

Changes in leaf water potential and photosynthesis of *Bauhinia forficata* Link under water deficit and after rehydration

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ABSTRACT - (Changes in leaf water potential and photosynthesis of *Bauhinia forficata* Link under water deficit and after rehydration). To evaluate the influence of different intensities of water deficit and rehydration on water relations and gas exchanges of *Bauhinia forficata* Link, plants were grown in a greenhouse for three months under the following water regimes: daily watered (control) and watered every 7 (7D) and 15 days (15D) returning to daily watering on 7D and 15D treatments at 75 days of the experiment. Aiming to evaluate short-term responses to re-hydration, plants of 7D and 15D treatments were re-watered 2 days before measurements and sampling was carried out at the 45th day of experiment. At fortnightly intervals (15, 30, 45, 60, 75, and 90 days) soil moisture (U_{soil}), leaf water potential (Ψ_{wf}), photosynthesis in response to photosynthetically active radiation ($A \times PPF$) to obtain the maximum net photosynthesis (A_{max}), and light saturation point (PAR_{sat}) were evaluated. The water deficit has affected water relations and photosynthesis with the lowest values observed in the treatments U_{soil} 7D, and 15D respectively, coinciding with the lowest Ψ_{wf} and A_{max} . Changes in PAR_{sat} in response to water deficit were observed showing mean values of 665, 275 and 254 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in control, 7D and 15D respectively. The return of daily watering after 75 days of experiment, promoted the recovery of A_{max} (7.8 and 9.6 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and PAR_{sat} (588 and 643 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) in 7D and 15D respectively with values higher than control plants (4.7 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ and 631 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), suggesting a strong dependence of photosynthesis of *Bauhinia forficata* to the soil water availability.

Key words: Brazilian Orchid-tree, drought tolerance, plasticity

RESUMO - (Alterações no potencial hídrico foliar e fotossíntese de *Bauhinia forficata* Link sob déficit hídrico e após reidratação). Para avaliar a influência de déficits hídricos de diferentes intensidades e da reidratação nas relações hídricas e trocas gasosas, plantas de *Bauhinia forficata* Link foram cultivadas em casa de vegetação durante três meses e submetidas aos regimes de regas diárias (controle) e regas a cada 7 (7D) e 15 dias (15D) retornando as regas diárias nos regimes 7D e 15D aos 75 dias de experimento. Com o objetivo de avaliar respostas de curto prazo à re-hidratação, plantas dos tratamentos 7D e 15D foram re-irrigadas 2 dias antes das medidas realizadas no 45º de experimento. Em intervalos quinzenais (15, 30, 45, 60, 75 e 90 dias) foram avaliadas a umidade do solo (U_{solo}), potencial hídrico foliar (Ψ_{wf}), a fotossíntese em resposta a radiação fotossinteticamente ativa ($A \times PPF$) para obtenção da fotossíntese máxima (A_{max}) e da radiação fotossinteticamente ativa na saturação (PAR_{sat}). O déficit hídrico afetou as relações hídricas e fotossíntese, sendo que os menores valores de U_{solo} observados nos tratamentos 7D e 15D respectivamente, coincidiram com os menores Ψ_{wf} e A_{max} . Alterações nos PAR_{sat} em resposta ao déficit hídrico foram observadas apresentando valores médios de 665, 275 e 254 $\mu\text{mol fótons m}^{-2} \text{s}^{-1}$ no controle, 7D e 15D, respectivamente. O retorno das regas diárias após 75 dias de experimento promoveu a recuperação de A_{max} (7,8 e 9,6 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) e dos PAR_{sat} (588 e 643 $\mu\text{mol fótons m}^{-2} \text{s}^{-1}$) das plantas 7D e 15D, respectivamente, aos 90 dias, com valores maiores daqueles observados nas plantas controle (4,7 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ e 631 $\mu\text{mol fótons m}^{-2} \text{s}^{-1}$), sugerindo forte dependência da fotossíntese de *Bauhinia forficata* à disponibilidade hídrica no solo.

Palavras-chave: pata-de-vaca, plasticidade, tolerância a seca

INTRODUCTION

The distribution of plants on Earth's surface is controlled basically by two abiotic factors, air temperature and water availability in soil. Since air

temperature allows, the amount and distribution of rain becomes the major limiting factor to plant development (Kramer & Boyer 1995). This ecological importance of water is a result of its physiological importance, being the only way by which an environmental factor

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such as water can affect the plant growth is influencing physiological processes (Koslowski & Pallardy 1997).

Due to the increase of carbon dioxide in atmosphere, which leads to an increase in air temperature, it is considered that there will raise the atmospheric demand for water and, on many regions, with higher occurrence, frequency, intensity and distribution of droughts. The climate change models show an high frequency of rainfall separated by long dry periods (Dore 2005). In this scenario, the projected climate changes for the coming years due to global warming, make studies on water use by native species critical, not only to preserve ecosystems, but also to define strategies for recovery of degraded areas, since the establishment of the species is a critical step to the recovery of these areas. Thus, among the environmental factors, water deficiency stands out as an adverse factor to the growth and crop production making it essential for studies to address the issue.

Water deficiency has been considered as one of the main factors limiting the productivity, both agricultural and natural ecosystems. In nature, the intensity and distribution of rainfall determine the water regime, from influencing the growth and productivity of individuals, to the distribution of populations and the biodiversity of ecosystems. The water deficit caused by drought is established when the water absorption from root system cannot meet the demands of the plant (Fan *et al.* 2006). Among the main demands are photosynthesis and transpiration, two essential processes for plant growth. Before the water deficit has been established, roots have to sense the dry soil and transmit this information to shoot, which creates an integrated response of the plant allowing its survival until the water availability increases. This communication is done by several means in addition to the reduction of the upward flow of water (Davies & Zhang 1991).

The main physiological processes that affect plants under water deficit, are stomatal conductance, mesophyll photosynthesis and, by extension, their growth. However, such effects depend of the species studied as well as the intensity and duration of the water deficit rate (Chaves & Pereira 1992).

Stomatal closure is in fact one of the first lines of defense against water deficits, since it is a fast and flexible process on relation to other alternatives, such as changes in the life cycle, root growth or leaf area, which constitute long term responses. The stomatal closure reduces water loss by the plant, but at the same

time decreases the entry of CO₂ from the atmosphere to the substomatal cavity, influencing the carbon assimilation (Chaves 1991).

The species *Bauhinia forficata* Link presents broad neotropical distribution being found in Argentina, Bolivia, Paraguay, Uruguay and Brazil (Fortunato 1986), thus occurring in different biomes. Moreover, it is recommended for projects of recovery of degraded areas, being a good model for studies on plant responses to environmental stresses such as water deficit.

Due to the wide distribution, we hypothesized that of *B. forficata* presents a high tolerance to drought allowing their occurrence and survival under different environments, mainly under water deficit conditions. Furthermore, since photosynthetic capacity plays an important role on plant establishment and growth, little is known about the effects of water stress in the photosynthesis of this species, considering that it is widely recommended for recovery of degraded areas.

This work aimed at evaluates changes in photosynthesis of *Bauhinia forficata* in response to different intensities of water deficits and after recovery by hydration.

Material and methods

Plant material and growing conditions - plants of *B. forficata* with 6 months of age were obtained in the nursery BioFlora Forest Restoration in the city of Piracicaba, São Paulo State, Brazil and transplanted into individual pots of 20 L, containing organic soil substrate (Tropstrato, HT[®]). Plants were daily watered and received Clark nutrient solution (Clark 1975), once a week until beginning of the experiment. After, nutrient solution was applied in fortnightly intervals. The pot-plant sets were maintained in a greenhouse at the Núcleo de Pesquisa em Fisiologia e Bioquímica do Instituto de Botânica (IBt/SMA/SP) throughout the experimental period. After three months the different water regimes were imposed on plants in the following treatments: daily watered plants (control), watered every 7 days (7D) and every 15 days (15D) returning to daily water regimes at 75th days of the experiment. Aiming to evaluate short-term responses to re-hydration, plants of 7D and 15D treatments were re-watered 2 days before measurements and sampling carried at 45th days of the experiment. In each treatment of watering regimes water was provided until pot saturation aiming to elevate soil moisture close to the field capacity in pots.

The watering frequencies of 7 and 15 days were defined previously on a pilot experiment where water supply to 10 potted plants distinct from that used in the main experiment. was totally suspended and leaf water potential was measured aiming to ensure the establishment of water deficit and avoid plant death during the main experiment.

At fortnightly intervals (15, 30, 45, 60, 75 and, 90 days) soil moisture (U_{soil}), leaf water potential (Ψ_{wf}) at predawn, photosynthesis in response to photosynthetic photon flux density ($A \times$ PPF) to obtain the maximum net photosynthesis (A_{max}) and light saturation point (PAR_{sat}) were evaluated.

During the experiment, the temperature ($^{\circ}C$), relative humidity (RH, %) and the photosynthetic photon flux density (PPFD, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) were monitored inside the greenhouse using a temperature/humidity sensor (Li-1400-140, Li-Cor - Nebraska, USA) and a quantum sensor (Li-190SA, Li-Cor - Nebraska, USA) respectively. The sensors were connected to a datalogger (Li-1400, Li-Cor - Nebraska, USA), which was configured to perform the measurements at intervals of 10 minutes, calculating daily means for each parameter evaluated.

Ecophysiological Evaluations - Soil moisture (U_{soil} , %) was measured by time domain reflectometry, using a sensor model ML2 Delta-X-T Devices (ThetaProbe, Cambridge, UK). In order to quantify the intensity of water deficit imposed to the plants in the different treatments, leaf water potential (Ψ_{wf} , MPa) at predawn (5 and 6 h) were measured in the 2nd fully expanded leaf from the apex of each plant using a pressure pump type Scholander, Model 1000 (PMS Instrument Co., UTAH, USA). We performed instantaneous measurements of net carbon assimilation rates (A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (g_s , $\text{mol m}^{-2} \text{ s}^{-1}$) and transpiration (E , $\text{nmol m}^{-2} \text{ s}^{-1}$) in response to photosynthetically active radiation (PAR, $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), curves $A \times$ PPF. From these curves we defined the light point saturation (PAR_{sat} , $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and maximum net photosynthesis (A_{max} , $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) according to model proposed by Long & Hällgren (1993). Measurements were carried using an infrared gas analyzer (IRGA) model Li-6400 (Li-Cor - Nebraska, USA) in open system, between 8 to 11 h. Curves $A \times$ PPF were performed in the 3rd fully expand leaf from the apex of each plant, with a concentration of 380 ppm of CO_2 and a photosynthetic photon flux density (PPFD) of 0, 50, 100, 300, 500, 700, 1,000 and, 1,200 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in

order to verify possible changes in parameters of gas exchange in response to water deficit. Each point in the $A \times$ PPF curve represents a mean of five replicates for each PPF.

Experimental design and statistical analysis - The experiment was conducted between September and November 2010 arranged on completely randomized design with five replicates per treatment in each point of analyses. Six points of analyses were carried over these 3 months with a total of 30 plants per treatment. Data of ecophysiological parameters were subjected to variance analysis (ANOVA), and any contrast between means was evaluated by Tukey test at 5% level of probability, using the statistical package BioEstat 3.0 (Ayres *et al.* 2000). Normality tests were previously performed. The data were also subjected to Pearson correlation analyses between the parameters evaluated. Correlations were tested by *t* Student test.

Results and discussion

The mean air temperature during the experiment was $25.8^{\circ}C$ with minimum and maximum means of 21 and $31^{\circ}C$, respectively (Figure 1). Under natural and greenhouse conditions, with increasing radiation, the temperature rises and the relative humidity decreases (Medina *et al.* 1999) increasing the atmospheric demand for water. So, as expected, we observed a significant inverse correlation between the PAR and RH ($r = -0.705$; $p = 0.0229$), with the lowest mean values of PAR ($345.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$) coinciding with the highest mean values of RH (57%), reflecting the influence of high clouds characteristic of this time of year in these meteorological parameters.

Soil moisture (U_{soil}) presented low changes in the pots of control plants with values between 22 to 26% (Figure 2). However, for pots of plants subjected to 7D and 15D treatments, values ranged between 2 to 12%, and 1 to 8% respectively, showing statistical differences between these treatments only on the 15th day of the experiment. Notwithstanding the lowest values of U_{soil} observed coincided with low values of RH (57%) and high values of PAR ($405 \mu\text{mol m}^{-2} \text{ s}^{-1}$) on the 60th day (figure 1). With the returning of daily watering after the 75th day of experiment, in the treatments 7D and 15D until the end of the experiment, the values of U_{soil} reached 18% showing no statistical differences when compared to control.

The water treatments of 7D and 15D were sufficient to generate water deficits in plants leading

to a significant decreasing on leaf water potential (Ψ_{wf} , MPa) (Figure 3), net carbon assimilation rates (A) (Figure 4), stomatal conductance (g_s) (Figure 5) and, transpiration (E) (Figure 6) if compared to control plants. Controls plants did not change significantly in Ψ_{wf} , remaining always above -1.0 MPa, showing that daily watering was sufficient to maintain high values of U_{soil} (Figure 2) and low values of Ψ_{wf} (Figure 3) throughout the whole experiment. On the other hand, the plants in 7D and 15D treatments showed that the Ψ_{wf} values close to -1.0 to -1.45 MPa at the beginning of the experiment and -2.0 and -3.0 MPa after 30 days respectively. However, only plants in the 15D treatment showed statistical differences when compared to control in these days.

Aiming to evaluate short-term responses to re-hydration, the plants of 7D and 15D treatments were re-watered 2 days before measurements and sampling at 45th day. Two days after re-watering, plants of 7D and 15D treatments presented an increasing in Ψ_{wf}

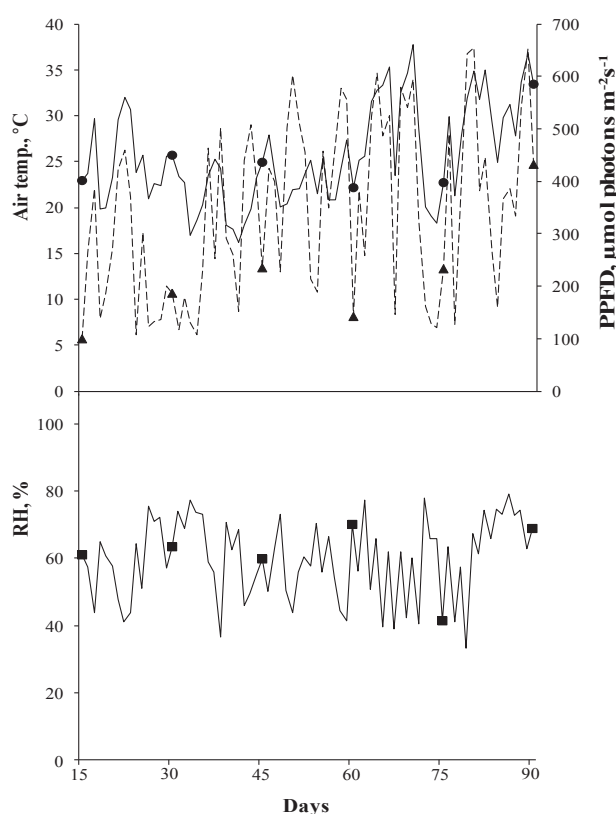


Figure 1. Air temperature (●), photosynthetically active radiation (PPFD) (▲), and air relative humidity (RH) (■) inside the greenhouse during the experimental period. The symbols indicate the days of ecophysiological evaluations.

reaching values of -1.0 and -1.12 MPa respectively, showing a rapid leaf rehydration. However, at 60th days, treatments 7D and 15D showed a fast decrease in Ψ_{wf} with mean values of -3.3 and -4.3 MPa respectively, with visible effects in g_s (Figure 5) and in E (Figure 6), but keeping positive A values (Figure 4). As expected, there was a positive correlation between variations in U_{soil} and in Ψ_{wf} in plants of 7D ($r = 0.916$; $p = 0.010$) and 15D ($r = 0.828$; $p = 0.042$) treatments, i.e. as soil water availability decreased, the Ψ_{wf} also decreased.

As observed for U_{soil} , the return of daily watering after 75 days of the experiment, allowed the increase in Ψ_{wf} from plants under water deficit to values similar to the control plants.

The water deficit imposed to the plants in this study was sufficient to generate changes in content and free energy of water in soils and plants, respectively, which in turn affected the photosynthesis of *B. forficata*. In fact, the decrease in water content is accompanied by loss of turgor and wilting, disruption in cell expansion, stomatal closure, reduced photosynthesis, affecting plant growth and productivity (Hu & Schmidhalter 1998, Kumar & Sing 1998, Kramer & Boyer 1995).

Associated to measurements of water potential (Figure 3), net carbon assimilation rates (A) (Figure 4) in response to photosynthetically active radiation (PAR) showed a positive relation of dependency of plants *B. forficata* to soil water availability.

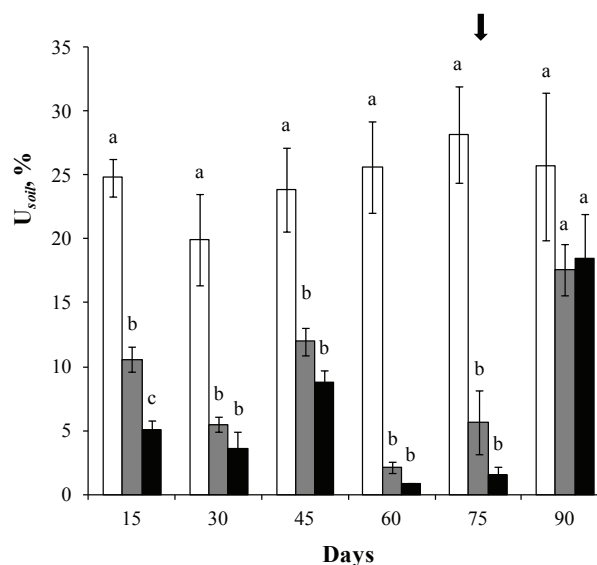


Figure 2. Soil Moisture (U_{soil}) in the pot of plants of *Bauhinia forficata* Link under daily watered (Control - □) and watered every 7-(7D - ■) and 15-day (15D - ■) conditions. The arrow indicates the return of daily watering in 7D and 15D treatments. Bars indicate the standard error ($n = 5$). Means followed by same letter in each sample do not differ significantly by Tukey's test ($P = 0.05$).

As observed in figure 4, A in 7D and 15D treatments was already affected at 15th days of the experiment with values always lower than the control, including negative rates observed on the 30th day of experiment. The re-watering of plants in 7D and 15D treatments two days before the 45th days favored the recovering of positive photosynthetic rates returning to zero and negative values at 60th and 75th days of experiment.

During the experiment the higher value of A_{max} in *B. forficata* was observed in control plants ($12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) that showed values always higher than plants of 7D and 15D treatments until the 75th day. However, with the return of daily watering, A_{max} of plants in the 7D and 15D treatments showed values of 7.8 and $9.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ respectively at the 90th day, which were significantly higher than control plants ($4.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

Light and water availability is one of the most important factors that affect the productivity of plants, mainly by reducing stomatal conductance and photosynthesis (Blum 1997). In this work we are showing that the maximum photosynthetic rates (A_{max}) of plants under water deficit (Figure 7A) presented a high and significant correlation with U_{soil} ($r = 0.806$; $p = 0.050$ and $r = 0.846$; $p = 0.034$) and Ψ_{wf} ($r = 0.887$; $p = 0.018$ and $r = 0.941$; $p = 0.005$) on the 7D and 15D

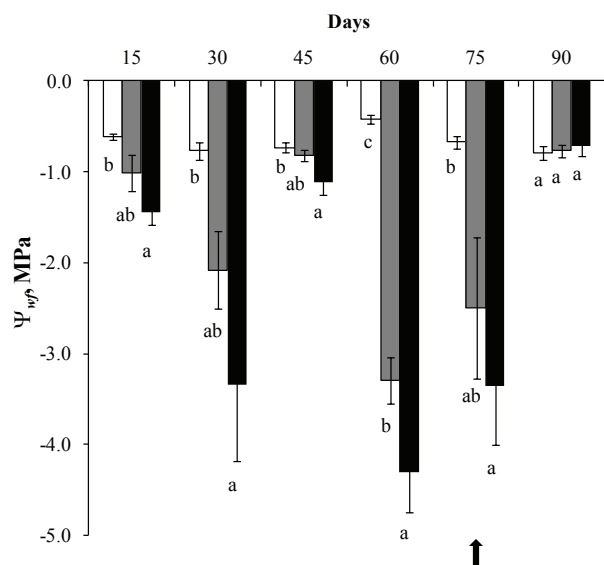


Figure 3. Leaf water potential (Ψ_{wf}) of plants of *Bauhinia forficata* Link grown under daily watered (Control - □) and watered every 7 (7D - ■) and 15 day (15D - ■) conditions. The arrow indicates the return of daily watering in 7D and 15D treatments. Bars indicate the standard error ($n = 5$). Means followed by same letter in each sample do not differ significantly by Tukey's test ($P = 0.05$).

treatments respectively. Such correlations associated with the fact that photosynthesis on 7D and 15D plants were higher than control after the return of daily watering reinforces the relation of dependence of photosynthesis of *B. forficata* to water availability, suggesting a high plasticity of its photosynthetic apparatus.

Also with respect to gas exchange, is observed in Figure 4 that the influence of water deficit decreasing A was partly due to reductions in g_s preventing, that plants from both 7D and 15D treatments achieved their photosynthetic compensation points. On the other hand, the recovery of positive values of A rates at 90th days in the plants 7D and 15D with higher values than the control, associated with the g_s data (Figure 5) and E (Figure 6) suggest rapid acclimation of the photosynthetic apparatus of plants 7D and 15D to the low availability of water in the soil and after water recovery.

The process of stomatal aperture and closure is mainly related to light intensity and state of leaf hydration. Thus, in situations of low water availability in soil, plants reduce their stomatal conductance in order to decrease water loss through transpiration, favoring the maintenance of cell turgor in drought conditions (Silva *et al.* 2004). However, when the stomata closes preventing water loss, simultaneously they restrict the diffusion of atmospheric CO_2 for substomatal chambers (Chaves 1991) affecting rubisco carboxylation and the rates of ribulose 1,5 bisphosphate regeneration (Bjorkman 1981), two important factors that define the minimum values of A (Farquhar *et al.* 1980). Figure 5 shows the stomatal conductance (g_s) of *B. forficata* plants submitted to water deficit, where the plants of 7D and 15D treatments kept their stomata constantly closed when soil water availability was less than 10%.

Figure 7B also shows that the photosynthetic saturation point (PAR_{sat}) was altered in response to water deficit imposed on plants in 7D and 15D treatments. Under optimal conditions of water availability, the PAR_{sat} showed mean values of $665 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in control while the 7D and 15D treatments showed minimum values of 43 and $18 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ respectively. In addition, as observed in A_{max} , the PAR_{sat} of plants 7D and 15D correlated significantly with U_{soil} ($r = 0.775$; $p = 0.050$ and $r = 0.881$; $p = 0.020$) and Ψ_{wf} ($r = 0.868$; $p = 0.025$ e $r = 0.929$; $p = 0.007$) respectively.

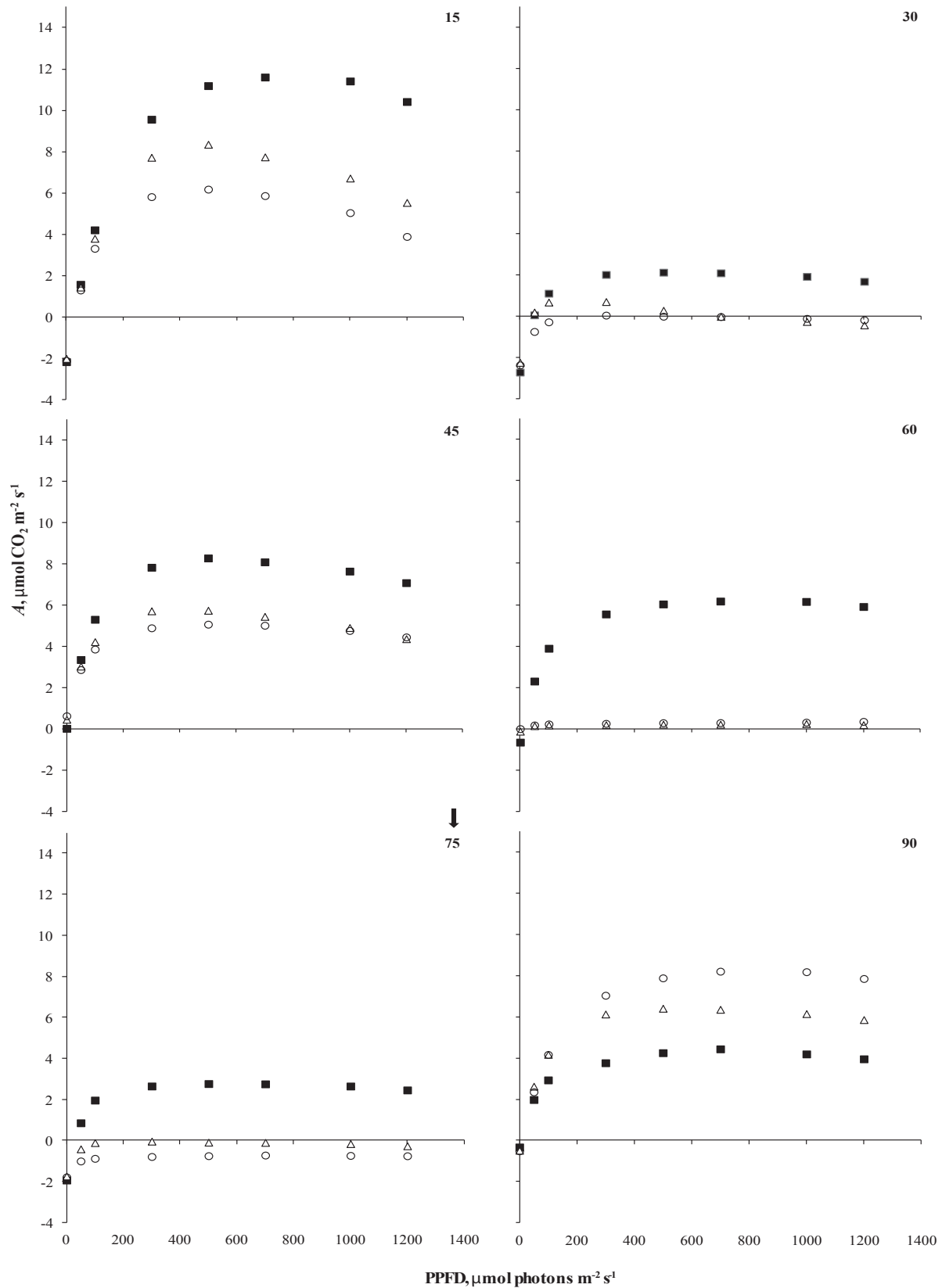


Figure 4. Curves of net carbon assimilation rates in response to photosynthetically active radiation ($A \times \text{PPFD}$) of plants of *Bauhinia forficata* Link under daily watered (Control - ■) and watered every 7-(7D - Δ) and 15-day (15D - \circ) conditions. The arrow indicates the return of daily watering in 7D and 15D treatments (n = 5).

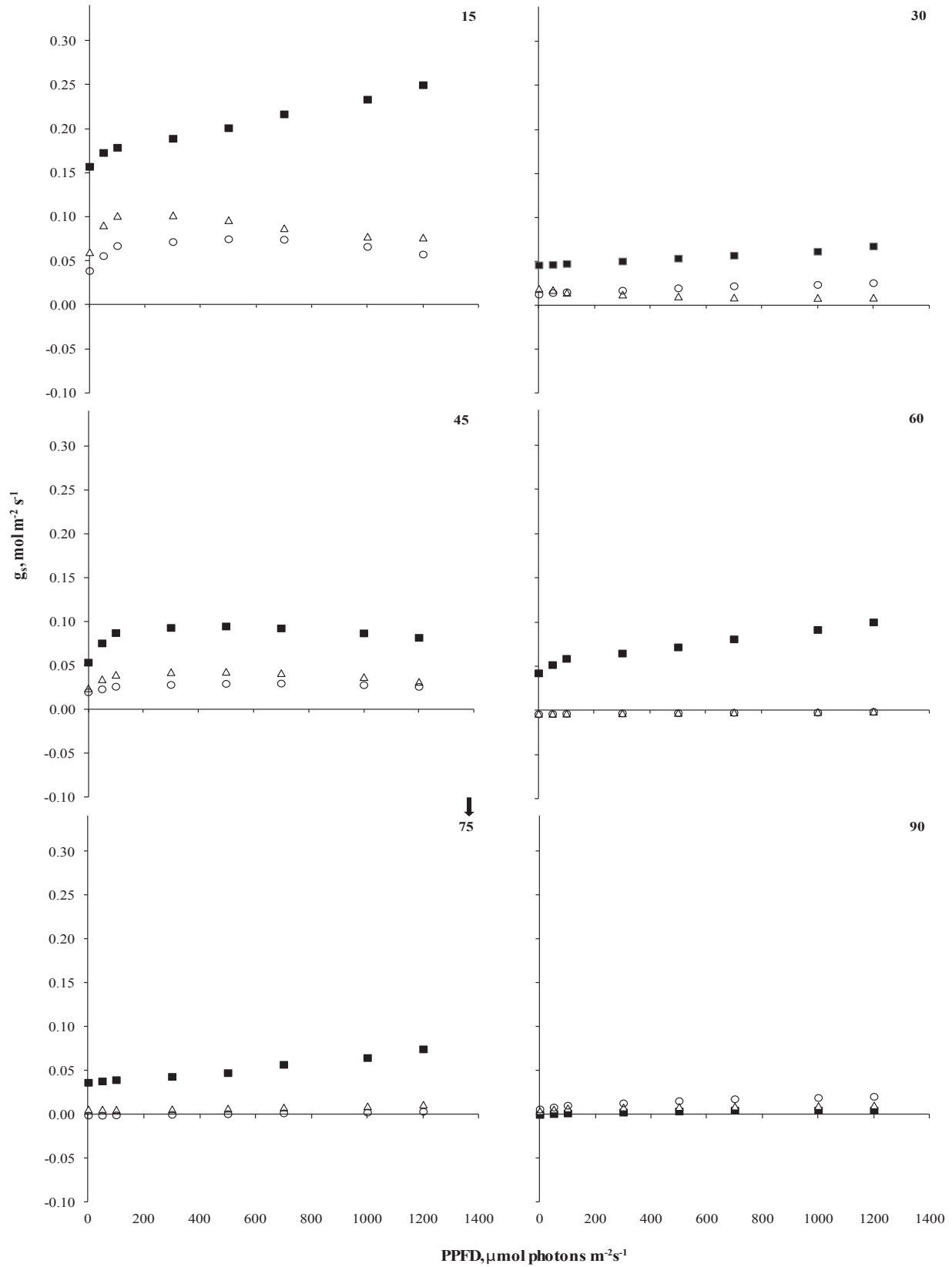


Figure 5. Curves of stomatal conductance (g_s) in response to photosynthetically active radiation ($g_s \times \text{PAR}$) of plants of *Bauhinia forficata* Link under daily watered (Control - ■) and watered every 7-(7D - △) and 15-day (15D - ○) conditions. The arrow indicates the return of daily watering in 7D and 15D treatments ($n = 5$).

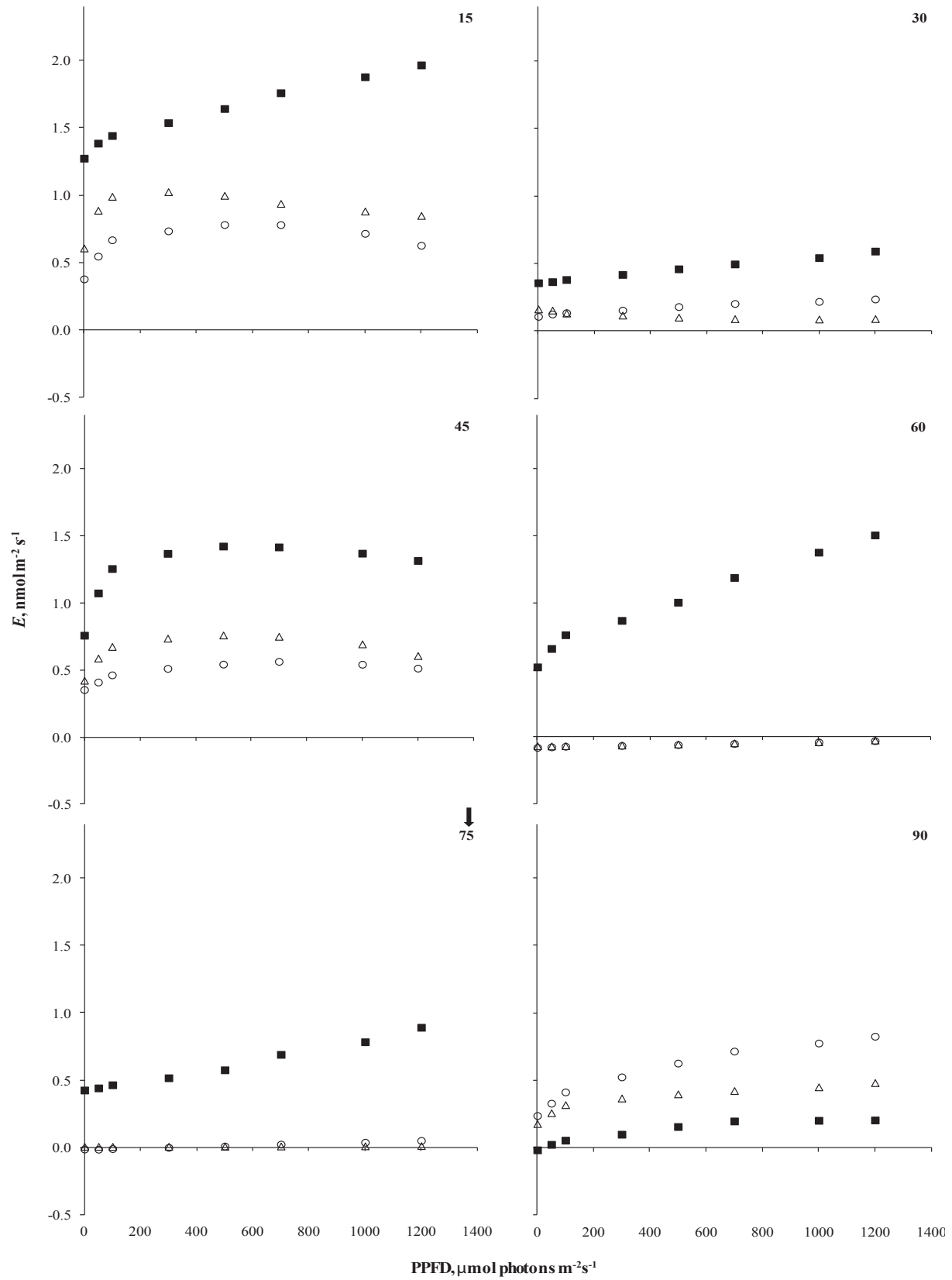


Figure 6. Curves of transpiration (E) in response to photosynthetically active radiation ($ExPAR$) of plants of *Bauhinia forficata* Link under daily watered (Control - ■) and watered every 7-(7D - Δ) and 15-day (15D - ○) conditions. The arrow indicates the return of daily watering in 7D and 15D treatments ($n = 5$).

The photosynthetic behavior of plants response to water deficit in our experiment are similar to those observed by Portes *et al.* (2006), who also evaluated under field conditions, the effect of water deficit on photosynthesis of *B. forficata* present in regions of clearing and understory. These authors showed that values of Ψ_{wf} between -2.47 and -3.3 MPa observed in clearing at the end of the dry season and after 45 days without rain, respectively, characterized a water deficit condition that reduced the photosynthetic rates of plants indicating that this environmental stress significantly affected the use of photosynthetic active radiation by *B. forficata*.

In same way our results showed that photosynthesis of *B. forficata*, a species that present a broad neotropical distribution is highly dependent of soil water availability. If not otherwise we also confirmed our hypothesis that the species *B. forficata* present a high

capacity to tolerate drought imposed by water deficits of different intensities during early development stage, rapidly recovering photosynthetic rates after the reestablishment of soil water availability. Such aspects should explain the wide territorial occurrence of the species and justify its application in restoration projects of degraded areas. Additional analyses about internal and external control of photosynthesis of *B. forficata* are necessary to elucidate the physiological and biochemical mechanisms involved in its drought tolerance.

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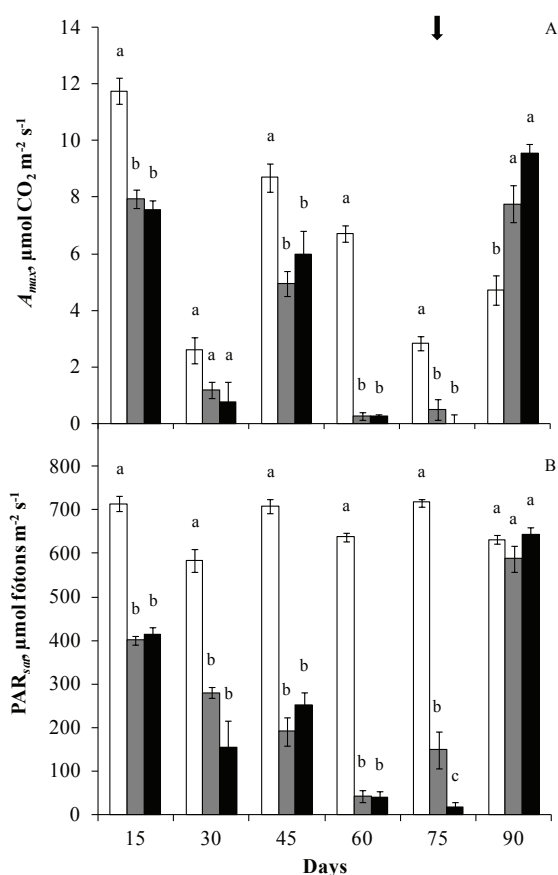


Figure 7 – Maximum net photosynthesis (A_{max}) and light saturation point (PAR_{sat}) of plants of *Bauhinia forficata* Link under daily watered (Control - □) and watered every 7-(7D - ■) and 15-day (15D - ■) conditions. The arrow indicates the day of daily watering return in 7D and 15D treatments. Bars indicate the standard error ($n = 5$). Means followed by same letter in each sample do not differ significantly by Tukey's test ($P = 0.05$).

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