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# Gas exchange of potted *Tabebuia aurea* plants under hydric stress

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**ABSTRACT.** To evaluate the effects of hydric stress on CO<sub>2</sub> and H<sub>2</sub>O exchange, five-month-old *Tabebuia aurea* seedlings cultivated in planting bags were subjected to hydric stress by suppressing irrigation for 21 days. After 14 days without irrigation, the rates of transpiration, stomatal conductance and net photosynthesis in leaves were zero, while the hydric potential of leaves reached -2.4 MPa. After this point, daily irrigation was resumed, and the values of the measured variables recovered to initial levels after 96 hours (transpiration rate from 3.2 to 3.5 mmol m<sup>-2</sup> s<sup>-1</sup>; stomatal conductance rate from 0.32 to 0.35 mol m<sup>-2</sup> s<sup>-1</sup> and photosynthesis rate from 8.0 to 9.8 μmol m<sup>-2</sup> s<sup>-1</sup>). Likewise, hydric potential values were similar to those at the beginning of the experiment (-0.6 MPa). These results demonstrate that *T. aurea* has mechanisms to tolerate a period of hydric deficit, which may be considered ecologically relevant.

**Keywords:** hydric deficit, photosynthesis, conductance, *Tabebuia*.

**RESUMO. Trocas gasosas em plantas envasadas de *Tabebuia aurea* sob estresse hídrico.** Visando avaliar os efeitos do estresse hídrico sobre as trocas gasosas de CO<sub>2</sub> e H<sub>2</sub>O, mudas de paratudo com cinco meses de idade cultivadas em sacos de plantio foram submetidas a estresse hídrico simulado pela supressão da irrigação durante 21 dias. Após 14 dias de supressão de irrigação, os valores de transpiração, condutância estomática e fotossíntese líquida das folhas foram nulos, enquanto o potencial hídrico das folhas atingiu -2,4 MPa. A partir deste ponto foi reiniciada a irrigação diária, sendo que após 96 horas as taxas voltaram a oscilar na faixa dos valores iniciais (transpiração - 3,2 a 3,5 mmol m<sup>-2</sup> s<sup>-1</sup>; condutância estomática - 0,32 a 0,35 mol m<sup>-2</sup> s<sup>-1</sup>; e, fotossíntese - 8,0 a 9,8 μmol m<sup>-2</sup> s<sup>-1</sup>), além do potencial hídrico voltar a apresentar valores similares ao início do experimento (-0,6 MPa), demonstrando que a espécie possui mecanismos para tolerar déficit hídrico durante um período que pode ser considerado ecologicamente relevante.

**Palavras-chave:** déficit hídrico, fotossíntese, condutância, ipê.

## Introduction

Environmental studies of woody tree species under conditions of hydric stress are of fundamental importance because the degree of stress tolerance varies by species, plant age and duration of stress. However, it is generally recognized that young plants are the most affected by adverse environmental factors (KRAMER; BOYER, 1995; LARCHER, 2004; MEDINA, 1998).

Water is the most common limiting factor for plant development (KRAMER; BOYER, 1995), and water deficit affects stomatal opening, which leads to a reduction in photosynthetic capacity and plant growth rates. However, because stomatal opening is a characteristic that is adaptable to environmental conditions, each species demonstrates different behavior when subjected to moderate or intense hydric deficit (LARCHER, 2004).

Photosynthetic activity can be limited by stomatal closing, by decreases in foliar hydric potential or by reduced relative air humidity. Lower photosynthetic activity can also result from stomatal responses to soil hydric deficit, light intensity, temperature, CO<sub>2</sub> concentration and nitrogen content in the leaves (MARENCO; LOPES, 2005).

Hydric stress affects plant development by reducing photosynthesis rates (through the restriction of CO<sub>2</sub> diffusion to the leaf mesophyll) and by limiting the chloroplast CO<sub>2</sub> fixation capacity. This reduction in photosynthesis is related to stomatal closing, causing a decrease in the partial CO<sub>2</sub> pressure and thereby limiting transpiration, which is an important mechanism to avoid water loss and dehydration under conditions of stress (KRAMER; BOYER, 1995; LARCHER, 2004).

The mechanisms that allow the survival of vegetation in areas where hydric restriction is common are stomatal closing during periods of increased water loss and the reduction of internal cellular hydric potential through solute accumulation that favors soil water absorption (LARCHER, 2004).

However, species have different hydric potential thresholds for the occurrence of stomatal closing, and a water potential of -1.0 to -2.0 MPa can lead to near zero transpiration and CO<sub>2</sub> assimilation rates for some species (KRAMER; BOYER, 1995; LARCHER, 2004).

Many species that have adapted to hydric stress employ intracellular solute accumulation to adjust for the decrease in water availability (TURNER, 1986), which allows for the maintenance of cell turgor, stomatal opening and, consequently, photosynthesis, even when there is low hydric availability in the soil (KRAMER; BOYER, 1995; TURNER, 1986). However, photosynthesis rates decrease when such plants are under stress (LARCHER, 2004).

Medina (1998) affirms that plantlet survival in savannas and dry forests is associated with the duration of hydric stress. Drought is usually a drastic change that imposes stress on organisms with unpredictable intensity and length. The flora of drought-prone areas has suffered from strong selective pressures, which have led to the evolution of mechanisms that allow survival under such harsh conditions. Although xerophytes normally have a number of adaptations to hydric stress (TURNER, 1986), mesophytes can also adapt in order to survive in environments where seasonal deficits occur (CALBO; MORAES, 2000).

Among the different regions that are subject to seasonal hydric stress, one of the most important is the Pantanal Matogrossense, which is paradoxically characterized by periodic floods. Nevertheless, drought conditions occur during part of the year because the evapotranspiration occurs more frequently than precipitation in this area (ALHO; GONÇALVES, 2005). According to Soares and Oliveira (2009), the Pantanal presents different vegetation formations adapted to diverse environmental conditions. Many formations are populated almost exclusively by a single species (known as monodominance), which often dominate extensive areas. The Paratudo is a region that exemplifies monodominance: it has as a single dominant tree species, the paratudo *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore, which is located in the region known as the Pantanal de Miranda.

Despite the great floristic richness of the Pantanal, there have only been a few ecophysiological studies focused on gas exchange mechanisms of Pantanal native tree species. Therefore, the present study aimed to investigate the gas exchange system of five-month-old plants of the paratudo tree species *T. aurea* after being exposed to conditions of induced hydric stress.

## Material and methods

*T. aurea* fruits were harvested from trees situated in the Miranda river sub-basin (upper Paraguay river basin) in the Pantanal de Miranda, municipality of Corumbá, Mato Grosso do Sul State, specifically in a region known as Passo do Lontra (19° 34' 37" S; 57° 00' 42" W). The collection was conducted with more than 30 matrices. After collection, the fruits were placed into paper bags and transported to the Universidade Federal de São Carlos (UFSCar) where they were kept at 25°C in the Vegetal Ecophysiology Laboratory of the Botany Department.

The seeds contained inside the dry fruits with natural dehiscence were collected and manually screened to separate those that were better preserved. Subsequently, the chosen seeds were set to germinate in petri dishes containing filter paper moistened with Captan fungicide solution (0.2%) and kept on laboratory shelves under environmental temperatures.

After germination, the seedlings were transferred to foil trays containing vermiculite and irrigated daily with distilled water. When they reached a height of 7 cm above the soil (11 days after germination), the seedlings were transplanted to planting bags (black plastic seedling bags, 7 kg capacity) already containing substrate. The substrate used was collected in Cerrado areas on the UFSCar campus between 0 and 20 cm in depth. The soil was classified as Eutrodox (Canchim unit) with a sandy texture (M.O.: 2.07%; pH: 4.33 CaCl<sub>2</sub>; P: Resin 2 µg cm<sup>-3</sup>; K<sup>+</sup>: 0.09 mg 100 cm<sup>-3</sup>; Ca<sup>2+</sup>: 0.72 mg 100 cm<sup>-3</sup>; Mg<sup>2+</sup>: 0.56 mg 100 cm<sup>-3</sup>; Al<sup>3+</sup>: 0.35 mg 100 cm<sup>-3</sup>). Analyses of soil properties were conducted in the Soil and Plant Chemical Analysis Laboratory of the Natural Resources Department at the Center of Agrarian Sciences of the UFSCar (Araras campus).

The substrate was sieved, placed onto plastic canvasses and dried outdoors. Each bag received a single seedling and was kept in a greenhouse (Doubly Poly Pad/Fan greenhouse model) set to average, minimum or maximum temperatures (20°C, 25 ± 2°C and 15 ± 2°C, respectively) at a relative humidity of 60 ± 10% and light intensity of 65% (compared to 100% in full daylight).

Five months after emergence, the plants were subjected to conditions of hydric stress simulated by the suppression of irrigation. The gas exchange of three control plants and three plants under stress was measured with a Hoddesdon model LCA-2 CO<sub>2</sub> infrared portable analyzer (IRGA, Analytical Development Company – ADC) connected to an air supply unit (ADC ASU; MF), processor and data storage unit (DL-2), with an air reference of 38%-40% adjusted for relative humidity. Daily measures of  $P_N$  (net photosynthesis,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) were taken, and after photosynthesis had reached a constant level, measurements of  $E$  (transpiration,  $\text{mmol m}^{-2} \text{s}^{-1}$ ) and  $G_s$  (stomatal conductance related to water steam,  $\text{mol m}^{-2} \text{s}^{-1}$ ) were conducted, using primary leaflets that remained in the chamber for 10 and 20 seconds. The measurements were conducted at a light intensity of  $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$  produced by an overhead light. A bowl containing water was placed between the light source and plants to avoid excessive heating of the leaves.

Evaluations were conducted in the morning, usually after 7:30 a.m., and attempts were made to use the same pairs of leaves for each evaluation. The measurements were conducted for 21 days, and irrigation occurred on day 14.

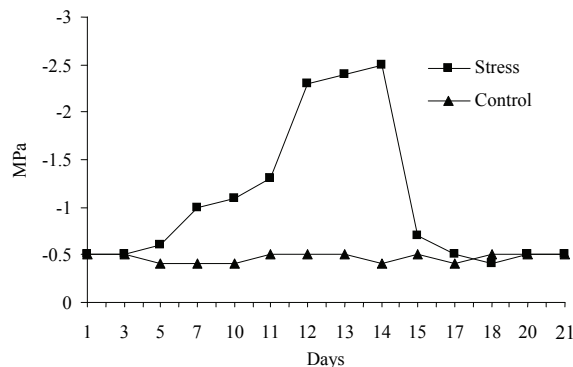
The leaf water potential ( $\Psi_w$ ) was obtained using the Scholander pressure chamber (PMS-1000, EUA). The experiment was completely randomized with two treatments (1-water omission; 2-dialy irrigation until load soil saturation), six replicates per treatment and daily evaluations for 21 days.

## Results and discussion

The leaf water potential values of the first five days were between -0.5 and -0.6 MPa. From day 7 onward, the hydric potential increased from -1.0 MPa until it reached -2.5 MPa on day 14, when net photosynthesis was  $0.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . This was the hydric potential value (-2.5 MPa) that limited photosynthesis for this species at five months of age. After this period, irrigation was resumed. On day 15, the hydric potential value reached -0.6 MPa but returned to the initial value on day 17 (-0.5 MPa) (Figure 1).

The minimum values for leaf water potential found for *T. aurea* are higher than those cited by Rocha and Moraes (1997), who had tested young *Stryphnodendron adstringens* (Mart.), Coville plants (-2.7 MPa) found in the Cerrado. Although *T. aurea* can also be found in different regions within the Cerrado, our samples were collected from the Pantanal where the environmental conditions are

different from those found in the savanna biome. This geographical difference might explain the higher value (i.e., a lower tolerance to hydric deficit) found for our plants when compared to other species of this biome.



**Figure 1.** Leaf water potential (MPa) in young *Tabebuia aurea* potted plants subjected the induced hydric stress.

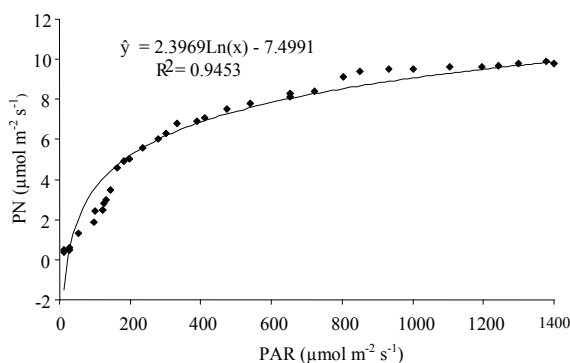
Plants found in different ecosystems can show differences in their genotype expression caused by environmental influences, which is a plasticity that can be manifested both morphologically and physiologically, allowing the species to adapt to different environments (SULTAN, 2000).

According to Larcher (2004), mesophytic plants from tropical forests with water potentials between -1.5 and -4.0 MPa can reach photosynthesis rates of zero, indicating that *T. aurea* exhibits mesophytic plant characteristics in response to hydric stress. In addition, the slow decrease in hydric potential and other evaluated parameters (transpiration, stomatal conductance and photosynthesis) indicate that this species can adapt to tolerate moderate hydric stress for a moderate period, which is also a typical behavior of mesophytic species.

The light compensation point (PCL, the light intensity at which CO<sub>2</sub> emission by transpiration and photorespiration equals the carbon fixed by photosynthesis) was  $53.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 2). The highest recorded PCL found by Calbo and Moraes (2000) was for four-month-old *Euterpe oleracea* Mart. palm trees ( $18.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), which was still lower than that observed by Rocha and Moraes (1997) for six-month-old *S. adstringens* ( $59 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

The maximum photosynthesis rate obtained for *T. aurea* was  $9.9 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 2), which was higher than that found by Calbo and Moraes (2000) for *E. oleracea* ( $4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). This rate, however, was lower than that observed by Rocha and Moraes (1997) for *S. adstringens* ( $12.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

When studying adult plants of 20 different Cerrado species, Prado and Moraes (1997) reported photosynthesis rates that varied between  $19.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  [*Tibouchina stenocarpa* (DC.) Cogn.] and  $6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  [*Tocoyena formosa* (Cham. et Sch.) K. Sch.], indicating a great diversity in the behaviors of species from areas under temporary hydric stress. In addition, Franco et al. (2005) studied 11 tree species from the Neotropical savannas (Cerrado) and found values ranging between  $16.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  (*Schefflera macrocarpa* Cham. & Schltdl. Frodin) and  $8.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  (*Vochysia elliptica* Mart.), which again demonstrates different behavioral strategies.



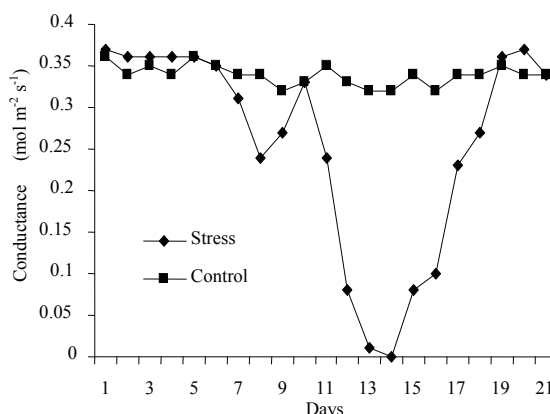
**Figure 2.** Net photosynthesis rate (PN,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) as a function of photosynthetically active radiation (PAR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in young and hydrated *Tabebuia aurea* potted plants.

For most plants, the rate of photosynthesis increases in response to increases in light up to approximately 25% of total sunlight. Above this value, the rates of photosynthesis are limited by the availability of reducing forces and ATP. However, photosynthesis is not limited when the saturating light intensity is reached unless there is less carbon fixation as a result of a decrease in carbon dioxide supply to carboxylation sites (AUSTIN, 1989).

Larcher (2004) has stated that the photosynthetic capacity is an intrinsic characteristic of each species and that rates change during plant growth. This capacity frequently depends on variations in environmental factors (e.g., light and temperature) to which plants are exposed.

The data obtained for stomatal conductance (Figure 3) showed initial values between 0.24 and  $0.37 \text{ mol m}^{-2} \text{s}^{-1}$  until day 11; afterward, these values varied between 0.08 and  $0.01 \text{ mol m}^{-2} \text{s}^{-1}$  until day 13. On day 14, conductance was  $0.0 \text{ mol m}^{-2} \text{s}^{-1}$  with a hydric potential of  $-2.4 \text{ MPa}$ , and irrigation was then resumed. Conductance rates were between 0.34 and  $0.36 \text{ mol m}^{-2} \text{s}^{-1}$  with a hydric potential of  $-0.5 \text{ MPa}$  at 96 hours after resuming irrigation, indicating a fast recovery. These results were

expected because an increase in hydric deficit always leads to a reduction in conductance or an increase in stomatal resistance. With greater water deficits, there is more intense stomatal closing, which is important to maintain the water transport system integrity and a favorable hydric potential for leaf development during the dry season or under conditions of hydric stress (DE MATTOS, 1998).



**Figure 3.** Conductance rates ( $\text{mol m}^{-2} \text{s}^{-1}$ ) in the two experimental groups (stress and control) of young *Tabebuia aurea* potted plants subjected to hydric stress through the suppression of irrigation.

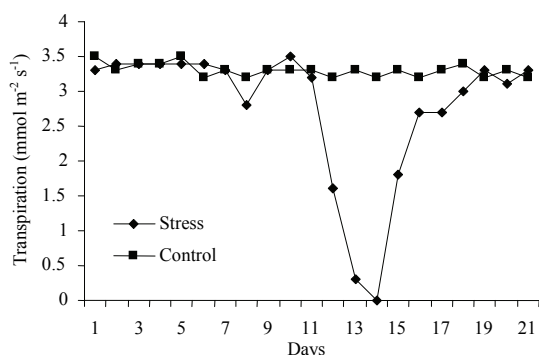
Rocha and Moraes (1997) had reported a decrease in conductance rates in *S. adstringens* under hydric stress. The authors observed that this species continually maintained its stomatal conductance rate between 0.10 and  $0.32 \text{ mol m}^{-2} \text{s}^{-1}$  until day 27, and these values reached zero on experimental day 30 with a hydric potential of  $-2.7 \text{ MPa}$ . After resuming irrigation, the conductance rate had returned to the initial values within two days, which was similar to that observed for *T. aurea*.

Calbo and Moraes (2000) also demonstrated a decrease in conductance rates for the Amazonian species *E. oleracea* under stress, which initially varied between 0.05 and  $0.12 \text{ mol m}^{-2} \text{s}^{-1}$  during the first 24 days of stress and decreased down to zero on day 61 (hydric potential of  $-2.4 \text{ MPa}$ ). However, the recovery of initial stomatal conductance rates was slow and was not achieved until day 14 after irrigation. Similar results were found by Tatagiba et al. (2007) for *Eucalyptus* clones in which a decrease in conductance rates occurred during the dry season and an increase occurred during the rainy season.

Research by Galmés et al. (2007) with eight Mediterranean species subjected to hydric stress also indicated a decrease in conductance as hydric failure increased, and recovery occurred after rehydration. Silva et al. (2008) also observed stomatal closing

during hydric stress and recovery after irrigation in *Schinus terebinthifolius* Raddi. Some species exhibit slow recovery of stomatal conductance due to the buildup of abscisic acid (ABA) during hydric stress. However, recovery times vary according to the species, and the rapid recovery observed for *T. aurea* could indicate low ABA buildup.

Transpiration rates varied between 2.8 and 3.5 mmol m<sup>-2</sup> s<sup>-1</sup> until day 11 and then varied between 0.3 to 1.8 mmol m<sup>-2</sup> s<sup>-1</sup> until day 14. On day 15, the lowest transpiration rate was observed (0.0 mmol m<sup>-2</sup> s<sup>-1</sup>). After this point (day 14), irrigation was resumed, and the rates increased once again, returning to initial values at 96 hours after irrigation (Figure 4).



**Figure 4.** Transpiration rates (mmol m<sup>-2</sup> s<sup>-1</sup>) in the two experimental groups (stress and control) of young *Tabebuia aurea* potted plants subjected to hydric stress through the suppression of irrigation.

Higher transpiration rates are associated with hydric excess in the soil. When the amount of water in the soil decreases, transpiration rates also decrease via restriction mechanisms (LARCHER, 2004) that prevent severe hydric reduction and the subsequent death of the plant. However, transpiration rates can decrease with a continuous decline in water until it reaches zero.

This decrease in water availability leads to an increase in hydric stress, which is expected for mesophytic species subjected to stress (KRAMER; BOYER, 1995; LARCHER, 2004). However, species adapted to regular periods of drought develop a resistance to this type of stress and are able to maintain transpiration for longer periods, despite the hydric restriction in the soil (LARCHER, 2004). The rapid recovery (Figure 4) observed in the studied species (*T. aurea*) indicates an adaptation to environments that are subject to periodical stress.

In *T. aurea*, a decrease in transpiration (Figure 4) correlates with a reduction in stomatal conduction (Figure 3), demonstrating that cuticular transpiration is minimal during this growth stage.

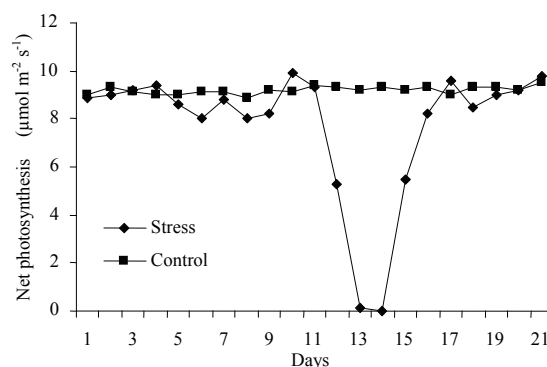
Therefore, the high cuticular resistance of this species is also an indication of drought tolerance.

Transpiration behavior in response to drought varies among plants. Rocha and Moraes (1997) reported that *S. adstringens* maintained high transpiration rates from 2.7 to 4.0 mmol m<sup>-2</sup> s<sup>-1</sup> until day 26, and then rates began to decrease until they reached 0.1 mmol m<sup>-2</sup> s<sup>-1</sup> on day 30. After irrigation was resumed, transpiration returned to the initial values.

In contrast, Calbo and Moraes (2000) found that transpiration rates in *E. oleracea* varied between 1.0 and 2.0 mmol m<sup>-2</sup> s<sup>-1</sup> during the first 30 days of stress. Afterward, transpiration rates continued to decrease, reached zero on day 61 and resumed to the initial values after 14 days of irrigation.

A decrease in transpiration values during hydric restriction was also observed by Silva et al. (2003) in a greenhouse with several tree species including *Mimosa caesalpinifolia* Benth., *Enterolobium contortisiliquum* (Vell.) Morong, and *Tabebuia aurea*. Furthermore, Tatagiba et al. (2007) observed a decrease in transpiration rates during periods of drought and an increase during rainy periods for *Eucaliptus* clones, while Silva et al. (2008) noted a similar pattern for *Schinus terebinthifolius* Raddi.

Initial net photosynthesis rates varied between 8.0 and 9.9 μmol m<sup>-2</sup> s<sup>-1</sup> until day 11 when they started to rapidly drop (5.3 μmol m<sup>-2</sup> s<sup>-1</sup> on day 12; 0.1 μmol m<sup>-2</sup> s<sup>-1</sup> on day 13) until reaching 0.0 μmol m<sup>-2</sup> s<sup>-1</sup> on day 14 with a hydric potential of -2.4 MPa. At this point, irrigation was resumed, and net photosynthesis rates were similar to initial values after 72 hours of irrigation (Figure 5). Similarly, the hydric potential was also recovered (-0.5 MPa), indicating that the leaf mesophyll was not affected during this period of stress.



**Figure 5.** Photosynthesis rates (μmol m<sup>-2</sup> s<sup>-1</sup>) in the two experimental groups (stress and control) of young *Tabebuia aurea* potted plants subjected to hydric stress through the suppression of irrigation.

A reduction in photosynthesis rates is common in species that are sensitive to hydric stress; this

reduction is initially mediated by stomatal closing and later by a reduction in photosynthetic capacity as well as other factors (KRAMER; BOYER, 1995; LARCHER, 2004). Rocha and Moraes (1997) confirmed this observation using *S. adstringens*, a species that maintained photosynthesis rates between  $8 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $11.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  until day 25 of hydric stress. The photosynthesis rates then declined starting on day 27 ( $3.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) until reaching zero on experimental day 30. A total recovery in photosynthesis rates occurred after 48 hours of irrigation.

Calbo and Moraes (2000) studied *E. oleracea* plants and found initial values of net photosynthesis varying between  $3.1$  and  $5.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  during 32 days of stress. The photosynthesis rate then decreased, reaching zero on day 61 with a hydric potential of  $-2.5 \text{ MPa}$ ; however, this species showed a slow recovery only returning to initial values on day 14 after irrigation.

Tatagiba et al. (2007) had also observed a decrease in *Eucalyptus* photosynthesis rates during the dry season and an increase during the rainy period.

Hydric restriction normally causes a parallel decrease in photosynthesis and conductance rates because stomatal closing leads to a decrease in  $\text{CO}_2$  entry (TURNER, 1986).

Larcher (2004) observed that when a decrease in hydric potential of leaves occurred, photosynthetic rates also decreased. However, the point where the decrease began to affect photosynthesis rates was variable from species to species due to genotype, habitat, environmental conditions and history of each plant.

*T. aurea* plants have the ability to survive short periods of drought without any loss in photosynthetic capability. This adaptation is linked to a reduction in stomatal opening that causes a reduction in transpiration rates and, consequently, in photosynthetic rates.

## Conclusion

*T. aurea* has evolved mechanisms to tolerate temporary hydric deficits, which may be considered ecologically relevant.

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