

Ecophysiology of water stressed  
*Handroanthus impetiginosus* (Mart. Ex. DC) Mattos) SeedlingsEcofisiologia de Mudanças de Ipê-Roxo (*Handroanthus impetiginosus*  
(Mart. ex. DC.) Mattos) Submetidas a Estresse HídricoJeferson Luiz Dallabona Dombroski<sup>1</sup>, Rômulo Magno Oliveira de Freitas<sup>2</sup>,  
Valmor Elias Tomczak<sup>3</sup>, José Rivanildo de Sousa Pinto<sup>4</sup> e Raul Martins de Farias<sup>5</sup>**Resumo**

O objetivo desse estudo foi avaliar o comportamento ecofisiológico de *Handroanthus impetiginosus* em resposta a estresse hídrico e à reidratação. Para isso foi realizado um experimento de supressão de irrigação por um período de 12 dias, até o início da queda das folhas. Após esse período a irrigação foi retomada. As variáveis avaliadas foram fotossíntese, condutância estomática, transpiração, eficiência instantânea e intrínseca de uso da água e o potencial hídrico foliar. As avaliações foram realizadas durante o período de suspensão da irrigação e após sua retomada, até que as taxas de fotossíntese das mudas que foram submetidas à suspensão da irrigação iguallassem as das que não foram submetidas. O estresse hídrico afetou a fotossíntese, a transpiração e a condutância estomática, com decréscimo dessas variáveis e rápidas recuperações após a reidratação. A eficiência do uso da água aumentou com o estresse hídrico. *H. impetiginosus* tem a capacidade de reduzir seu potencial hídrico foliar em condições estressantes, e recupera rapidamente a capacidade fotossintética após o período de estresse.

**Palavras-chave:** Fotossíntese, Potencial hídrico, Condutância estomática, Transpiração, Caatinga.

**Abstract**

The objective of this work was to evaluate the ecophysiological behavior of *Handroanthus impetiginosus* seedlings in response to water stress and rehydration. For this, an experiment was conducted, in which irrigation was suppressed for twelve days, up to the beginning of leaves fall, followed by irrigation resumption. The variables measured were photosynthesis, stomatal conductance, transpiration, instantaneous and intrinsic water use efficiency and leaf water potential. The evaluations were made during the irrigation suspension time and after resumption, until the photosynthesis values from water stressed plants equaled those which did not suffer water shortage. Water stress affected photosynthesis, transpiration and stomatal conductance, with diminution of its levels, and fast recovery after rehydration. The water use efficiency was higher with water stress. *H. impetiginosus* has the capability of reducing its water potential under stress, and has a fast recovery of photosynthetic rates after the end of the stress.

**Keywords:** Photosynthesis, Stomatal conductance, Water potential, Transpiration, Caatinga.

**INTRODUCTION**

*Handroanthus impetiginosus*, *Tabebuia impetiginosa* or *Tabebuia avellanadae* (TROPICOS, 2012), popularly known in Brazil as Ipe roxo or pau d'arco roxo is a tree species from the Bignoniaceae, found in Caatinga vegetation (BENEVIDES; CARVALHO, 2009; LIRA et al., 2007; SANTANA;

SOUTO, 2011). It has been used for furniture manufacturing and flooring (GEMAQUE et al., 2002), folk medicine (CASTELLANOS et al., 2009; LOURENÇO et al., 2010), urban afforestation (SANTOS et al., 2011) and has a potential as a bee forage plant (BENEVIDES; CARVALHO, 2009). It has also been indicated to be used in forest restoration programs (MAIA, 2004).

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The Caatinga plant species present physiological and morphological adaptations to withstand drought (SILVA et al., 2004). These adaptations show up in form, color, metabolism, vital cycles and social organization of all the organisms in this Biome (MAIA, 2004), and the plant composition is conditioned mainly by the water regime (ANDRADE et al., 2009).

Abiotic factors like high irradiances and temperatures and low water or nutrient availability, are all observed in the Caatinga Biome, making it difficult to establish juvenile plants (GONÇALVES et al., 2005; LIBERATO et al., 2006; SANTOS JUNIOR et al., 2006). Among these resources, water is considered the main factor that restrains the establishment potential for plants in general (ARAÚJO et al., 2007; MCLAREN; MCDONALD, 2003; NIPPERT et al., 2006; WEIEGAND et al., 2006;), and particularly for Caatinga plants (CABRAL et al., 2004; MARIANO et al., 2009; SOUZA et al., 2010).

Water stress is the most important problem in agriculture (SHAO et al., 2008), and understanding plant responses to water shortage is of great importance for the development of strategies that improve crop production under water stress (CATTIVELLI et al., FUSSELL et al., 1991; 2008; JALEEL et al., 2009), and also the irrigation programs in semiarid areas (FLEXAS et al., 2004a).

Water deficiency affects plant productive capability, initially due to stomatal closure, with its consequent reduction of CO<sub>2</sub> uptake (CHAVES et al., 2002; TANG et al., 2002), but as the stress grows up, a number of metabolic alterations occur (BAKER; ROSENQVIST, 2004; RIBEIRO et al., 2008; SANTOS JUNIOR et al., 2006; TAIZ; ZEIGER, 2009), culminating in leaf fall in deciduous species (SANTANA; SOUTO, 2011). Other aspects related to water stress include reduction of mineral nutrient absorption (FIRMANO et al., 2009; GONZALEZ-DUGO et al., 2010), and impairment of cell (CHAVES et al., 2009) and plant growth (BENGOUGH et al., 2011; SHAO et al., 2008).

There are only a few studies on the physiological responses of Caatinga plants to stresses (TROVÃO, 2007) and also a few studies on photosynthesis recovery capability after water stress (CHAVES et al., 2009; FLEXAS et al., 2006; FLEXAS et al., 2004a). In this way, the aim of this study was to evaluate the ecophysiological behavior of *Handroanthus impetiginosus* in response to water stress and rehydration.

## MATERIAL AND METHODS

The experiment was conducted from November 2010 to September 2011, in a greenhouse at the Department of Plant Sciences of the Semiarid Federal Rural University in Mossoro (UFERSA), state of Rio Grande do Norte, Brazil, located at 5°11'S and 37°20'W, and at 18 m altitude. The climate is classified as Köppen's BSw<sub>h</sub>, i.e., dry and very hot (CARMO FILHO et al., 1991), the mean annual temperature is 27.4 and the relative humidity is 68.9%. The greenhouse was covered with plastic film and 50% shade cloth.

The fruits were collected from mother plants at the UFERSA campus in Mossoro, the seeds were extracted and three seeds were planted in each plastic bag with 1.5L substrate capacity. The substrate used was a Neossolo Quartzarenico Distrofíco (by Brazilian system of soil classification), also collected at the UFERSA campus, in an area under natural forest restoration, which was mixed with 25% manure. The plants were thinned 40 days after seeding, leaving one per bag. The irrigation was made daily, always at the end of the afternoon.

When seedlings reached nine months, in the dry season, an experiment in random complete blocks was installed, with two water regimes (with and without water stress) and three replications. Each replication was represented by three plants. Irrigation was suspended for 12 days, up to the beginning of leaves fall, and resumed after that. Evaluations were made at a three-day interval, since before irrigation suspension and until the photosynthetic rates from the two water regimes were equal. The variables measured were pre-dawn and midday leaf water potential ( $\Psi_w$ ; MPa); photosynthesis ( $A$ ;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ); stomatal conductance ( $g_s$ ;  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and transpiration ( $E$ ;  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ).

For the photosynthesis measurement we used a LI-6400 photosynthesis system (LI-COR Biosciences) with CO<sub>2</sub> levels fixed at 400  $\mu\text{moles m}^{-2} \text{ s}^{-1}$  and light intensity at 1500  $\mu\text{moles m}^{-2} \text{ s}^{-1}$  of PAR. The instantaneous water use efficiency ( $A/E$ ) was determined and also intrinsic water use efficiency ( $A/g_s$ ) (MEDRANO; GALMÉS, 2009). For water potential measurement we used a pressure pump (PMS Instrument).

The results were submitted to variance analysis by the F test, 5% probability, in each evaluation time, with the SISVAR statistical software (FERREIRA, 2008).

## RESULTS AND DISCUSSION

The beginning of leaves fall occurred on the 12th day, then irrigation was resumed and, after six days, the photosynthesis rates between the two water regimes were equal.

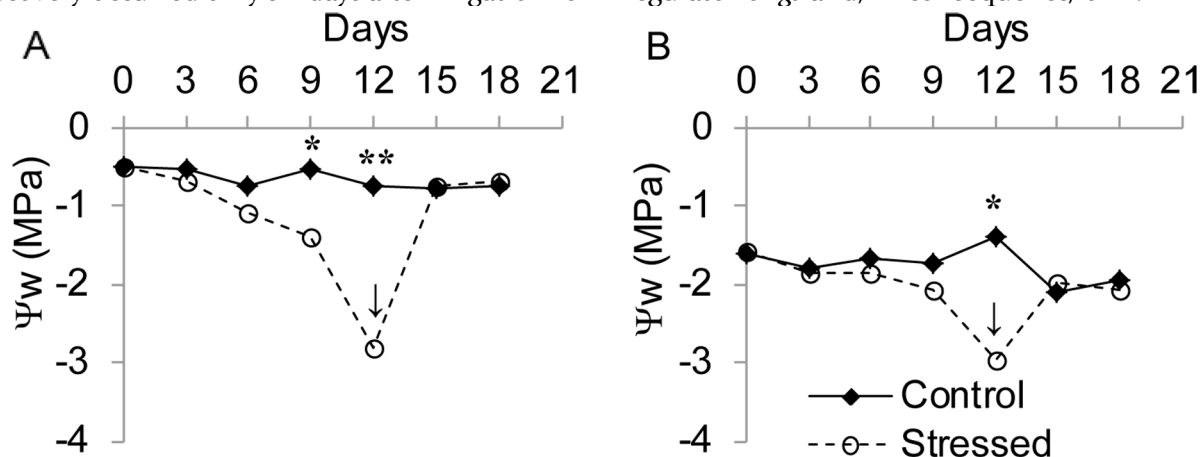
Minimum pre-dawn and midday water potential observed were -1.9 and -3.0 MPa (Figure 1) which indicates a good investment capability as a drought resistance strategy. Similar water potential levels were observed by Dombroski et al. (2011) with other Caatinga species in the dry season. For *Caesalpinia ferrea* e *Calliandra spinosa*, the authors observed a mean leaf  $\Psi_w$  of -1 and -1.3 Mpa in pre-dawn and -2.2 and -2.7 Mpa at midday, respectively. In the same work, the authors observed that, for other tree species, the water potential ranged from -0.5 Mpa to -3.5 Mpa, characterizing varied investment strategies. Lowering internal  $\Psi_w$  allows water absorption to occur for some time after the rain, with consequent stomatal opening and photosynthesis (LARCHER, 2004).

Irrigation suspension affected pre-dawn and midday water potential in different ways. In pre-dawn there was a significant difference of  $\Psi_w$  between the two water regimes after three days of suspension, indicating the beginning of water deficit in soil. This difference remained until the 12th day when irrigation was resumed and, on the 15th day, no more  $\Psi_w$  differences between the treatments were observed. For midday  $\Psi_w$ , a difference between treatments was seen only on the 12th day, so the plants kept a leaf  $\Psi_w$  near -2.0MPa in less severe conditions; but when water availability was even more reduced, the plant reduced its leaf  $\Psi_w$  even more. Midday leaf  $\Psi_w$  recovery occurred only six days after irrigation re-

turned, which may indicate a loss in xylem water conductivity (BRODRIBB; COCHARD, 2009).

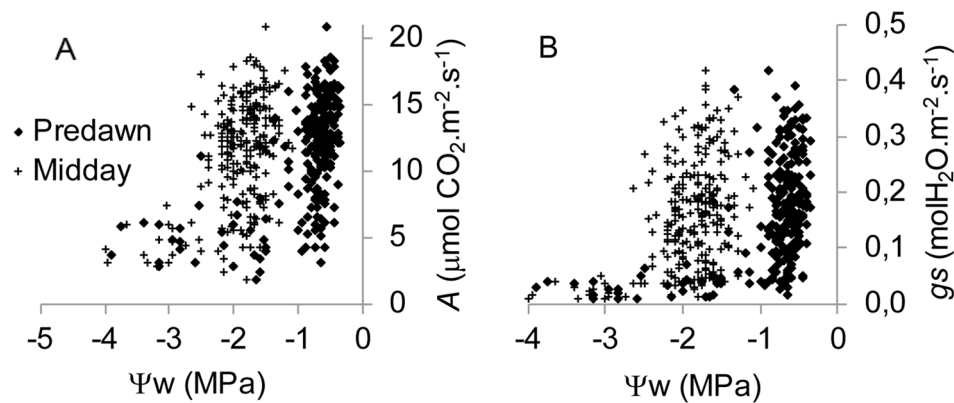
In figures 2A and 2B the relationship between  $A$  and  $g_s$  with pre-dawn and midday leaf  $\Psi_w$  is shown. It can be seen that there is a pattern, both for  $A$  and for  $g_s$  relationship with leaf  $\Psi_w$ . For leaf  $\Psi_w$  values in pre-dawn higher than -1.0 MPa, and in midday, higher than -2.5 MPa, the relation is very weak, with small  $\Psi_w$  variation related to strong variations in  $g_s$  and  $A$ . Below these  $\Psi_w$  threshold values,  $A$  and  $g_s$  values are lower than  $7.0 \mu\text{moles CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  for  $A$  and lower than  $0.05 \text{mmoles H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  for  $g_s$ . Similar results were obtained for *Chilops* and *Encelia*, both desert bushes, by Odening et al. (1974). Values of  $g_s$  below  $0.10 - 0.15 \text{mmoles H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  are considered indicators of severe water stress (FLEXAS et al., 2004a).

There are strong differences in stomatal behavior among species related to water deficits in soil and atmosphere (BOND et al., 1999). The stomatal conductance is affected by a series of factors related to plant water status, like leaves' and roots' water potential, abscisic acid levels and other hormones, xylem hydraulic conductivity (MEDRANO et al., 2002), the photosynthetic metabolism type (OSBORNE; SACK, 2012), and also by environmental factors, like the vapour pressure deficit (YU et al., 2009), temperature (SALVUCCI; CRAFTS-BRANDNER, 2004), atmosphere  $\text{CO}_2$  levels (MIRI et al., 2012), and light availability and intensity (HORTON et al., 1996).  $G_s$  responds to a complex net of factors linked to the plant water status so that Flexas et al. (2004b) propose the use of  $g_s$  as an indicator of plants water stress level. Leaf  $\Psi_w$  is a strong regulator of  $g_s$  and, in consequence, of  $A$ .



**Figure 1.** Effect of irrigation suspension on *H. impetiginosus* seedlings at pre-dawn (A) and midday (B)  $\Psi_w$ . The arrow indicates the irrigation resuming time. Asterisks indicate significant differences at 1% (\*\*) and 5% (\*) of probability.

**Figura 1.** Efeito da suspensão da irrigação em mudas de ipê-roxo sobre o  $\Psi_w$  foliar, antes do amanhecer (A) e ao meio dia (B). A seta indica o momento da retomada da irrigação. Os asteriscos indicam diferenças significativas entre os regimes hídricos a 1% (\*\*) e 5% (\*) de probabilidade.

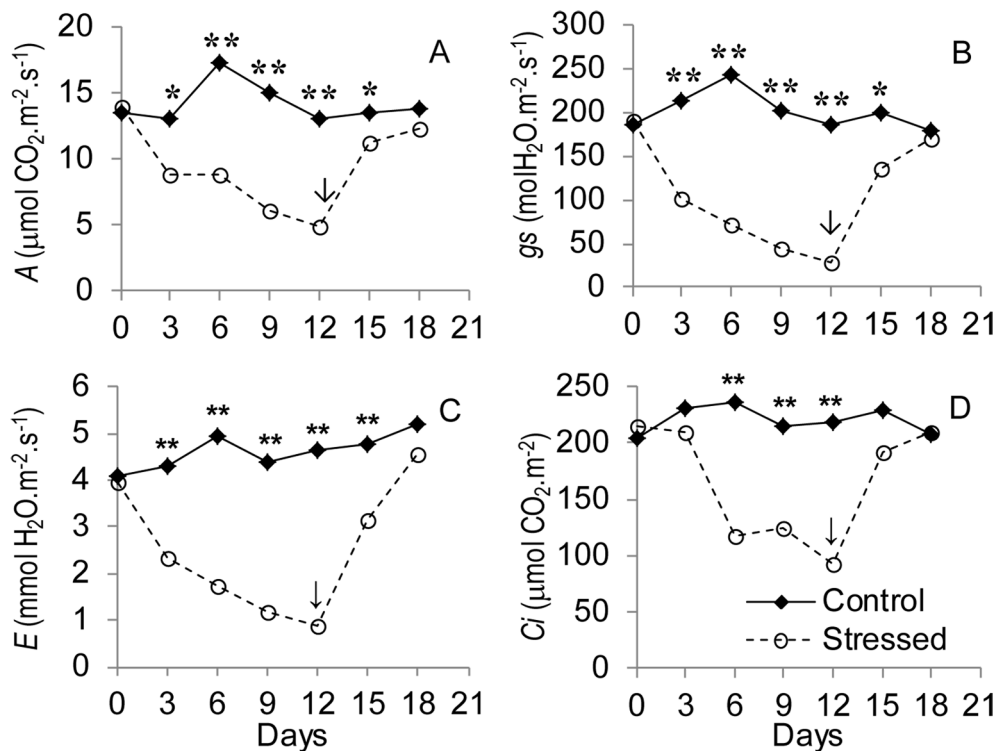


**Figure 2.** Relationship between photosynthesis (A) and stomatal conductance (B) with leaf water potential at two evaluation times (pre-dawn and midday) in *H. impetiginosus* young plants under various water availability conditions.

**Figura 2.** Relação da fotossíntese (A) e da condutância estomática (B) com o potencial hídrico obtido em dois horários (antes do amanhecer e meio-dia) em plantas de ipê roxo submetidas a diferentes condições hídricas.

A mild water stress affects A (Fig 3a) and gs (Fig. 3b), which affects directly E (Fig. 3c). A decrease in A, gs and E three days from the beginning of irrigation suspension was observed, but without a decrease in  $C_i$ . Water stress can affect A related to  $\text{CO}_2$  limitation (Fig. 3c), caused by the decrease in gs, as was observed in the present work, but in this case there would be a decrease in  $C_i$ , suggesting that the limitation of A is not from  $\text{CO}_2$  shortage. Although the reliability of  $C_i$  mensuration under water stress has been

questioned (Flexas et al.; 2004b; Lawlor and Tezara; 2009), the possibility of non gs limitations cannot be disregarded. In more severe cases, the water deficit has been reported to cause decrease in A by a restriction of mesophyll conductance of  $\text{CO}_2$  (Lawlor and Tezara, 2009); metabolic alterations in chlorophyll content; ATP levels; content of Ribulose biphosphate; Rubisco activity (LAWLOR, 2002; BOTA et al., 2004; Flexas et al., 2004b), oxidative damage and/or photoinhibition (Galmés et al., 2007).



**Figure 3.** Effect of irrigation suspension of young *H. impetiginosus* plants on A (A), gs (B), E (C), and  $C_i$  (D). The arrow indicates the irrigation resumption day. Asterisks indicate significant differences between treatments at 1% (\*\*) and 5% (\*).

**Figura 3.** Efeito da suspensão da irrigação em mudas de ipê-roxo sobre A(A), gs(B), E(C), e  $C_i$  (D). A seta indica o momento da retomada da irrigação. Os asteriscos indicam diferenças significativas entre os tratamentos a 1% (\*\*) e 5% (\*).

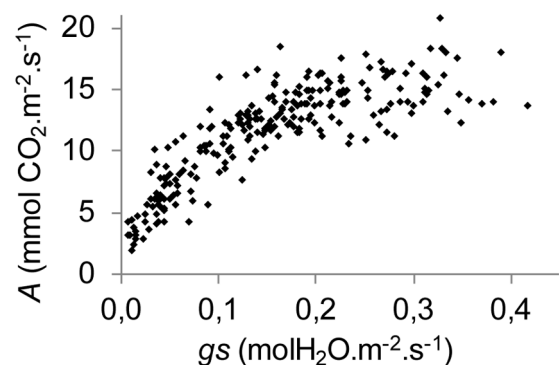
Six days after irrigation resumption, the treatments showed no more significant differences among the variables  $A$ ,  $g_s$ ,  $E$  and  $C_i$  (figure 4). Similar results were found for *Minquartia guianensis* (LIBERATO et al., 2006), also with recuperation six days after irrigation resumption. In a work with *Carapa guianensis*, Gonçalves et al. (2009) observed a recuperation of  $A$  levels eight days after the water levels were restored. Despite the beginning of leaves fall, the full recuperation of  $A$  is an evidence of a low damage to the photosynthetic apparatus, different of what was observed in other species (MIYASHITA et al., 2005). In cases of severe water stress, it may occur that the plants take a long time or do not recover its pre-stress photosynthetic capability (FLEXAS et al., 2004a).

Instantaneous ( $A/E$ ) and intrinsic ( $A/g_s$ ) water use efficiency were affected by the treatments. Higher values at the 6th, 9th and 12th days after irrigation suspension were observed (Fig 4A and 4B). Gonçalves et al. (2009), in a work with *Carapa guianensis* did not observe differences in  $A/E$  between irrigated and non irrigated plants, with maximum values near  $4.0 \text{ mmol CO}_2 \cdot \text{mol H}_2\text{O}^{-1}$ , lower than the highest values observed in the present work (average of  $5.7 \text{ mmol CO}_2 \cdot \text{mol H}_2\text{O}^{-1}$ ). The higher *H. impetiginosus* efficiency may be due to the fact that *C. guianensis* is a humid tropical climate plant, in which water is not a scarce resource, when compared to the Caatinga climate.

Six days after irrigation resumption,  $A/E$  and  $A/g_s$  values equaled the control treatment (Fig. 4), which means that the water use efficiency observed during the water restriction period was not kept after irrigation resumption. A raise in  $A/E$  in moderate water stress conditions had already been observed (SAUSEN; ROSA, 2010). Still

when the stress is severe, with the decrease of mesophile cells water content, the metabolism is impaired, affecting photosynthesis, and water use efficiency decreases (TAIZ; ZEIGER, 2009).

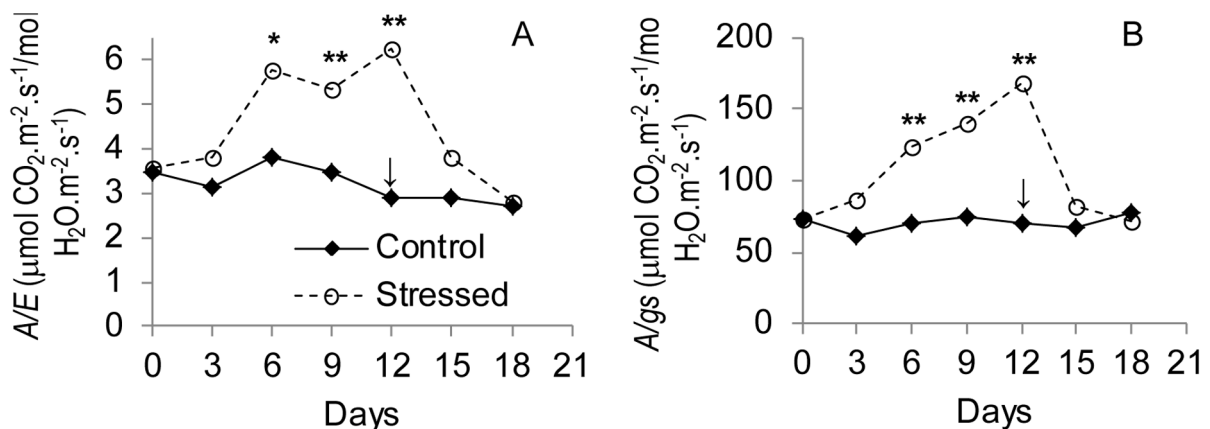
There was a linear relationship between  $A$  and  $g_s$  for  $g_s$  values below  $200 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , (data not shown,  $R^2 = 0.91$ ), Flexas et al., 2004a indicates that  $A$  is possibly limited mainly by  $g_s$  in this range, but there are other factors that can limit  $A$ , especially under  $g_s$  values of 50 to  $100 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , like those cited before. Costa and Marengo (2007) and Gonçalves et al. (2009) in works with *C. guianensis*, and Janoudi et al. (1993) with pumpkin also observed a restraint in  $A$  for  $g_s$  values below  $256 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ .



**Figure 5.** Relationship between  $A$  and  $g_s$  for young *H. impetiginosus* plants under several water conditions.

**Figura 5.** Relação entre fotossíntese ( $A$ ) e a condutância estomática de plantas jovens de ipê sob diferentes condições hídricas.

The behavior of the  $A/g_s$  relationship followed a similar pattern to the three stages pattern described by Flexas et al. (2004a), as a characteristic pattern for plants in general, with a small decrease of  $A$  until  $150 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , a stronger reduction between  $150$  and  $50 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ,



**Figure 4.** Effect of irrigation suspension in young *H. impetiginosus* plants on A: Instantaneous water use efficiency ( $A/E$ ) and B: intrinsic water use efficiency ( $A/g_s$ ). The arrow indicates the irrigation resumption date. Asterisks indicate significant differences between treatments at 1% (\*\*) and 5% (\*).

**Figura 4.** Efeito da suspensão da irrigação em mudas de ipê-roxo sobre a eficiência instantânea de uso da água ( $A/E$ , A) e eficiência intrínseca de uso da água ( $A/g_s$ , B). A seta indica o momento da retomada da irrigação. Os asteriscos indicam diferenças significativas entre os regimes hídricos a 1% (\*\*) e 5% (\*).

and an even higher reduction below this  $g_s$  level. This tendency was also observed for grapevines by Medrano et al. (2002), which is a species well adapted to water stress (FLEXAS et al., 2004a).

## CONCLUSIONS

*H. impetiginosus* has a full photosynthetic recovery after a severe water stress.

Water stress affects photosynthesis, transpiration and stomatal conductance, with the decrease of these variables; and fast recovery after rehydration.

Instantaneous and intrinsic water use efficiency raise under water stress.

## ACKNOWLEDGEMENTS

To FAPEMAT - Fundação de Amparo à Pesquisa do Estado de Mato Grosso, which enabled the Matas de Galeria Project, to the Programa de Pós-graduação em Ecologia e Conservação - UNEMAT, and the entire staff of the Laboratório de Ecologia Vegetal, at Universidade do Estado de Mato Grosso, Nova Xavantina campus.

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Recebido em 31/05/2013

Aceito para publicação em 06/02/2014