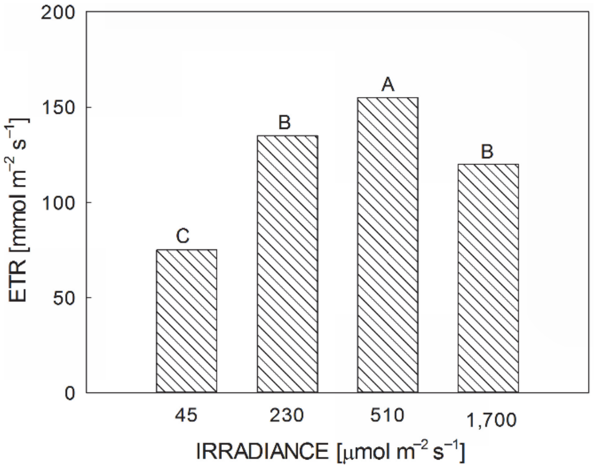

Fig. 1. Electron transport rate (ETR) in young *Hymenaea stigonocarpa* plants as a function of irradiance during growth. Averages followed by *the same letters* do not differ according to *Tukey*'s test ($P<0.05$). The data are given as means ($n = 10$).

performed well photosynthetically. However, under irradiance of L45, low $\Delta F/F_m'$ and ETR values suggest that this condition might be limiting to plant growth.

The decreases in F_v/F_m under high irradiance might be explained by the plant low ability to protect against excess absorbed light, as shown by the low values for $\Delta F/F_m'$ and ETR, in plants grown at LF. The high NPQ values indicate the occurrence of a mechanism used by plants to minimize photoinhibition damage to photosynthetic apparatus under high irradiance conditions (Franco *et al*. 2007, Dos Anjos *et al*. 2012). However, this increase in nonphotochemical energy dissipation as heat was not sufficient to minimize stress, indicating that these plants possessed a reduced ability to endure high irradiances at a juvenile age. The decrease in $\Delta F/F_m'$ as a function of increased irradiance was similar to the behavior observed for ETR in the present study. The reduction of $\Delta F/F_m'$ was also observed in the tropical, arboreous species *Cariniana legalis* and *Rhamnidium elaeocarpum* under high irradiance (Ribeiro *et al*. 2005).

Under water-deficit conditions, other stress factors, such as temperature (Aranda *et al*. 2012), irradiance (Adibah and Ainuddin 2011), and salinity (Munns 2002), have their effects intensified. Drought in a combination with high irradiances can cause lower values of F_v/F_m, *i.e.*, reducing photosynthetic efficiency (Lemos Filho 2000) of tropical plants. However, in this study, water deficit did not intensify photoinhibition in plants of *H. stigonocarpa* under high irradiance, as evidenced by the lack of interaction between these two factors in the statistical analysis. On the other hand, when analyzed together,

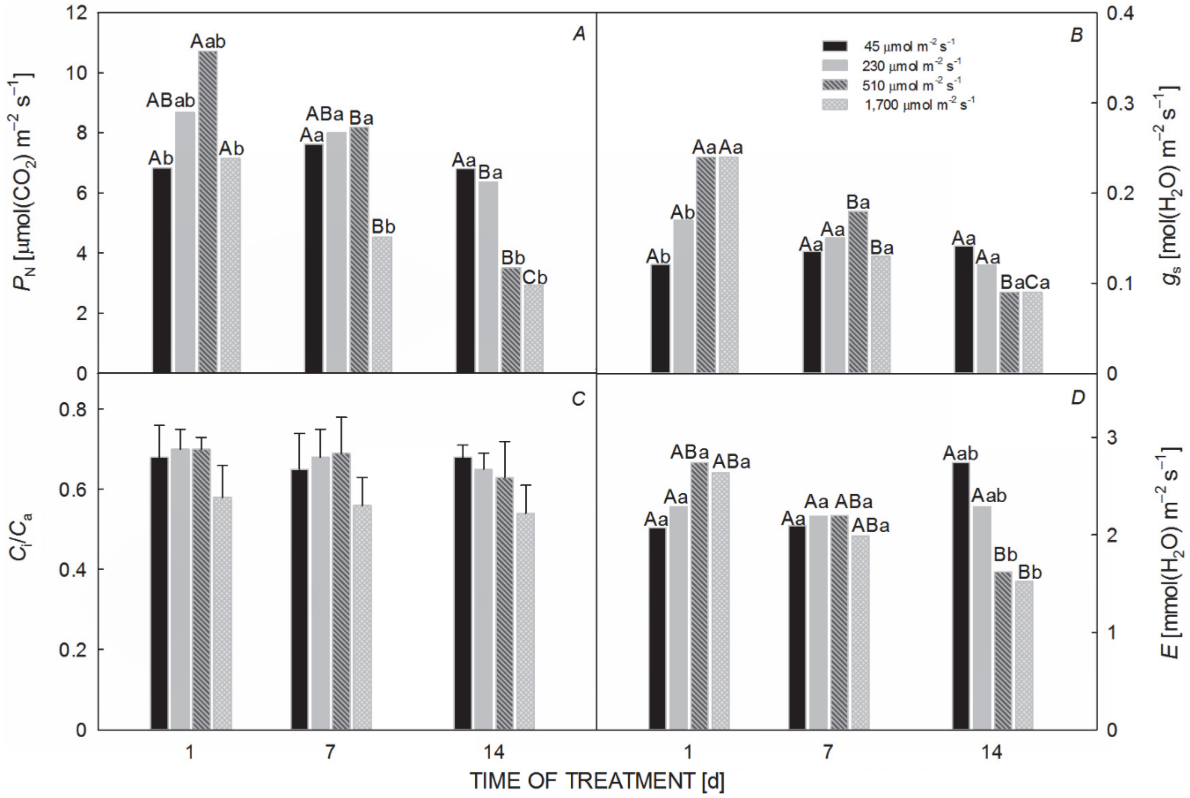

Fig. 2. (*A*) Net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) ratio of intercellular and ambient concentration of CO2 (C_i/C_a), and (*D*) transpiration rate (*E*) in young *Hymenaea stigonocarpa* plants as a function of irradiance during growth and the time of treatment. Averages that are followed by the same *uppercase letters* between days and *lowercase letters* between irradiance levels are not different according to *Tukey*'s test ($P<0.05$). The given data are means ($n = 10$).

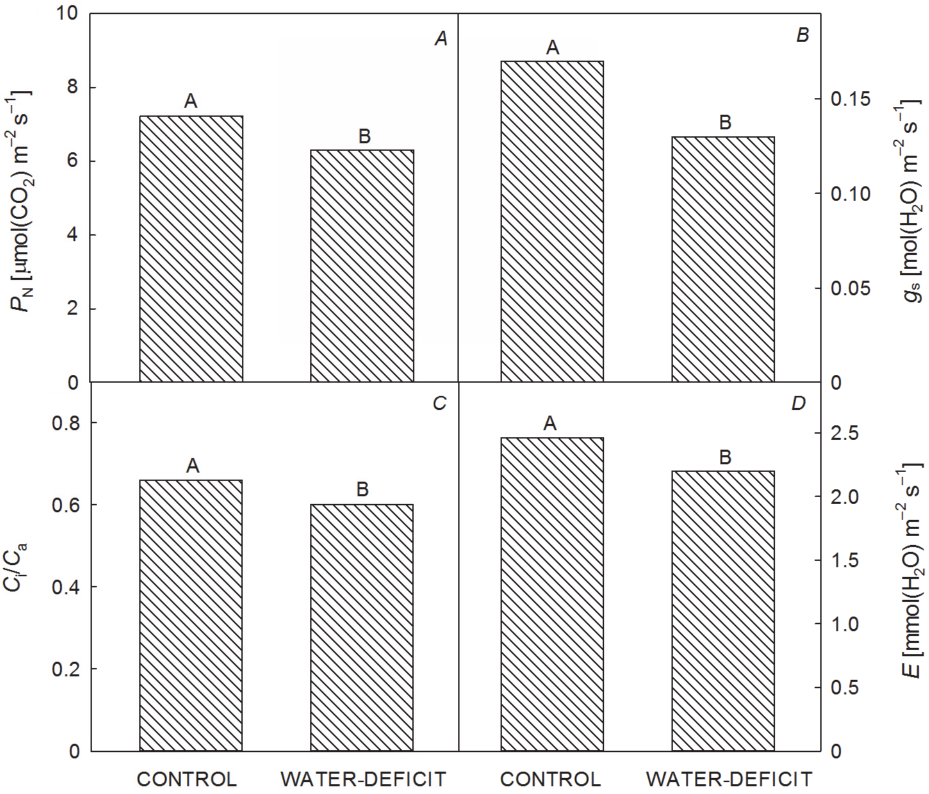

Fig. 3. (*A*) Net photosynthetic rate (P_N), (*B*) stomatal conductance (g_s), (*C*) ratio of intercellular and ambient concentration of CO_2 (C_i/C_a), and (*D*) transpiration rate (*E*) in young *Hymenaea stigonocarpa* plants as a function of the water regime. Averages followed by *the same letters* are not different according to *Tukey*'s test ($P<0.05$). The data presented here are means ($n = 60$).

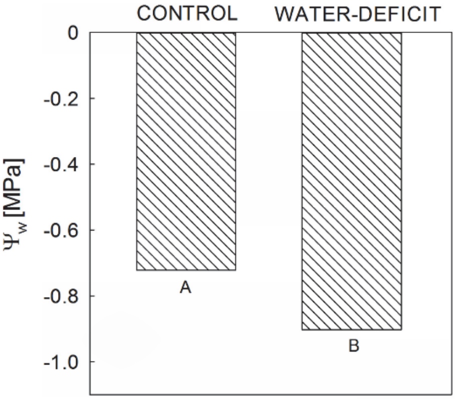

Fig. 4. Water potential (Ψ_w) in young *Hymenaea stigonocarpa* plants as a function of the water regime. Averages followed by *the same letter* are not different according to *Tukey*'s test ($P<0.05$). The data given here are averages ($n = 60$).

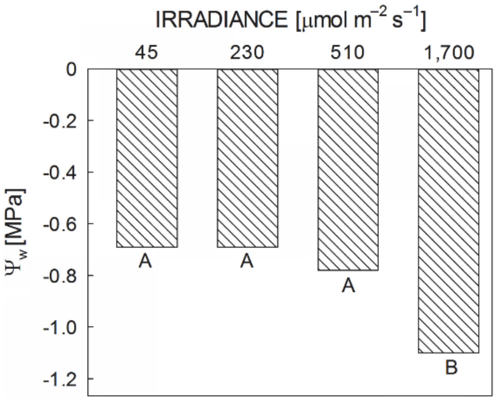

Fig. 5. Water potential (Ψ_w) in young *H. stigonocarpa* plants as a function of irradiance during growth. Averages followed by *the same letter* are not different according to *Tukey*'s test ($P<0.05$). The data shown here are averages ($n = 40$).

the long exposure period and high irradiance intensified the damage to the photosynthetic apparatus in plants grown under LF. The decrease in all characteristics of gas exchange and Chl *a* fluorescence, independent of water regime, confirmed that exposure time and irradiance were the determining factors for photoinhibition of these plants.

Although we did not find a statistical interaction between water regime and irradiance, water deficit caused a reduction in P_N, g_s, C_i/C_a, and *E*. The effect of water deficit on reduced *E* was related to stomata closing in response to reduced water availability, showing a direct relation between g_s and photosynthesis. Environments with a high incidence of luminous energy generally experience higher temperatures and higher VPD, intensifying the water-deficit effects. When plants are exposed to those conditions, stomata normally close to prevent water loss, which results in a decrease in intercellular CO_2 concentrations and inhibits photosynthesis (Favaretto *et al.* 2011, Júnior *et al.* 2011).

Both irradiance and water stress independently affected the Ψ_w in young *H. stigonocarpa* plants. Lower Ψ_w values were observed in water-restricted plants and

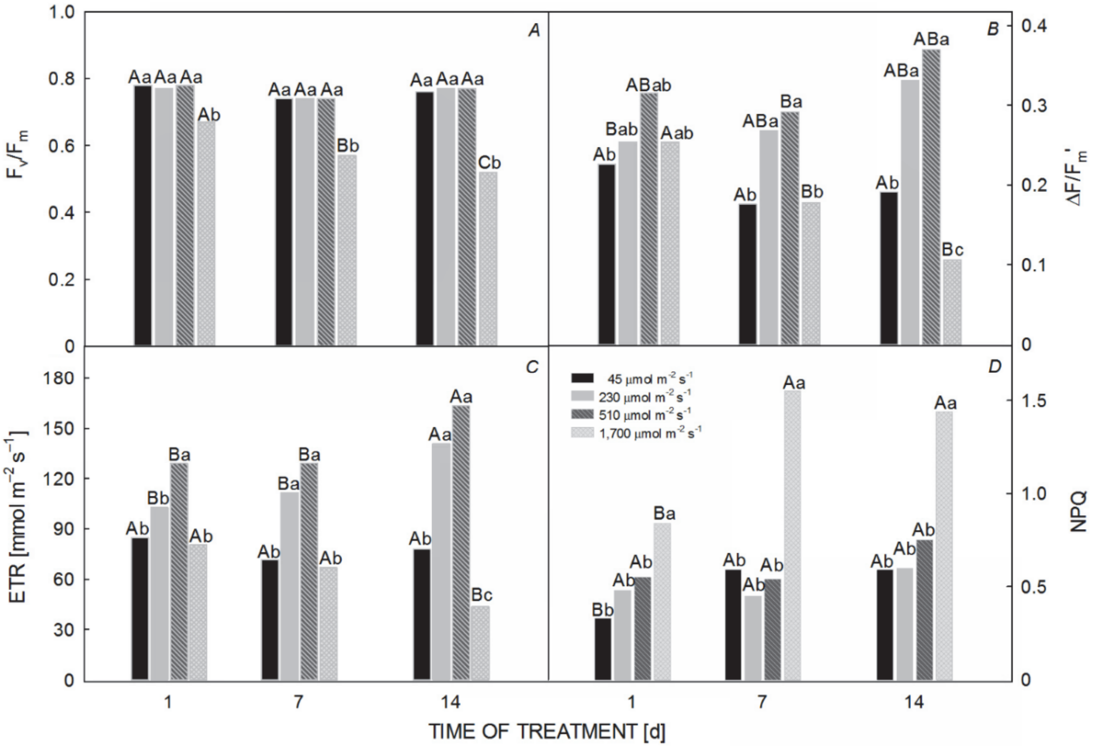

Fig. 6. (*A*) Maximal quantum yield of PSII photochemistry (F_v/F_m), (*B*) effective quantum yield of photosystem II ($\Delta F/F_m'$), (*C*) electron transport rate (ETR), and (*D*) nonphotochemical quenching (NPQ) in young *H. stigonocarpa* plants as a function of irradiance and time of treatment. Averages followed by the same *uppercase letters* between days and *lowercase letters* between irradiances are not different according to *Tukey*'s test ($P<0.05$).The data are the averages ($n = 10$).

Table 3. Maximal quantum yield of PSII photochemistry (F_v/F_m) in young *Hymenaea stigonocarpa* plants that were exposed to different irradiance levels for 68 d. Averages followed by the same *uppercase letters* are between the measurement times, and *lowercase letters* are between the irradiances at the same time-point and are not significantly different according to *Tukey*'s test ($P<0.05$). The data are averages ($n = 10$).

Irradiance [µmol m^{-2} s^{-1}]	F_v/F_m Measurement time	
	12:00 h	8:00 h
45	0.82^{Aa}	0.82^{Aa}
230	0.81^{Aa}	0.81^{Aa}
510	0.79^{Bb}	0.80^{Ab}
1,700	0.59^{Bc}	0.69^{Ac}

those grown under the LF irradiance, regardless of the water regime. High light intensity causes a higher evaporative demand and consequent desiccation of the soil, which leads to a lower leaf water potential. Despite reducing Ψ_w approximately by –1.0 MPa under high irradiance and water deficit, this value is close to that found in other plants from Cerrado (Mattos *et al.* 1997, Franco 1998, Prado *et al.* 2004) under conditions not characterized as stress.

Water stress did not affect fluorescence under any of the experimental conditions. Although water deficit may change the dynamics of Chl *a* fluorescence in plants (Zhang *et al*. 2011, Campos *et al*. 2014), studies show that PSII keeps its functionality under water-deficit conditions (Cornic and Fresneau 2002, Snider *et al*. 2014) and the F_v/F_m is little affected under such circumstances (Tezara *et al*. 2003). In other arboreous species from tropical environments, such as *Myracrodruon urundeuva* (Queiroz et *al*. 2002), *Bertholletia excelsa*, and *Dipteryx odorata* (Morais *et al*. 2007), no changes in F_v/F_m ratio were observed under water deficit.

The parameters of Chl *a* fluorescence, in this study, were not influenced by water deficit, suggesting that this species has an efficient mechanism to tolerate seasonal drought, because even when subjected to this stress factor, acclimation occurred in plants growing under intermediate irradiance. However, young plants of *H. stigonocarpa* are susceptible to light stress, although the combination with water stress does not intensify photoinhibition. This behavior can be related to a survival strategy of these plants in the savanna formations of the Brazilian Cerrado.

In conclusion, young *H. stigonocarpa* plants showed the increased ability of photosynthetic acclimation under intermediate light intensities as observed through fluorescence parameters, such as $\Delta F/F_m$' and ETR. Plants exposed to high irradiance exhibited low values of F_v/F_m and high values of NPQ, which indicated the occurrence of photoinhibition under these conditions.

References

Antunes Júnior M.Z.A., Lobo F.A., Dalmagro H.J. *et al.*: [Microclimate effect on potential gas exchange of cambara (*Vochysia divergens* Pohl) and lixeira (*Curatella americana* L.) in Brazilian Savanna area.] – Rev. Bras. Bioci. **9**: 77-85, 2011. [In Portuguese]

Aranda I., Forner A., Cuesta B., Valladares F.: Species-specific water use by forest tree species: From the tree to the stand. – Agr. Water Manage. **114**: 67-77, 2012.

Bauer H., Thöni W.: Photosynthetic light acclimation in fully developed leaves of the juvenile and adult life phases of *Hedera helix*. – Physiol. Plantarum **73**: 31-37, 1988.

Bilger W., Björkman O.: Role of xanthophyll cycle in photoprotection elucidated by measurements of light induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. – Photosynth. Res. **25**: 173-185, 1990.

Bilger W., Schreiber U., Bock M.: Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. – Oecologia **102**: 425-432, 1995.

Campos H., Trejo C., Peña-Valdivia C.B. *et al.*: Stomatal and non-stomatal limitations of bell pepper (*Capsicum annuum* L.) plants under water stress and re-watering: Delayed restoration of photosynthesis during recovery. – Environ. Exp. Bot. **98**: 56-64, 2014.

Capuzzo J.P., Rossatto D.R., Franco A.C.: Differences in morphological and physiological leaf characteristics between *Tabebuia aurea* and *T. impetiginosa* is related to their typical habitats of occurrence. – Acta Bot. Bras. **26**: 519-526, 2012.

Carvalho P.E.: [Jatobá-do-Cerrado - *Hymenaea stigonocarpa* Embrapa Forestry. Technical Report, n. 133]. Pp. 8. Embrapa Forestry. Colombo 2007. [In Portuguese]

Cornic G., Fresneau C.: Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. – Ann. Bot.-London **89**: 887-894, 2002.

De-Carvalho P.S., de Miranda S.C., dos Santos M.L.: [Germination and biometrical data of *Hymenaea stigonocarpa* Mart. ex Hayne (Leguminosae Caesalpinoideae) - jatobá-do-cerrado]. – Rev. Anh. **6**: 101-116, 2005. [In Portuguese]

Dos Anjos L., Oliva M.A., Kuki K.N.: Fluorescence imaging of light acclimation of brazilian atlantic forest tree species. – Photosynthetica **50**: 95-108, 2012.

Ehleringer J.: Leaf absorptances of Mohave and Sonoran desert plants. – Oecologia **49**: 366-370, 1981.

EMBRAPA: [Brazilian Soil Classification System]. Pp. 412. Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA. Centro Nacional de Pesquisas de Solos. Rio de Janeiro, 1999. [In Portuguese]

Favaretto V.F., Martinez C.A., Soriani H.H., Furriel R.P.M.: Differential responses of antioxidant enzymes in pioneer and late successional tropical tree species grown under sun and shade conditions. – Environ. Exp. Bot. **70**: 20-28, 2011.

Franco A.C., Matsubara S., Orthen B.: Photoinhibition, carotenoid composition and the co-regulation of photochemical and non-photochemical quenching in neotropical savanna trees. – Tree Physiol. **27**: 717-725, 2007.

Franco A.C.: Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen savanna species. – Plant Ecol. **136**: 69-76, 1998.

Genty B., Briantais J.M., Baker N.R.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Gonçalves J.F.C., Santos Junior U.M.: Utilization of the chlorophyll a fluorescence technique as a tool for selecting tolerant species to environments of high irradiance. – Braz. J. Plant Physiol. **17**: 307-313, 2005.

Gonçalves J.F.C., Silva C.E., Guimarães D.G. *et al.*: [Analysis of the transient of chlorophyll a fluorescence of *Carapa guianensis* and *Dipteryx odorata* seedling submitted to two light environments.] – Acta Amaz. **40**: 89-98, 2010. [In Portuguese]

Jones H. G. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology. 2nd Ed. Pp. 85. Cambridge University. Press, Cambridge 1992.

Kanegae M. F., Braz V. S., Franco A. C.: [Seasonal drought effects and light availability on the survival and gowth of *Bowdichia virgilioides* in two typical vegetation types of the savanna of Central Brazil]. – Rev. Bras. Bot. **23**: 459-468, 2000. [In Portuguese]

Laisk A., Loreto F.: Determining photosynthetic parameters from leaf CO_2 exchange and chlorophyll fluorescence. – Plant Physiol. **110**: 903-912, 1996.

Lemos Filho J.P.: [Photoinhibition in three species of the savanna (*Annona crassifolia*, *Eugenia dysenterica* and *Campomanesia adamantium*) in the dry and rainy season].– Rev. Bras. Bot. **23**: 45-50, 2000. [In Portuguese]

Lorenzi H.: [Brazilian Trees: Manual of Identification and Cultivation of the Wood Plants Native from Brazil.] Pp 352. Instituto Plantarun de Estudos da Flora, São Paulo, Nova Odessa 2000. [In Portuguese]

Mattos E. A. de, Reinert F., de Moraes J.A.P.V.: Comparison of carbon isotope discrimination and CO_2 and H_2O gas exchange between the dry and wet seasons in leaves of several cerrado woody species. – Rev. Bras. Fisiol. Veg. **9**: 77-82, 1997.

Maxwell K., Johnson G. N.: Chlorophyll fluorescence: a practical guide. – J. Exp. Bot. **51**: 659-668, 2000.

Melis A.: Photosystem-II damage and repair cycle in chloroplasts: what modulates the rate of photodamage in vivo? – Trends Plant Sci. **4**: 130-135, 1999.

Morais R.R. de, Gonçalves J.F.C., Santos Júnior U.M. *et al.*: Chloroplastid pigment contents and chlorophyll a fluorescence in Amazonian tropical three species. – Rev. Árvore **31**: 959-966, 2007.

Müller P., Li Xiao-Ping, Niyogi K. K.: Non-photochemical quenching. A response to excess light energy. – Plant Physiol. **125**: 1558-1566, 2001.

Munns R.: Comparative physiology of salt and water stress. – Plant Cell Environ. **25**: 239-250, 2002.

Murata N., Takahashi S., Nishiyama Y., Aakhverdiev S.I.: Photoinhibition of photosystem II under environmental stress. – BBA-Bioenergetics **1767**: 414-421, 2007.

Myers N., Mittermeier R.A., Mittermeier C.G. *et al.*: Biodiversity *hotspots* for conservation priorities. – Nature **403**: 853-858, 2000.

Niinemets Ü.: Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. – Forest Ecol. Manag. **260**: 1623-1639, 2010.

Pereira S.R., Giraldelli G.R., Laura V.A., de Souza A.L.T.: [Fruit and seeds size and its influence on jatobá-do-cerrado (*Hymenaea stigonocarpa* var. *stigonocarpa* Mart. ex Hayne, Leguminosae - Caesalpinoideae).] – Rev. Bras. Sementes **33**: 141-148, 2011. [In Portuguese]

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

Prado C.H.B.A., Wenhui Z., Cardoza-Rojas, M.H., Souza G.M.: Seasonal leaf gas exchange and water potential in a woody cerrado species community. – Braz. J. Plant Physiol. **16**: 7-16, 2004.

Queiroz C.G.S., Garcia Q.S., Lemos Filho, J.P. [Photosynthetic activity and peroxidation of membrane lipids in aroeira-do-sertão plants under water stress and followed of rehydration]. – Braz. J. Plant Physiol. **14**: 59-63, 2002. [In Portuguese]

Rascher U., Liebig M., Lüttge U.: Evaluation of instant light-responses curves of chlorophyll parameters obtained with a portable chlorophyll fluorometer on site in the field. – Plant Cell Environ. **23**: 1397-1405, 2000.

Ribeiro R.V., Souza G. M., Oliveira R. F., Machado E.C.: Photosynthetic responses of tropical tree species from different successional group sunder contrasting irradiance conditions. – Rev. Bras. Bot. **28**: 149-161, 2005.

Ruzana Adibah M.S., Ainuddin A.N.: Epiphytic plants responses to light an water stress. – Asian J. Plant Sci. 10: 97-197, 2011.

Silva A.S., Oliveira J.G., da Cunha M., Vitória A.P.: Photosynthetic performance and anatomical adaptations in *Byrsonima sericea* DC. under contrasting light conditions in a remnant of the Atlantic forest. – Braz. J. Plant Physiol. **22**: 245-254, 2010.

Silvestrini M., Válio I.F.M., de Mattos E.A.: Photosynthesis and carbon gain under contrasting light levels in seedlings of a pioneer and a climax tree from a Brazilian Semideciduous Tropical Forest. – Rev. Brasil. Bot. **30**: 463-474, 2007.

Snider J.L., Collins G. D., Whitaker J. *et al.*: Electron transport through photosystem II is not limited by a wide range of water deficit conditions in field-grown *Gossypium hirsutum*. – J. Agro. Crop. Sci. **200**: 77–82, 2014.

Takahashi S., Badger M.R.: Photoprotection in plants: a new light on photosystem II damage. – Trends Plant Sci. **16**: 53-60, 2011.

Tezara W., Martínez D., Rengifo E., Herrera A.: Photosynthetic responses of the tropical spiny shrub *Lycium nodosum* (Solanaceae) to drought, soil salinity and saline spray. – Ann. Bot.-London **92**: 757-765, 2003.

Thach B., Shapcott A., Schmidt S., Critchley C.: The OJIP fast fluorescence rise characterizes *Graptophyllum* species and their stress responses. – Photosynth. Res. **94**: 423-436, 2007.

Valladares F., Pearcy R.W.: Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. – Plant Cell Environ. **20**: 25-36, 1997.

Wong S.L., Chen C.W., Huang H.W., Weng J.H.: Using combined measurements of gas exchange and chlorophyll fluorescence to investigate the photosynthetic light responses of plant species adapted to different light regimes. – Photosynthetica **50**: 206-214, 2012.

Yamashita N., Koike N., Ishida A.: Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status.– Plant Cell Environ. **25**: 1341-1356, 2002.

Zhang L.T., Zhang Z.S., Gao H.Y. *et al.*: Mitochondrial alternative oxidase pathway protects plants against photoinhibition by alleviating inhibition of the repair of photodamaged PSII through preventing formation of reactive oxygen species in *Rumex* K-1 leaves. – Physiol. Plantarum **143**: 396-407, 2011.