DOI: 10.1007/s11099-014-0038-5 PHOTOSYNTHETICA 52 (3): 351-357, 2014

Photosynthetic acclimation in shade-developed leaves of *Euterpe edulis* Mart (Arecaceae) after long-term exposure to high light

A.O. LAVINSKY*, F.P. GOMES**,+, M.S. MIELKE**, and S. FRANÇA***

Departamento de Biologia Vegetal, Universidade Federal de Viçosa, Av. PH Rolfs s/n,
*Viçosa, MG, 36570-000, Brazil**
*Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, BA, 45662-900, Brazil***
Departamento de Ciências Agrárias e Ambientais, Universidade Estadual de Santa Cruz,
*Ilhéus, BA, 45662-900, Brazil****

Abstract

To analyze acclimation of *Euterpe edulis* seedlings to changes in light availability, we transferred three-year-old seedlings cultivated for six months under natural shade understory [≈ 1.3 mol(photon) m^{-2} d^{-1}] to a forest gap [≈ 25.0 mol(photon) m^{-2} d^{-1}]. After the transfer, changes in chlorophyll fluorescence and leaf gas-exchange parameters, as well as in the light-response curves of photosynthesis and photosynthetic induction parameters, were analyzed during the following 110 days. Simultaneously measured photosynthetic characteristics in the shaded seedlings grown in understory served as the control. Despite the fact that the understory seedlings were under suboptimal conditions to achieve their light-saturated net photosynthetic rate (P_{Nmax}), light-response curves and photosynthetic induction parameters indicated that the species had the low respiration rate and a fast opening of stomata in response to the intermittent occurrence of sunflecks, which exerted a feed-forward stimulation on P_{Nmax}. Sudden exposure to high light induced photoinhibition during the first week after the transfer of seedlings to gap, as it was shown by the abrupt decline of the maximal quantum yield of PSII photochemistry (F_v/F_m). The photoinhibition showed the time-dependent dynamics, as the F_v/F_m of the seedlings transferred to the forest gap recovered completely after 110 days. Furthermore, the net photosynthetic rate increased 3.5-fold in relation to prior-exposure values. In summary, these data indicated that more than 21 days was required for the shade-acclimated seedlings to recover from photoinhibition and to relax induction photosynthetic limitations following the sudden exposure to high light. Moreover, the species responded very quickly to light availability; it highlights the importance of sunflecks to understory seedlings.

Additional key words: Arecaceae; jussara; photosynthetic induction; shade tolerance.

Introduction

E. edulis Mart. (Arecaceae), known as heart of palm or simply Juçara palm, is one of the most valuable palm species endemic to the Brazilian Atlantic Forest, occurring from southern Bahia to Rio Grande do Sul states, always associated with the rainforests along the Atlantic Ocean coast (Lorenzi 1996). This species produces a high-quality heart of palm that is harvested from the core of the palm and represents an important fresh and/or canned product in the Brazilian food industry. However, the extraction of this product causes death of the plant. *E. edulis* is classified as an endangered, vulnerable plant due to its overuse and the absence of replacement cultivations, as well as the deforestation of the Atlantic Forest (Reis *et al.* 2000). As a typical understory species, *E. edulis* requires the

---

Received 4 July 2013, *accepted* 22 October 2013.

+Corresponding author; phone: (55) (73) 3680 5285, fax: (55) (73) 3680 5226; e-mail: gomes@uesc.br

Abbreviations: C_a – atmospheric CO_2 concentration; C_i – intercellular CO_2 concentration; F_0 – minimal fluorescence of the dark-adapted state; F_m – maximal fluorescence of the dark-adapted state; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance to water vapor; IS_{60} – photosynthetic induction state measured 60 s after an increase in PAR; PAR_C – photosynthetic compensation PAR; PAR_S – photosynthetic saturation PAR; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate; $T_{90\%}$ – the time required to reach 90% of the P_{Nmax}; α – apparent quantum efficiency of photosynthesis.

Acknowledgements: Financial support for the investigation was provided by Universidade Estadual de Santa Cruz and Fundação de Amparo à Pesquisa do Estado da Bahia. We also thank Dr. A.-A.F. de Almeida and Dr. R.F. Ribas for significant contributions to improve the manuscript. Dr. M.S. Mielke and Dr. F.P. Gomes gratefully acknowledges the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil, for the concession of a fellowship of scientific productivity.

presence of a forest environment for successful regeneration and initial growth (Nakazono *et al.* 2001). The full-sunlight cultivation is impracticable and this reinforces the necessity for Atlantic Forest conservation as a whole (Reis *et al.* 2000).

Leaf-level photosynthetic characteristics have been widely used as a tool for indicating environmental stress and selection of growth conditions suitable for different plant species (Pastenes *et al.* 2004). It has been commonly observed that the capacity of plants to growth in light regimes different from their original habitats depends on their ability to acclimate to changing environment (Cai *et al*. 2005). Moreover, it has been long recognized that monocots can acclimate to light similarly as dicots (Reyes *et al.* 1992). Based on a glasshouse experiment, Nakazono *et al.* (2001) reported that *E. edulis* plants transferred from shade (4% of full sun) to high light (30% of full sun) showed higher biomass, growth rate, root/shoot ratio, unit leaf rate, number of leaves, and leaf area, when compared to plants maintained in shade. They concluded that it indicates that the regeneration of this species can take advantage of a medium gap opening.

In general, more important than morphology, physiological acclimation and plasticity have been considered to describe light availability responses (Leakey *et al.* 2005). Fluctuations of light may lead to a series of stress reactions known as photoinhibition, especially in understory species (Cai *et al*. 2005). Recent studies have explored limitations of the optimal net photosynthetic rate (P_N) based on responses to sunflecks (Leakey *et al.* 2005, Urban *et al.* 2007, Way and Pearcy 2012), but none is specific to *E. edulis*. Photosynthetic utilization of sunflecks requires a quick and dynamic physiological response, which depends on several regulatory factors, each working at a different time scale and exhibiting remarkable variation among species and individuals grown under different environments (Urban *et al.* 2007, Way and Pearcy 2012). These factors influence three features of the photosynthetic response to fluctuating light: (*1*) photosynthetic induction response to light increase; (*2*) ability to maintain photosynthetic induction under low light, and (*3*) vulnerability to photoinhibition under an increased light through the formation of a forest gap. Quantification of the enhanced energy gain in understory seedlings during sunflecks may also contribute to understanding carbon gain and, consequently, growth of a species. An evaluation and understanding of these responses are necessary to establish adequate management practices and to ensure effective cultivation and conservation of understory species such as *E. edulis*.

In the present study, we investigated how *E. edulis* leaves, fully developed in the understory, responded to increasing light due to gap formation. We hypothesized that *E. edulis* is a shade-tolerant species, but it is also able to acclimate to the higher light doses than that in understory. To test this hypothesis, the gap formation was mimicked by transferring potted seedlings, cultivated under natural shade, to a high light environment (gap). We carried out samplings throughout changes in light environment to find the suitable light conditions for *E. edulis* growth. Changes on leaf-level photosynthetic characteristics after gap formation were determined by simultaneous measurements of chlorophyll (Chl) fluorescence and leaf gas-exchange parameters, as well as light-response curves of photosynthesis and photosynthetic induction parameters.

Materials and methods

Plants and experimental conditions: Three-year-old individuals of *E. edulis* were used in this study. In total, 30 seedlings were obtained from a regional nursery and transplanted to polyethylene pots containing 10 kg of soil (oxisoil, variation 'Nazaré', collected from A horizon, 20 cm depth, rich in organic matter, sand-clay texture). Fertilization with 20 g of 4-14-8 (N, P_2O_5, K_2O) was performed 30 d after transplantation. The seedlings were cultivated for six months in the shade of cocoa trees (*Theobroma cacao* L.) in a rustic agroforestry system (Sambuichi and Haridasan 2007). After 6 months of the cultivation under the shade (understory environment), a group of 15 randomly selected seedlings was transferred to a forest gap with the area of about 400 m^2. To eliminate the influence of the water deficit, the seedlings were irrigated regularly to maintain moisture close to field capacity in the root zone. PAR in both different environments was quantified using *SLIA-M003* quantum sensors, coupled to *HOBO* weather stations (*Onset Computer*, Bourne, Massachusetts, USA). The weather stations were programmed to register PAR data simultaneously every 1 min.

Photosynthetic characteristics were evaluated in eight seedlings per treatment by measurements of the Chl fluorescence parameters, leaf gas exchange, and photosynthetic induction parameters, using a portable photosynthesis system (*LI-6400*, *LI-COR Inc.*, Lincoln, NE, USA). Measurements were performed always from 8:30 to 11:30 h on the main leaflet of healthy and fully expanded leaves of the first pair of pinnae. Leaf gas exchange and Chl fluorescence parameters were measured at 0, 7, 14, 21, and 110 d after transfer (DAT). We measured light-response curves at 110 DAT in the same leaflets.

Chl fluorescence parameters were measured using a portable fluorometer (*Leaf Chamber Fluorometer LI-6400-40, LI-COR Inc.*, Lincoln, NE, USA) coupled to the photosynthesis system. Before Chl fluorescence measurements, leaves were covered with a dark-adapting clip in the evening to ensure the electron carriers being in the oxidized state. The fluorescence parameters were recorded by the data acquisition system of the device that automatically calculated the minimal (F_0) and maximal (F_m) fluorescence of the dark-adapted state. The difference between F_m and F_0 is defined as the variable fluorescence, F_v, and maximal quantum yield of PSII photochemistry (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_0)/F_m$.

Net photosynthetic rate (P_N), stomatal conductance to water vapor (g_s), and intercelullar CO_2 concentrations (C_i) were measured using the portable photosynthesis system equipped with an artificial light source of *6400-02 B RedBlue*. PAR, atmospheric CO_2 concentration (C_a), and leaf temperature were fixed at 600 μmol(photon) m^{-2} s^{-1}, 400 μmol(CO_2) mol^{-1}, and 27ºC, respectively, using the equipment accessories. Readings became stable within 1–2 min and then the data were saved by the *LI-6400*.

The light-response curves were created based on measurements at seven different values of PAR from 600 to 0 μmol(photon) m^{-2} s^{-1}, with the portable photosynthesis system equipped with an artificial light source of *6400-02 B RedBlue*. The apparent quantum yield of the photoynthesis (α) and the respiration rate (R_D) were estimated using a linear regression model $P_N = \alpha \text{ PAR} - R_D$ for the values when PAR < 100 μmol(photon) m^{-2} s^{-1}. Photosynthetic compensation light (PAR_c) was calculated as $PAR_c = R_D/\alpha$. The light-saturated photosynthetic rate (P_{Nmax}) was estimated using the equation:

$$P_N = P_{Nmax} \left[1 - \exp(-\alpha \text{ PAR}/P_{Nmax})\right] - R_D.$$

The photosynthetic saturation light (PAR_s) was calculated by the same equation as the value of PAR, when P_N reached 90% of P_{Nmax}. The exponential model used was suitable for this purpose in other Arecaceae, such as *Cocos nucifera* (Gomes *et al.* 2006) and *Attalea funifera* (Pamponet *et al.* 2013).

Photosynthetic induction time was determined on thesame leaves used for the leaf gas exchange using the same portable photosynthesis system. To ensure sufficient acclimation before measurements, a leaf was sealed in the chamber and exposed to 5 μmol(photon) m^{-2} s^{-1} for 20 min. Then, the P_{Nmin} value was recorded and PAR was increased to saturating values of 600 μmol(photon) m^{-2} s^{-1}. P_N was recorded sequentially at 1, 5, 10, and 30-s intervals for the first 2 min and the following 1-, 1-, and 2-min periods, respectively. Then, the equipment was programmed to record automatically 20 readings at 60-s intervals. The induction state measured 60 s after the increase in PAR (IS_{60}) was calculated as described by Pearcy *et al.* (1996). The time required to reach 90% of the P_{Nmax} ($T_{90\%}$) was estimated by fitting an exponential curve, as described by Valladares *et al.* (1997), or by fitting a sigmoidal curve, as described by Zipperlen and Press (1997). Biomass, obtained by weighing the seedlings material after drying at 75°C until a constant mass was reached, was also quantified at the end of the experiment.

Statistics: The experiment was conducted in a completely randomized design, with two light environments (understory and gap), five evaluations (0, 7, 14, 21, 110 DAT), and eight repetitions per treatment. The photosynthetic characteristics of seedlings were compared between light environments by one-way analysis of variance (Steel *et al.* 1997). Estimation of parameters derived from photosynthetic induction curves was performed by nonlinear regression using minimum square method (Draper and Smith 1998).

Results

Mean values of PAR were 38.8 and 770.7 μmol(photon) m^{-2} s^{-1}, daily means of 1.3 and 25.0 mol(photon) m^{-2} d^{-1}, with mean PAR peaks at *ca.* 11:00 h of 67.2 and 1,504.2 μmol(photon) m^{-2} s^{-1} in the understory and gap, respectively, during the experimental period (Table 1). The seedlings grown under the canopy of cocoa trees received only 5% of gap PAR. Although PAR values found in the understory were 84% of the time near 6.7 μmol(photon) m^{-2} s^{-1}, the seedlings also received PAR peaks due to sunflecks during the day, which varied from 51.3 to 1,523.8 μmol(photon) m^{-2} s^{-1}, contributing 67.4% of the PAR daily total (Table 1). In understory, the daily duration of PAR ≥ 38.8 and 770.7 μmol(photon) m^{-2} s^{-1} were 499.7 min (16.4% of time) and 7.4 min (0.25% of time), respectively. In turn, PAR values found in the gap were 95 and 37% of the time above 38.8 and 770.7 μmol (photon) m^{-2} s^{-1}, and these daily-PAR duration were of 2,888.7 and 1,129.0 min, respectively (Table 1).

Table 1. Photosynthetically active radiation (PAR) availability and its distribution in understory and forest gap environments. Values are means (± SE) of 10 replicates.

	Understory	Gap
Mean PAR [mol(photon) m^{-2} s^{-1}]	38.8 ± 0.06	770 ± 1.24
Mean daily PAR [mol(photon) m^{-2} d^{-1}]	1.30 ± 0.02	25.0 ± 0.05
% of gap	5 ± 0.01	100
Mean daily duration with PAR ≥ 770.7 μmol(photon) m^{-2} s^{-1} [min]	7.40 ± 0.37	1,129 ± 0.49
Mean daily duration with PAR ≥ 38.8 μmol(photon) m^{-2} s^{-1} [min]	499 ± 0.50	2,888 ± 0.58
PAR ≥ 770.7 μmol(photon) m^{-2} s^{-1} [% of time]	0.30 ± 0.01	37.4 ± 0.02
PAR ≥ 38.8 μmol(photon) m^{-2} s^{-1} [% of time]	16.4 ± 0.02	95.0 ± 0.01
Mean daily duration with PAR ≥ PAR_S [min]	117 ± 0.02	2,183 ± 0.43
Daily PAR due to sunflecks [%]	67.4 ± 0.01	-

The mean values of F_v/F_m remained near 0.82 over the whole experimental period in the understory seedlings (Fig. 1*A*); the mean P_N was 1.20 µmol(CO$_2$) m^{-2} s^{-1} (Fig. 2*A*), which represented 57% of P_{Nmax}, because P_N was strongly limited by g_s. Exposure of shade-acclimated seedlings to high PAR caused abrupt decline in F_v/F_m during the first week after transfer, reaching a minimum value of approximately 0.49 at 7 DAT (Fig. 1*A*). This decline was accompanied by a significant increase in F_0 (Fig. 2*B*) and by the insignificant decrease in F_m (Fig. 2*C*). However, this initial period was followed by a period of recovery and acclimation. At 21 DAT, all seedlings achieved near 80% of their prior-exposure F_v/F_m values; the complete recovery was observed at 110 DAT (Fig. 1*A*).

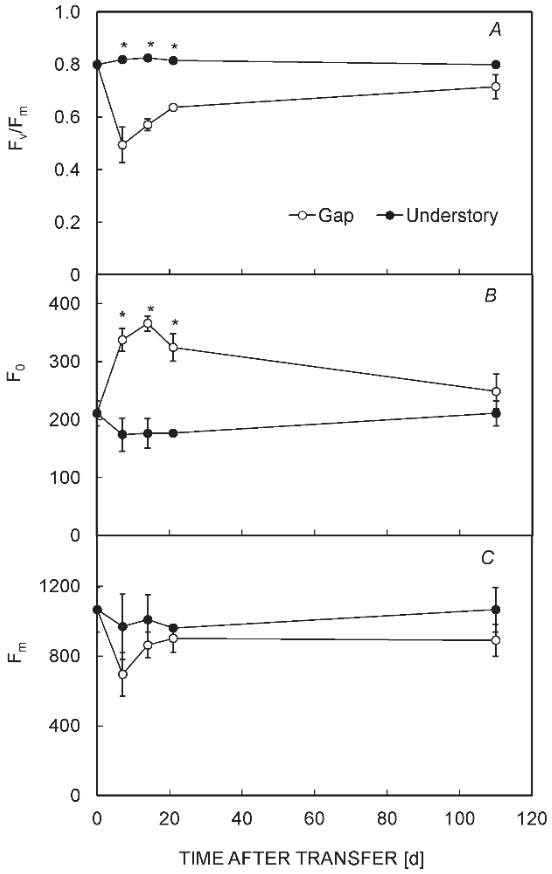

Fig. 1. Maximal quantum efficiency of PSII photochemistry (F_v/F_m), minimal (F_0) and maximal fluorescence (F_m) parameters measured in leaflets of six-month, potted *Euterpe edulis* seedlings maintained in understory (*black circles*) or transferred to a gap (*white circles*) during 110 days after transfer. Values are means (± SD) of eight seedlings. Significant differences between environment at each time are indicated by * $P<0.05$, *F-ANOVA*.

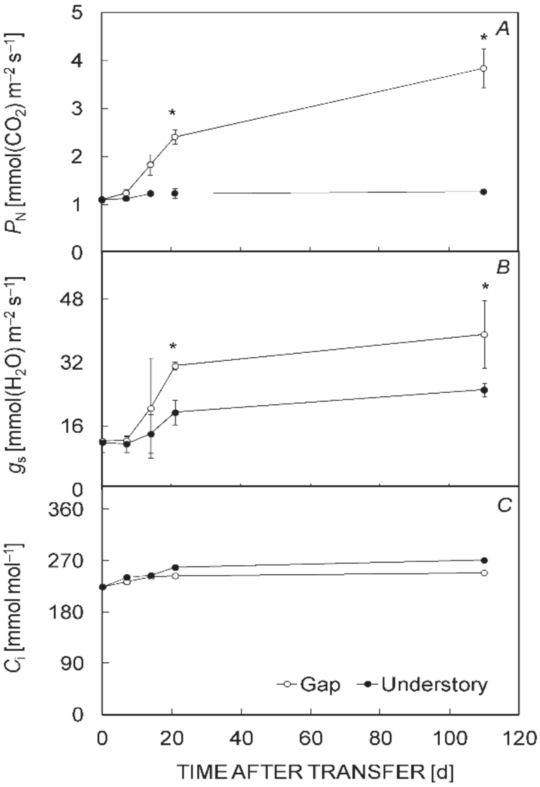

Fig. 2. Net photosynthetic rate (P_N) and stomatal conductance to water vapor (g_s) measured in leaflets of six-month, potted *Euterpe edulis* seedlings maintained in understory (*black circles*) or transferred to a gap (*white circles*) during 110 days after transfer. Values are means (± SD) of eight seedlings. Significant differences between environment at each time are indicated by * $P<0.05$, *F-ANOVA*.

Despite the photodamage during the first week after the transfer, the mean P_N of the seedlings transferred to the gap was 2.09 µmol(CO$_2$) m^{-2} s^{-1} (Fig. 2*A*), which corresponded to approximately 84% of P_{Nmax}. The mean values of P_N increased 3.46-fold in relation to prior-exposure values, but a significant increase in P_N was proved from 21 DAT, with maximal values at 110 DAT [3.85 µmol(CO$_2$) m^{-2} s^{-1}], when the photochemistry was completely recovered (Fig. 1*A*). Insignificant differences in P_{Nmax}, α, PAR$_c$, PAR$_s$, and R_D were observed between environments (Table 2). We also detected that P_N was largely governed by g_s, at least in the seedlings exposed to higher PAR (Fig. 3).

Leaflets of six-month-old *E. edulis* seedlings transferred from understory to the gap showed a significant increase of IS_{60}, when compared to those kept in the understory (Fig. 4*A*). However, differences in $T_{90\%}$ were not statistically significant between environments (Fig. 4*B*).

In addition, no significant increase in biomass was found (4.18 *vs*. 3.29 g in the gap and understory seedlings, respectively).

Discussion

The pattern of fluctuating light may be considered as an important determinant for performance of obligatory shade species in understory, which in addition to gap regeneration dynamics, is the key determinant of forest regeneration and the maintenance of high biodiversity (Leakey *et al.* 2005). In our experiment, the contribution of sunflecks to daily PAR was similar to that found by Leakey *et al.* (2005) in short sunflecks (≤ 10 min) in an Asian tropical forest (61% of PAR total). The colonization strategy of *E. edulis* is characterized by an abundant, natural distribution of seedlings around the adult palms, which has deleterious effect, since seedlings could be overshaded. Thus, the sunflecks were essential to maintain a positive carbon balance for the seedlings cultivated in the understory. In addition, following a long period of shade in understory, deactivation of enzyme Rubisco and stomata closure limits the induction state of a leaf (Way and Pearcy 2012). In most of the time, the seedlings were for six months under suboptimal conditions to achieve its P_{Nmax}, because P_{N} was strongly limited by g_{s}.

Table 2. Photosynthetic light-response curve parameters estimated from field measurements in leaflets of *Euterpe edulis* seedlings maintained in the forest understory or transferred to a gap after 110 days. P_{Nmax} – light-saturated net photosynthetic rate; R_{D} – dark respiration rate; α – apparent quantum yield of photosynthesis; PAR – photosynthetically active radiation; PAR_{C} – photosynthetic compensation PAR; PAR_{S} – photosynthetic saturation PAR. Each value represents the mean (± SD) of eight replicates. For all variables $P<0.01$, *F-ANOVA*.

Variable	Gap	Understory	% of value in the gap
P_{Nmax} [µmol(CO$_2$) m^{-2} s^{-1}]	4.37 ± 0.14	4.03 ± 0.13	92
R_{D} [µmol(CO$_2$) m^{-2} s^{-1}]	0.52 ± 0.02	0.34 ± 0.02	65
α [µmol(CO$_2$) µmol(photon)$^{-1}$]	0.06 ± 0.00	0.05 ± 0.01	88
PAR_{C} [µmol(photon) m^{-2} s^{-1}]	8.98 ± 0.25	6.65 ± 0.35	74
PAR_{S} [µmol(photon) m^{-2} s^{-1}]	182.50 ± 6.41	188.13 ± 7.92	103

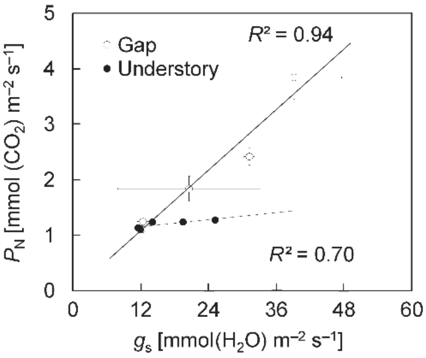

Fig. 3. Relationship between net photosynthetic rate (P_{N}) and stomatal conductance to water vapor (g_{s}) measured in leaflets of six-month, potted *Euterpe edulis* seedlings maintained in understory or transferred to a gap. Measurements were done at 0, 7, 14, 21, and 110 days after transfer. Points are means (± SD) of 10 seedlings.

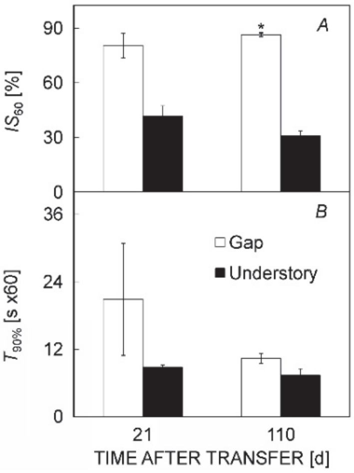

Fig. 4. Induction state measured after 60 s of increase in PAR (IS_{60}, *A*), and the time required to reach 90% of the P_{Nmax} ($T_{90\%}$, *B*) estimated from the field data measured in leaflets of six-month, potted *Euterpe edulis* seedlings maintained in understory or transferred to a gap. Measurements were done at 21 and 110 days after transfer. Values are means (± SD) of eight seedlings. Significant differences between growth environment at each time are indicated by * $P<0.05$, *F-ANOVA*.

Although PAR values found in understory were 84% of the time slightly bellow PAR_{c}, values of PAR_{s} were achieved only during 117 min. It corresponded to 3.84% of time, a magnitude not sufficient to trigger a photosynthetic process limitation due to the photoinhibition. Associated with this, the stomata opening was very fast in *E. edulis* seedlings in response to sunflecks, which, in turn, allowed achieving P_{Nmax} values similar to those found in the seedlings transferred to the gap. On the other hand, the mean PAR_{s} was 130.5 µmol(photon) m^{-2} s^{-1} and its duration was of 2,183 min (data not shown) in the seedlings transferred to the gap. It could explain photoinhibition of the seedlings transferred to this environment during the first week after the transfer. The higher values of PAR in the gap were associated to high T_{air} and depression in RH, especially at midday, which also contributed to the limitation of photosynthetic processes (Kitao *et al.* 2006). Parallel measurements of the Chl fluorescence parameters led to a clear interpretation of photosynthetic changes associated to the transfer of seedlings to the high light environment. Data from F_0 and F_v/F_m showed that the photosynthetic limitation under high PAR was due to downregulation of the photochemical machinery in seedlings transferred to gap.

During the first week after the transfer, photoinhibition restrained leaf photosynthetic acclimation to higher PAR (P_N increase was limited). In this experiment, more than 21 d from the sudden transfer to the gap were needed for the recovery from photoinhibition and the decrease of the limitation to photosynthetic induction (*e.g.*, increase in g_s). Such changes led to increase of P_N to near P_{Nmax} values. Guo *et al.* (2006) consider that photoinhibition was the main cause of P_N suppression in three *Garcinia* species after a transfer to a simulated gap. They also reported that P_N was higher or recovered completely to the values of seedlings kept in understory after two months of acclimation to the gap condition, although F_v/F_m did not recovered completely. Bungard *et al.* (2000) observed that F_v/F_m declined within one to three days after the transfer from understory to gap in four dipterocarp species, recovering toward the end of the 17 DAT, with all seedlings achieving more than 75% of their prior-exposure values. The complete recovery was observed after 20 DAT, indicating acclimation to high light.

Ecophysiological and demographic studies are relevant to palms growing under natural conditions and help explain the success of *E. edulis* in the forest understory and its absence in large gap openings. Based on a glasshouse experiment, Nakazono *et al.* (2001) considered the lower performance of *E. edulis* in full sunlight and deep shade an indication of a limited competitive capacity of the species in large gaps and in extremely closed canopies. In our experiment, leaf gas exchange and Chl fluorescence parameters showed this endangered species being able to recover from photoinhibition after long-term exposure to high light in large gaps. In addition, the lack of correlation between the parameters $T_{90\%}$ and IS_{60} could be a sign of the strategy to use better the short-time exposure to high light during sunfllecks. As P_{Nmax} did not increase in the seedlings transferred to the gap, it is possible that the enzymes involved in acclimation of photosynthetic machinery were not completely activated. In fact, photosynthetic induction kinetics is influenced by the previous light environment (Cai *et al.* 2005), which affects the rate of photosynthetic activation of Rubisco.

In summary, the shade-acclimated *E. edulis* seedlings adjusted their photosynthetic machinery to high light, despite the observed photochemical damages that could occur in foliage when suddenly exposed. The fast opening of stomata guaranteed the ideal utilization of available light during sunflecks, thus maximizing P_{Nmax} during this period. It indicated the species is also fast responsive to sunflecks. Moreover, the photoinhibition of photosynthesis occurred in a dynamic form showing that the shade-acclimated leaves adjusted the photosynthetic machinery after the transfer from low to high light.

References

Bungard, R.A., Scholes, J.D., Press, M.C.: The influence of nitrogen on rain forest dipterocarp seedlings exposed to a large increase in irradiance. – Plant Cell Environ. **23**: 1183-1194, 2000.

Cai, Z.Q., Rijkers, T., Bongers, F.: Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. – Tree Physiol. **25**: 1023-1031, 2005.

Draper, N.R., Smith, H.: Applied Regression Analysis. 3rd ed. Pp. 505-553. John Wiley & Sons, Inc., New York 1998.

Gomes, F.P., Oliva, M.A., Mielke, M.S., Almeida, A-A.F., Leite, H.G.: Photosynthetic irradiance-response in leaves of dwarf coconut palm (*Cocos nucifera* L. '*nana*', Arecaceae): Comparison of three models. – Sci. Hortic. **109**: 101-105, 2006.

Guo, X.R., Cao, K.F., Xu, Z.F.: Acclimation to irradiance in seedlings of three tropical rain forest *Garcinia* species after simulated gap formation. – Photosynthetica **44**: 193-201, 2006.

Kitao, M., Lei, T.T., Koike, T., Tobita, H., Maruyama, Y.: Tradeoff between shade adaptation and mitigation of photoinhibition in leaves of *Quercus mongolica* and *Acer mono* acclimated to deep shade. – Tree Physiol. **26**: 441-448, 2006.

Leakey, A.D.B., Scholes, J.D., Press, M.C.: Physiological and ecological significance of sunflecks for dipterocarp seedlings. – J. Exp. Bot. **56**: 469-482, 2005.

Lorenzi, H., Souza, H.M., Medeiros-Costa, J.T., Cerqueira, L.S.C., Behr, N.V.: [Palm trees in Brazil: natives and exotic]. Pp. 84. Editora Plantarum, São Paulo 1996. [In Portuguese]

Nakazono, E.M., da Costa, M.C., Futatsugi, K., Paulilo, M.T.S.: [Early growth of *Euterpe edulis* Mart. in different light environments.] – R. Bras. Bot. **24**: 173-179, 2001. [In Portuguese]

Pamponet, T.C., Gomes, F.P., Almeida, A-A.F. *et al.*: Photosynthetic characteristics and fibre production following defoliation in A*ttalea funifera* Mart., Arecaceae, growing under full sun and forest understorey. – Exp. Agr. **49**: 435-447, 2013.

Pastenes, C., Pimentel, P., Lillo, J.: Leaf movements and photoinhibition in relation to water stress in field-grown beans. – J. Exp. Bot. **56**: 425-433, 2004.

Pearcy, R.W., Krall, J.P., Sassenrath-Cole, G.F.: Photosynthesis in fluctuating light environment. – In: Baker, N.R. (ed.): Advances in Photosynthesis: Photosynthesis and the Environment. Pp. 321-346. Kluwer, Amsterdam. 1996.

Reis, M.S., Fantini. A.C., Nodari, R.O., *et al*: Management and conservation of natural populations in Atlantic Rain Forest: The case study of palm heart (*Euterpe edulis* Martius). – Biotropica **32**: 894-902, 2000.

Reyes, T., Nell, T.A., Conover, C.A., Barrett, J.E.: The effects of light intensity and fertilizer rate on the acclimatization potential of *Chamaedorea elegans*. – HortScience **27**: 583, 1992.

Sambuichi, R.H.R., Haridasan, M.: Recovery of species richness and conservation of native Atlantic forest trees in the cacao plantations of southern Bahia in Brazil. – Biodivers. Conserv. **16**: 3681-3701, 2007.

Steel, R.G.D., Torrie, J.H., Dickey, D.A.: Principles and Procedures of Statistics: A Biometrical Approach. 3rd Ed. Pp. 328-345. McGraw-Hill Book Co., New York 1997.

Urban, O., Košvancová, M., Marek, M.V., Lichtenthaler, H.K.: Induction of photosynthesis and importance of limitations during the induction phase in sun and shade leaves of five ecologically contrasting tree species from the temperate zone. – Tree Physiol. **27**: 1207-1215, 2007.

Valladares, F., Allen, M.T., Pearcy, R.W.: Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. – Oecologia **111**: 505-514, 1997.

Way, D.A., Pearcy, R.W.: Sunflecks in trees and forests: from photosynthetic physiology to global change biology. – Tree Physiol. **32**: 1066-1081, 2012.

Zipperlen, S.W., Press, M.C.: Photosynthetic induction and stomatal oscillations in relation to the light environment of two dipterocarp rain forest tree species. – J. Ecol. **85**: 491-503, 1997.