GAS EXCHANGE IN YOUNG PLANTS OF *Tabebuia aurea* (Bignoniaceae Juss.) SUBJECTED TO FLOODING STRESS[1]

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ABSTRACT – The Paratudo (*Tabebuia aurea*) is a species occurring in the Pantanal of Miranda, Mato Grosso do Sul, Brazil, an area characterized by seasonal flooding. To evaluate the tolerance of this plant to flooding, plants aged four months were grown in flooded soil and in non-flooded soil (control group). Stomatal conductance, transpiration and CO_2 assimilation were measured during the stress (48 days) and recovery (11 days) period, totalling 59 days. The values of stomatal conductance of the control group and stressed plants at the beginning of the flooded were 0.33 mol m^{-2} s^{-1} and reached 0.02 mol m^{-2} s^{-1} (46 th day) at the end of this event. For the transpiration parameter, the initial rate was 3.1 mol m^{-2} s^{-1}, and the final rate reached 0.2 or 0.3 mol m^{-2} s^{-1} (47/48 th day). The initial photosynthesis rate was 8.9 mmol $m^{-2}s^{-1}$ and oscillated after the sixth day, and the rate reached zero on the 48th day. When the photosynthesis rate reached zero, the potted plants were dried, and the rate was analyzed (11th day). The following values were obtained for dried plants: stomatal conductance = 0.26 mol m^{-2} s^{-1}, transpiration rate = 2.5 mol m^{-2} s^{-1} and photosynthesis rate = 7.8 mmol m^{-2} s^{-1}. Flooded soil reduced photosynthesis and stomatal conductance, leading to the hypertrophy of the lenticels. These parameters recovered and after this period, and plants exhibited tolerance to flooding stress by reducing their physiological activities.

Keywords: CO_2 assimilation; Hydric stress; Hypoxia tolerance.

TROCAS GASOSAS EM PLANTAS JOVENS DE Tabebuia aurea (Bignoniaceae Juss.) SUBMETIDAS A ESTRESSE POR ALAGAMENTO

RESUMO – O paratudo, *Tabebuia aurea*, é uma espécie de larga ocorrência no Pantanal de Miranda, Mato Grosso do Sul, uma área de inundação sazonal. Para determinar o grau de tolerância da espécie ao alagamento, um grupo de plantas com quatro meses de idade foi mantido em vasos alagados, além do grupo controle, com as taxas de condutância estomática, transpiração e assimilação de CO_2 determinadas durante o período de estresse (48 dias) e de recuperação (11 dias), totalizando 59 dias. Em relação aos valores obtidos, a condutância estomática, no início do alagamento, atingiu 0,33 mol m^{-2} s^{-1}, decrescendo até 0,02 mol m^{-2} s^{-1} (46º dia). No parâmetro transpiração, os valores máximos iniciais foram de 3,1 mmol m^{-2} s^{-1} e, ao final do período de estresse (47-48º dia), estavam entre 0,2 e 0,3 mmol m^{-2} s^{-1}. Quanto à assimilação de CO_2, o valor máximo inicial foi de 8,9 mmol m^{-2} s^{-1}, atingindo zero no 48º dia. Após a redução de 100% da assimilação de CO_2 (48º dia), as plantas foram retiradas da condição de alagamento (vasos drenados) e iniciaram sua recuperação (11 dias). Os valores obtidos ao final do processo foram: condutância estomática = 0,26 mol m^{-2} s^{-1}, transpiração = 2,5 mmol m^{-2} s^{-1} e assimilação de CO_2 = 7,8 mmol m^{-2} s^{-1}, indicando que o alagamento do solo reduziu a assimilação de CO_2, a condutância estomática

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e induziu a hipertrofia das lenticelas, ocorrendo a recuperação dos parâmetros avaliados após a supressão do alagamento, demonstrando tolerância da espécie ao estresse induzido, através da redução de suas atividades fisiológicas.

Palavras-chave: Assimilação de CO_2; Estresse hídrico; Tolerância a hipoxia.

1. INTRODUCTION

The study of tree species behaviour in response to hypoxic stress conditions in the soil environment is of fundamental importance with regard to the preservation or restoration of riparian formations, which are subject to seasonal flooding, because the degree of tolerance varies by species, plant age and stress intensity. Some tolerant species can survive under flooding conditions during the growth phase, whereas other, more sensitive plants die soon after the soil becomes anaerobic (PAROLIN, 2009; PAREEK et al., 2010; TAIZ; ZIEGER, 2010).

Saturating the soil with water immediately and rapidly decreases the oxygen levels available due to the low diffusion of O_2 in water. Furthermore, the poor aeration of roots decreases the absorption of water by plants. Under normal conditions, this type of phenomenon occurs frequently in areas subject to periodic flooding, such as the Pantanal wetland (a periodically flooded area). In this environment, the soil is anaerobic for periods ranging from 3 to 8 months, depending on the region, and the spaces previously occupied by air are suddenly padded with water due to flooding. Within a few hours, the oxygen available to the respiratory process disappears, and the root system of the vegetation takes on a hypoxic or anoxic environment (SCREMIN-DIAS et al., 2011).

Several researchers have studied the effects of flooding during certain periods by considering the morphological, anatomical, physiological and biochemical changes in plants, such as changes in gas exchange (MOMMER et al., 2004; EZIN et al., 2010; SCREMIN-DIAS et al., 2011; KATO; OKAMI, 2011; PARLANTI et al., 2011; among others). Stressed plants adapt to disturbances caused by hypoxia or anoxia in the root have different adaptations; the most common of these adaptation strategies being increased stomatal conductance, reducing photosynthesis, changes in transpiration rates, the inhibition of growth, the wilting and/or abscission of leaves, and reduced leaf water potential (KOZLOWSKI, 1997; PAROLIN; WITTMANN, 2010; PAREEK et al., 2010).

Flooding areas usually impose one stress of unpredictable intensity and duration on organisms due to rapid changes. The flora of flooded areas often suffer strong selection pressure that has led to the evolution of mechanisms that enable their survival in these conditions, with the most adapted species avoiding hypoxia by developing mechanisms that include physiological, metabolic and morphological plasticity (SCREMIN-DIAS et al., 2011).

The maintenance of photosynthetic rates under conditions of flooding is used as a criterion to assess tolerance to flooding. For example, Mielke et al. (2005b) showed that araticum (*Annona glabra* L.) did not exhibit significant reductions in the photosynthetic rate after 56 days of stress due to flooded soil when compared with the control group. Batista et al. (2008) showed that embaúba (*Cecropia pachystachya* Trec.) exhibited a pronounced reduction in the photosynthetic rate after 15 days of stress. These data indicate that some species can maintain their photosynthetic rates for certain periods despite drought stress, whereas others suffer from the effects of hypoxia or anoxia in the root system after a short period of time.

The Pantanal wetland, a flood plain, harbours different vegetation types that consist almost exclusively of one species (intercropping), which dominates vast expanses as a result of edaphic and/or hydrological factors. The paratudal, whose dominant tree species is the paratudo (*Tabebuia aurea* (Silva Manso) Benth. & Hook.f ex. S. Moore Bignoniaceae) (POTT et al., 2011), is an example of this type of environment found in the Pantanal of Miranda (between the different regions that make up the wetland), a flooded formation; its flooding time varies, but it remains flooded for 4 to 5 months, usually from December to March/April. However, few studies have examined the mechanisms by which species adapt to this periodic stress (SOARES; OLIVEIRA, 2009; POTT et al., 2011).

Given the importance of studies that focus on native species, the main objective of this study was to determine the degree of tolerance of *T. aurea* to artificial flooding. To this end, we examined the effect of root hypoxia on the gas exchange of *T. aurea*.

2. MATERIALS AND METHODS

T. aurea fruits were harvested from 10 trees located in the sub-basin of the Rio Miranda (Upper Paraguay River Basin) in the Pantanal of Miranda, Municipality of Corumbá, Mato Grosso do Sul, Brazil, in the region known as Passo do Lontra (19°34’37" S; 57°00’42" W).

The seeds were removed from the dried fruit and allowed to germinate in Petri dishes lined with a filter paper moistened with Captan fungicide solution (0.2%). The dishes were maintained on a laboratory bench at room temperature.

After germination, the seedlings were placed in aluminium trays containing vermiculite and irrigated daily with distilled water. When they reached a height of 7 cm, they were transplanted into black 7-kg polystyrene bags containing sifted and dry red yellow latosol as the substrate, which was obtained from the experimental development site of the campus of the Federal University of São Carlos (UFSCar), São Paulo, Brazil. The soil was sandy in texture (OM: 2.07%; pH: 4.33 $CaCl_2$; P: Resin 02 mg/cm^3; K: 0.09 emg/100 cm^3; Ca: 0.72 emg/100 cm^3; Mg: 0.56 emg/100 cm^3; Al: 0.35 emg/100 cm^3) according to analyses carried out at the Laboratory of Chemical Analysis of Soil and Plant of the Department of Natural Resources at the Centre for Agricultural Sciences UFSCar, *Campus* Araras.

Each bag received a single seedling and was maintained in a greenhouse with an average, maximum and minimum temperature of 20 °C, 25±2 °C and 15±2 °C, respectively. The relative humidity was 60 ± 10%, and the light intensity was 65%.

One hundred and twenty days after emergence, 15 of 30 total plants were subjected to water stress due to flooding the soil by placing the seedlings in plastic buckets containing 2-3 cm of water (above-ground), which was covered with dark plastic. When necessary, the water was replaced.

A completely randomized design was used for this study, with plants placed on countertops and three randomly selected individuals per group. The evaluated parameters were measured daily with a portable infrared-based CO_2 analyzer (Hoddesdon model LCA-2 CO_2); the light intensity was 1.200 µmol m^{-2} s^{-1}, and light was provided by a lamp; an aquarium containing water was placed between the light source and the plant to avoid excessive heating.

Taking into account the displacement of the plastic buckets to the reading room and the time required for this process, readings were taken from three plants during the early morning hours, usually after 7:30, and attempts were made to evaluate the same pairs of leaves for each measurement.

The P_N (Assimilation of CO_2, µmol m^{-2} s^{-1}), and (Transpiration, mmol m^{-2} s^{-1}) and gs (Stomatal conductance in relation to water vapour, mol m^{-2} s^{-1}) were measured daily using three or four registers per leaves. After the CO_2 assimilation reached a constant value, three primary leaflets that remained in the chamber were measured for a period between 10 and 20 seconds. The light compensation point was determined based on a response curve of CO_2 assimilation versus the light intensity (there was no net carbon assimilation).

The leaf water potential (Øw) was also assessed using a Scholander pressure chamber (PMS-1000, USA), and measurements were made immediately after the evaluation of gas exchange.

The experimental group was subjected to flooding for 48 days, and the water was removed on the 49th day. The experimental and control groups were measured for up to 59 days. The heights of all plants in both groups were also measured from the neck to the plant apex at the beginning and at the end of the experiment using a graduated ruler, and values are reported in centimetres.

3. RESULTS

The effect of flooding on root growth was first observed in the shoot, which exhibited arrested development and did not produce new leaves during flooding; epinasty or chlorosis signals were also observed (data not shown). The heights of control plants increased throughout the experiment, from 25 cm (beginning of the experiment) to 32 cm (end of the experiment), whereas stressed plants did not exhibit increases in height, measuring 25 cm at the beginning and end of the experiment (data not shown). Morphological changes in response to stress included the hypertrophy of lenticels

The leaf water potential ranged from -0.4 to -0.5 MPa until the 19th day. This value changed to -0.35 MPa after the 20th day and oscillated between -0.35 and -0.4 MPa thereafter until the 56th day (suppression of stress on the 49th day). The water potential again returned to the initial values thereafter (data not shown).

The light compensation point (LCP) in control and stressed plants (beginning of the experiment) was 51.4 µmol m^{-2} s^{-1}, with a maximum of 9.8 µmol m^{-2} s^{-1} at the beginning of the experiment (Figure 1).

The rate of assimilation of CO_2 (P_N) by control plants rapidly increased until reaching 200 PAR (photosynthetically active radiation); after this point, the P_N began to decrease at accelerating rates, exhibiting gradual stabilization. Stressed plants exhibited stabilization 20 and 40 days after a small increase in P_N, and the increase in PAR did not produce an increase in the P_N (Figure 1).

The assimilation of CO_2 was similar in stressed and control plants until the sixth day, varying from 7.8 and 8.9 µmol m^{-2} s^{-1}. From the 7th to the 15th day, the stressed plants exhibited P_N values that strongly oscillated between 8.5 and 2.4 µmol m^{-2} s^{-1}. In the 16th day, these values exhibited continuous decreases with some fluctuations, reaching 0.0 µmol m^{-2} s^{-1} on the 47th and 48th days (Figure 2).

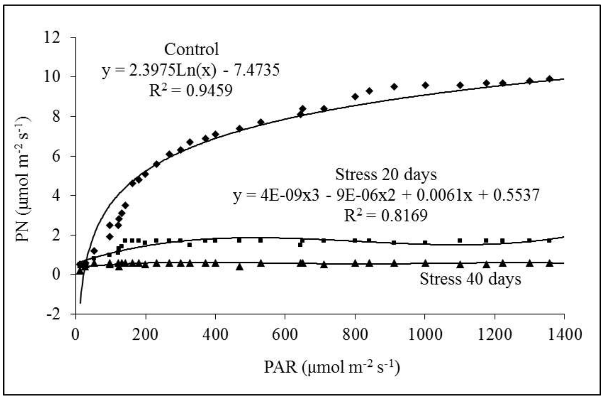

Figure 1 – CO_2 assimilation (P_N) as a function of photosynthetically active radiation (PAR) in two groups of young *Tabebuia aurea* potted plants (control and hydric stress due to flooding).

Figura 1 *– Taxa de assimilação de CO_2 (PN) em função da radiação fotossinteticamente ativa (PAR) em dois grupos de plantas jovens envasadas (controle e plantas submetidas a estresse hídrico por enchente 20 e 40 dias) de* ***Tabebuia aurea****.*

On the 49th day, the rates began to increase upon the removal of water and reached 3.7 µmol m^{-2} s^{-1}. On the 59th day, they reached similar values to those measured at the beginning of the experiment (7.8 µmol m^{-2} s^{-1}), indicating that 10 days of recovery after flooding are sufficient to allow rates to return to initial levels (Figure 2).

The stomatal conductance of flooded and control plants did not significantly differ until the 6th day of treatment, with values of 0.24 and 0.30 mol m^{-2} s^{-1}, respectively (Figure 3). After the 7th day, the conductance of stressed plants decreased to 0.12 mol m^{-2} s^{-1}, remaining between 0.05 and 0.20 mol m^{-2} s^{-1} until the 17th day. The values decreased thereafter, ranging from 0.02 to 0.08 mol m^{-2} s^{-1} until the 37th day. Between the 38th and 49th days, the values were between 0.02 and 0.05 mol m^{-2} s^{-1}, and the photosynthetic rate was minimized during this period. On the first day after the suppression of stress (49th day), the value increased to 0.07 mol m^{-2} s^{-1}, and the photosynthetic rate fully recovered to 0.26 mol m^{-2} s^{-1} on the 59th day, similar to the conductance. During this growth phase, the conductance values of individual plants require 10 days to recover, demonstrating that this parameter is resilient (Figure 3).

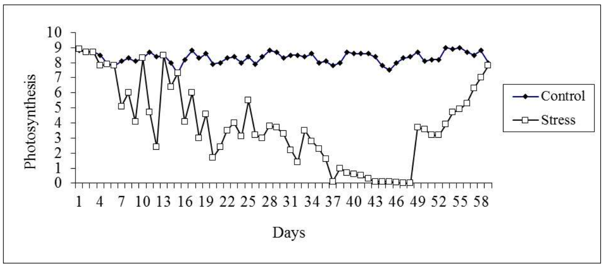

Figure 2 – Photosynthesis rates (ìmol m^{-2} s^{-1}) in the two experimental groups (control and hydric stress due to flooding) of young *Tabebuia aurea* potted plants.

Figura 2 *– Valores médios das taxas de assimilação de CO_2 (mmol m^{-2} s^{-1}) em dois grupos (estresse hídrico por excesso de água e controle) de plantas jovens envasadas de* ***Tabebuia aurea****.*

The initial transpiration values of experimental and control plants ranged from 2.4 to 3.0 mmol m^{-2} s^{-1} until the 11th day (Figure 4), but these values began to vary thereafter due to flooding. Specifically, they decreased and ranged from 2.6 to 0.6 mmol m^{-2} s^{-1} until the 35th day. Transpiration remained low after this period, with values between 0.2 and 0.3 mmol m^{-2} s^{-1} until the 48th day. On the 49th day (first day after the removal of stress), this rate reached 0.9 mmol m^{-2} s^{-1}, and it recovered to 2.5 mmol m^{-2} s^{-1} on the 59th day. Given that the water was removed on the 49th day, the transpiration rates required 10 days to completely recover, similar to the recovery period for stomatal conductance. Thus, transpiration also rapidly recovered.

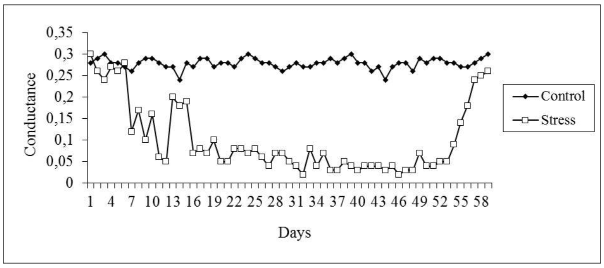

Figure 3 – Conductance rates (mol m^{-2} s^{-1}) in the two experimental groups (control and hydric stress due to flooding) of young *Tabebuia aurea* potted plants.

Figura 3 – *Valores médios de condutância (mol m^{-2} s^{-1}) em dois grupos (estresse hídrico através do excesso de água e controle) de plantas jovens envasadas de* ***Tabebuia aurea****.*

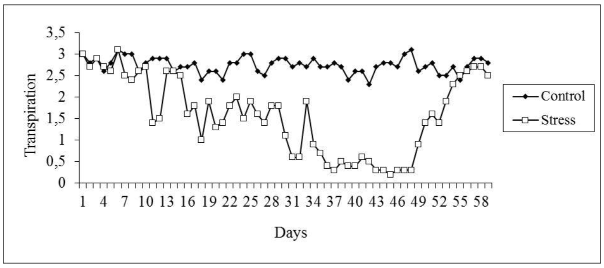

Figure 4 – Transpiration rates (mmol m^{-2} s^{-1}) in the two experimental groups (control and hydric stress due to flooding) of young *Tabebuia aurea* potted plants.

Figura 4 – *Valores médios de taxas de transpiração (mmol m^{-2} s^{-1}) em dois grupos (estresse hídrico por enchente e grupo controle) de plantas jovens envasadas de* ***Tabebuia aurea****.*

4. DISCUSSION

Normally, studies of plants growing in flooded areas indicate that the adaptation of the species permits its growth, as reported by Batista et al. (2008) for *Cecropia pachystachya*. Specifically, plants growing in a waterlogged environment maintained a growth rate equal to that displayed by plants in the control group. Similar results were cited by Kolb and Joly (2008), who studied caixeta seedlings (*Tabebuia cassinoides* (Lam.) DC) subjected to stress for different periods; they reported that the duration of flooding directly correlated with the biomass of the root system and aerial parts.

However, Davanso et al. (2002) reported different results for ipê-roxo (*Tabebuia avellanedae* Lor. ex Griseb.). Specifically, stress negatively affected on the growth of roots and leaves, but the height of plants was not affected. Conversely, Pelecani et al. (1998), demonstrated that plants of a different species stopped growing when subjected to stress, and this behaviour was also observed in *Tabebuia aurea*, indicating that some species decrease their ability to produce new structures in response to flooding.

The lack of growth in response to flooding is probably due to decreases in the availability of energy. Specifically, this strategy allows the species to prioritize what little energy generated for its maintenance, as reported by Medri et al. (2002). Responses to oxygen deficiency in the soil include stomatal closure, damage to photosystem II and a decrease in photosynthesis (KOZLOWSKI; PALLARDY, 1984; PEZESHKI, 1994).

Flooding also causes changes in the synthesis activity of the root system and consequently restricts the absorption of water and nutrients and reduces the production of certain growth hormones, such as auxins, citocianinas and gibberellins. These changes can reduce or halt growth (PEZESHKI, 1994; TAIZ; ZEIGER, 2010).

Plants in flooded soils cannot easily absorb water because flooding increases resistance to absorption. Therefore, a water deficit and a reduction in the cell turgor of the plant occur, which limits the growth of tissues (leaf expansion) (KOZLOWSKI, 1997). In accordance with Pareek et al. (2010) and Taiz and Zeiger (2010), leaf growth may also be affected by abscisic acid accumulation in the leaves and a reduction in the production and translocation of assimilates to places of greater enzyme activity.

Visual signs of chlorosis, which is common in plants experiencing root flooding, were absent in the leaves of *T. aurea* subjected to stress. This absence indicates that the species tolerates stress because intolerant plants exhibit root system death, leaf abscission, etc., which did not occur in *T. aurea*. Intolerant species undergo leaf chlorosis, as reported by Reyna et al. (2003) for soy (*Glycine max* (L.) Merr.) and Ezin et al. (2010) for the tomato (*Lycopersicon esculentum* Mill.).

The hypertrophy of lenticels observed in stressed plants also indicates flooding tolerance because this behaviour is common in tree species tolerant to this type of stress (PAROLIN, 2009). This modification is induced by endogenous ethylene, which is formed in response flooding and involves the dissolution of cell walls and cell proliferation; the hypertrophied lenticels can eliminate the ethylene that is produced and accumulated during an anaerobic state that is potentially toxic and could, for example, lead to the death of roots (HE et al., 1996; KOZLOWSKI, 1997).

However, Arruda and Calbo (2004) assessed the ability of carnaúba (*Copernicia prunifera* (Mill.) H. E. Moore), a species that occurs in flood plains, to withstand flooding stress and indicated that this species did not develop structures that could facilitate the aeration of the roots, such as pneumatophores, adventitious roots and hypertrophied lenticels. Thus, species subject to seasonal flooding exhibit different adaptive strategies.

The leaf water potential of flooded plants was similar to that reported for control plants at 5 months by Oliveira et al. (2011). The results obtained from this study indicated that the water potential of *T. aurea* is not strongly affected by flooding and remains constant. Silva et al. (2003) cited values of -0.71 MPa for control plants aged 2 months, and these values were obtained from a water-suppression experiment in Caatinga. The small differences in behaviour were likely related to the origin of plants.

The maintenance of the water potential, according to Kozlowski (1997), is due to difficulties in water absorption during flooding, which will result in a water-deficient physiological condition. Waldhoff and Furch (2002) studied seven species of the Amazon floodplain and cite that this behaviour occurs when species is subjected to flooding.

The light compensation point of control plants was similar to that reported by same by Oliveira et al. (2011) for 5-month-old plants of the same species and smaller than that described by Rocha and Moraes (1997) for six-month-old barbatimão (*Stryphnodendron adstringens* (Mart.) Coville) plants (59 µmol m^{-2} s^{-1}). These differences indicate that the photosynthetic strategies differ by environment due to differences in adaptation among species or differences in the ecological group, as indicated by Ceulemans and Saugier (1991) and Press et al. (1996).

The maximum rate of CO_2 assimilation for control plants in this study was similar to that reported by Oliveira et al. (2011) for five-month-old plants of the same species. However, the rates inversely correlated with the duration of flooding, resulting in lower values after 20 and 40 days of stress.

The initial values found for *Tabebuia aurea* were lower than those cited for Rocha and Moraes (1997) for *S. adstringens* (12.9 µmol m^{-2} s^{-1}). Franco et al. (2005) examined 11 tree species of Neotropical Savannahs (Cerrado) and reported values that demonstrate different strategies, ranging from 16.3 µmol m^{-2} s^{-1} (mandiocão-do-cerrado *Schefflera macrocarpa* (Cham. & Schltdl.) Frodin to 8.8 µmol m^{-2} s^{-1} (pau-doce *Vochysia elliptica* Mart.). This variation indicates significant diversity in the assimilation of CO_2 of these species

In accordance with Kozlowski and Pallardy (1984), flooding is one of the factors that reduces the photosynthetic rate by decreasing the efficiency with which radiation is utilized. This behaviour was observed for *T. aurea* and reported by Mielke et al. (2003, 2005ab) for *Annona glabra*, jenipapo (*Genipa americana* L.), aroeira-vermelha (*Schinus terebinthifolius* Raddi) and capororoca (*Rapanea ferruginea* (Ruiz & Pavon) Mez).

According to Pezeshki (1994), this decrease may be due to a reduction in oxygen in the rhizosphere. In accordance with Lavinsky et al. (2007) and Mielke and Schaffer (2010), the stress tolerance of the species depends on the growth stage. Furthermore, according to Dias-Filho and Carvalho (2000), plants respond differently to flooding, with this acclimation capacity possibly being determined by the efficiency of the plant in maintaining a net gain of carbon.

The type of soil used for the experiment, Red Yellow Latosol, is not found in the collection area, which features Albaqualf soil (SOARES; OLIVEIRA, 2009). The use of another type of soil may have decreased the resistance to flooding. Nevertheless, the surface layer of the soil in the study area is acidic (pH between 4.2 and 5.8), similar to the pH of the soil used in this study (4.3). Latosol also contains high levels of aluminium, which may increase the acidity of the soil via hydrolysis, which generates H^+ ions (TAIZ; ZEIGER, 2010). However, because both soils are acidic and contained Al, these factors likely did not strongly interfere with the effect of stress on the plant.

The photosynthetic rates of flooded plants gradually decreased and exhibited some oscillation during collection. This behaviour is expected because different individual plants were used for each sample. According to Medri et al. (2012), the genetic variability of the population may affect the results obtained.

Decreases in photosynthesis after the seventh day were also reported by Davanço et al. (2002), who studied flooded *Tabebuia avellanedae* plants. Other authors, such as Arruda and Calbo (2004), who examined *Copernicia prunifera*, Mielke et al. (2005b), who studied *Annona glabra*, and Batista et al. (2008), who studied *Cecropia pachystachya*, also found a reduction in photosynthesis in plants subjected to flooding, a result similar to that found for *Tabebuia aurea*.

The conductance and transpiration rates show the photosynthetic rate decreased along with others rates, indicating that CO_2 uptake expectedly depends conductance and transpiration.

A reduction in stomatal conductance can reduce the CO_2 assimilation rate, but flooding stress can directly affect the photosynthetic apparatus, irrespective of stomatal conductance. The decreases in photosynthesis in response to flooding are, among other factors, attributed to the reduction of the activity and regeneration of ribulose 1,5-bisphosphate carboxylase (rubisco) and the inhibition of CO_2 assimilation due to starch accumulation (GIBBS; GREENWAY, 2003; PAROLIN, 2009; PAROLIN; WITTMANN, 2010; PAREEK et al., 2010).

The stomatal conductance was negatively affected by flooding. Specifically, it inversely correlated with the duration of stress, which negatively affected the photosynthetic rate, as cited by Kozlowski (1997).

In accordance with Cabral et al. (2004), *T. aurea* plants exhibit stomata on both surfaces (adaxial and abaxial) and the species is consequently classified as amphistomatic, but exhibits more stomata on the abaxial surface (bottom). The same authors write that water stress may increase or decrease the number of stomata depending on the duration of stress. Fahn and Cutler (1992) indicate that the number and location of stomata are an important response to the water availability of the medium and vary by situation.

Plants that do not tolerate oxygen deficits in the soil commonly exhibit stomatal closure resulting from several factors, such as increases in the concentration of abscisic acid, ethylene synthesis or leaf dehydration. Plants that have adapted to long periods of flooding can maintain constant rates of stomatal conductance by developing structures that allow the absorption of water and soil ions, such as high porosity roots (KOZLOWSKI, 1997; GIBBS; GREENWAY, 2003; PAREEK et al., 2010). This behaviour was not observed for *T. aurea*, despite the ability of this species to maintain low conductance values for nearly two months.

The results found for *Tabebuia aurea* indicated that the species can maintain its conductance values for only the first 6 days of flooding at this stage of development. After this period, the conductance decreases. This behaviour was also reported by Oliveira et al. (2000) for gerbera plants (*Gerbera jamesonii* Adlam): conductance was significantly reduced in individuals flooded for 6 days. Furthermore et al. (2004), who studied *Copernicia prunifera*, and Batista et al. (2008), who studied *Cecropia pachystachya*, found a reduction in stomatal conductance in plants subjected to flooding, a result similar to that found in this study for *T. aurea*. Similarly, Davanso et al. (2002), who studied *Tabebuia avellanedae*, found a reduction in this parameter in plants subjected to stress.

Mielke et al. (2005b) observed an increase in the conductance of flooded *Annona glabra* plants. This increase was directly correlated with the length of the stress period, indicating that the survival of a seedling in adverse environments may be related to its ability to maintain high levels of stomatal conductance, a fact not observed for *T. aurea* during the study period. Moreover, the authors of this study reported hypertrophied lenticels, a response that may be related to improved root aeration. According Medri et al. (1998), hypertrophy allows for the uptake and diffusion of oxygen to the roots; in addition, it eliminates volatile substances, such as ethanol, which may be damaging to the plant.

The presence of lenticels due to flooding was also reported by Mielke et al. (2005a), who studied *Annona glabra*, Povh et al. (2005), who studied paineira (*Chorisia speciosa* A. St.-Hil.), and Batista et al. (2008), who studied *Cecropia pachystachya*.

Furthermore, the decrease in transpiration is expected for species qualified as sensitive to water stress. In *T. aurea*, the reduction in transpiration was directly related to the closing of the stomata, which resulted from the reduction or complete deficiency of oxygen in the soil; transpiration resumed upon the opining of the stomata (KOZLOWSKI, 1997; PAROLIN, 2009; PAROLIN; WITTMANN, 2010).

Parolin (2001) and Mielke et al. (2005ab) also reported decreases in transpiration in tree species subjected to flooding. In other species that are less tolerant to flooding, such as *Gerbera jamesonii*, six days of flooding significantly reduced the transpiration rate (OLIVELLA et al., 2000). Furthermore Davanço et al. (2002), also reported decreases in this parameter in *Tabebuia avellanedae* in response to stress.

However Arruda and Calbo (2004), who examined *Copernicia prunifera*, and Pezeshki and Anderson (1997), who studied three woody species of wetlands, did not find reductions in transpiration in plants subjected to flooding, which contradicts the results obtained for *Tabebuia aurea*.

In accordance with Chapin III et al. (1993), species adapt to adverse conditions, like flooding, by reducing the level of activity of most of its physiological functions, such as photosynthesis, conductance and transpiration. This strategy allows the plant to survive and preserve its vital activities, as observed for *T. aurea*. Because seeds disperse and germinate in September, the seedlings are established when flooding begins in December. However, the seedlings may die if they are submerged due to flooding, despite their ability to survive certain periods of flooding.

5. CONCLUSION

The responses of this species indicate that it can survive certain periods of flooding (up to 48 days) by reducing its activity levels, such as photosynthesis and conductance, and rapidly recovering after the cessation of stress. This ability is likely due to structural changes, such as the hypertrophy of lenticels and absence of vegetative growth, indicating that the species is partially tolerant to water stress, which allows it to occupy flooded areas.

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7. REFERENCES

ARRUDA, G.M.T.; CALBO, M.E.R. Efeitos da inundação no crescimento, trocas gasosas e porosidade radicular da carnaúba (*Copernicia prunifera* (Mill.) H.E. Moore). **Acta Botanica Brasilica**, v.18, n.2, p.219-224, 2004.

BATISTA, C.U.N.; MEDRI, M.E.; BIANCHINI, E.; MEDRI, C.; PIMENTA, J.A. Tolerância à inundação de *Cecropia pachystachya* Trec. (Cecropiaceae): aspectos ecofisiológicos e morfoanatômicos. **Acta Botanica Brasilica**, v.22, n.1, p.91-98, 2008.

CABRAL, E.L.; BARBOSA, D.C.A.; SIMABUKURO, E.A. Crescimento de plantas jovens de *Tabebuia aurea* (Manso) Benth. & Hook. f. ex S. Moore submetidas a estresse hídrico. **Acta Botanica Brasilica**, v.18, n.2, p.241-251, 2004

CEULEMANS, R.J.; SAUGIER, B. Photosynthesis. In. RAGHAVENDRA, A.S. **Physiology of trees**. Chichester: John Wiley & Sons, 1991. p.21-50.

CHAPIN III, F.S.; AUTUMN, K.; PUGNAIRE, F. Evolution of suites of traits in response to environmental stress. **The American Naturalist**, v.14 (supplement), p.78-92, 1993.

DAVANSO, V.M.; SOUZA, L.A.; MEDRI, M.E.; PIMENTA, J.A.; BIANCHINI, E. Photosynthesis, growth and development of *Tabebuia avellanedae* Lor. Ex Griseb. (Bignoniaceae) in flooded soil. **Brazilian Archives of Biology and Technology**, v.45, n.3, p.375-384, 2002.

DIAS-FILHO, M.B.; CARVALHO. J.R. Physiological and morphological responses of

Brachiaria spp. to flooding. **Pesquisa Agropecuária Brasileira**, v.35, p.1959-1966, 2000.

EZIN, V.; DE LA PENA, R.; AHANCHEDE, A. Flooding tolerance of tomato genotypes during vegetative and reproductive stages. **Brazilian Journal of Plant Physiology**, v.22, n.1, p.131-142, 2010.

FAHN, A.; CUTLER, D.F. Xerophytes. In: ENCYCLOPEDIA of plant anatomy. Berlin: Gebrüder Borntraeger, 1992. p.87-98.

FRANCO, A.C.; BUSTAMANTE, M.; CALDAS, L.S.; GOLDSTEIN, G.; MEINZER, F.C.; KOZOVITS, A.R.; RUNDEL, P.; CORADIN, V.T.R. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. **Trees - Structure and Function**, v.19, n.3, p.326-335, 2005.

GIBBS, J.; GREENWAY, H. Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. **Functional Plant Biology**, v.30, n.1, p.1-47, 2003.

HE, C.; FINLAYSON, S.A.; DREW, M.C.; JORDAN, W.R.; MOTGAN, P.W. Ethylene biosynthesis during aerenchyma formation in roots of maize subjected to mechanical impedance and hypoxia. **Plant Physiology**, v.112, n.4, p.1679-1685, 1996.

KATO, Y.; OKAMI, M. Root morphology, hydraulic conductivity and plant water relations of high-yielding rice grown under aerobic conditions. **Annals of Botany**, v.108, n.3, p.575-583, 2011.

KOLB, R.M.; JOLY, C.A. Germination and anaerobic metabolism of seeds of *Tabebuia cassinoides* (Lam.) DC subjected to flooding and anoxia. **Flora**, v.205, n.2, p.112-117, 2010.

KOZLOWSKI, T.T. Responses of woody plants to flooding and salinity. **Tree Physiology Monograph**, v.1, n.1, p.1-29, 1997.

KOZLOWSKI, T.T.; PALLARDY, S.G. Effect of flooding on water, carbohydrate, and mineral relations. In: KOZLOWSKI, T.T. (Org.). **Flooding and plant growth**. Orlando: Academic Press, 1984. p.165-193

LAVINSKY, A.O.; SANT'ANA, C.S.; MIELKE, M.S.; ALMEIDA, A-A.F.; GOMES, F.P.; FRANÇA, S.; SILVA, D.C. Effects of light availability and soil flooding on growth and photosynthetic characteristics of *Genipa americana* L. seedlings. **New Forest**, v.34, n.1, p.41–50, 2007.

MEDRI, M.E.; BIANCHINI, E.; PIMENTA, J.A.; DELGADO, M.F.; CORREA, G.T. Aspectos morfo-anatômicos e fisiológicos de *Peltophorum dubium* (Spr.) Taub. submetida ao alagamento e à aplicação de etrel. **Revista Brasileira de Botânica**, v.21, n.3, p.261-267, 1998.

MEDRI, M.E.; BIANCHINI, E.; PIMENTA, J.A.; COLLI, S.; MULLER, C. Estudos sobre a tolerância ao alagamento em espécies arbóreas nativas da bacia do rio Tibagi. In: MEDRI, M.E.; BIANCHINI, E.; SHIBATTA, O.A.; PIMENTA, J.A. (Eds.). **A bacia do Rio Tibagi**. Londrina: Edição dos editores, 2002. p.133-172.

MEDRI, C.; PIMENTA, J.A.; RUAS, E.A.; SOUZA, L.A.; MEDRI, P.S.; SAYHUN, S.; BIANCHINI, E.; MEDRI, M.E. O alagamento do solo afeta a sobrevivência, o crescimento e o metabolismo de *Aegiphila sellowiana* Cham. (Lamiaceae)? **Semina:** Ciências Biológicas e da Saúde, v.33, n.1, p.123-134, 2012.

MIELKE, M.S.; ALMEIDA, A.F.; GOMES, F.P.; AGUILAR, M.A.G.; MANGABEIRA, P.A.O. Leaf gas exchange, chlorophyll fluorescence and growth responses of *Genipa americana* seedlings to soil flooding. **Environmental and Experimental Botany**, v.50, n.3, p.221-231, 2003.

MIELKE, M.S.; ALMEIDA, A-A.F.; GOMES, F.P.; MANGABEIRA, P.A.O.; SILVA, D.C. Effects of soil flooding on leaf gas exchange and growth of two neotropical pioneer tree species. **New Forest**, v.29, n.2, p.161-168, 2005a.

MIELKE, M.S.; MATOS, E.M.; COUTO, V.B.; ALMEIDA, A.A.F.; GOMES, F.P.; MANGABEIRA, P.A.O. Some photosynthetic and growth responses of *Annona glabra* L. seedlings to soil flooding. **Acta Botanica Brasilica**, v.19, n.4, p.905-911, 2005b.

MIELKE, M.S.; SCHAFFER, B. Photosynthetic and growth responses of *Eugenia uniflora* L. seedlings to soil flooding and light intensity. **Environmental and Experimental Botany**, v.68, n.2, p.113-121, 2010.

MOMMER, L.; PEDERSEN, O.; VISSER, E.J.W. Acclimation of a terrestrial plant to submergence facilitates gas exchange under water. **Plant, Cell and Environment**, v.27, n.10, p.1281-1287, 2004.

OLIVEIRA, C.; BIEL, C.; VENDREL, M.; SAVÉ, R. Hormonal and physiological responses of *Gerbera jamesonii* to flooding stress. **HortScience**, v. 35, n. 2, p. 222-225, 2000.

OLIVEIRA, A.K.M.; GUALTIERI, S.C.J.; BOCCHESE, R.A. Gas exchange of potted *Tabebuia aurea* plants under hydric stress. **Acta Scientiarum Agronomy**, v.33, n.4, p.641-647, 2011.

PARLANTI, S.; KUDAHETTIGE, N.P.; LOMBARDI, L.; MENSUALI-SODI, A.; ALPI, A.; PERATA, P.; PUCCIARIELLO, C. Distinct mechanisms for aerenchyma formation in leaf sheaths of rice genotypes displaying a quiescence or escape strategy for flooding tolerance. **Annals of Botany**, v.107, n.8, p.1335-1343, 2011.

PAREEK, A.; SOPORY, S.K.; BOHNERT, H.J.; GOVINDJEE (Ed.). **Abiotic stress adaptation in plants:** physiological, molecular and genomic foundation. Dordrecht: Springer, 2010. 526p.

PAROLIN, P. Morphological and physiological adjustaments to waterlogging and drought in seedlings of Amazonian floodplain trees. **Oecologia**, v.128, n.3, p.326-335, 2001.

PAROLIN, P. Submerged in darkness: adaptation to prolonged submergence by woody species of the Amazonian floodplains. **Annals of Botany**, v.103, n.2, p.359-376, 2009.

PAROLIN, P.; WITTMANN, F. Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. **AoB Plants**, plq003, p.1-19, 2010.

PELECANI, C.R.; OLIVEIRA, L.E.M.; CRUZ, J.L. Respostas de algumas espécies florestais à baixa disponibilidade de oxigênio no meio de cultivo. I - Alterações em algumas características de crescimento. **Revista Árvore**, v.22, n.1, p.61-67, 1998.

PEZESHKI, S.R. Plant responses to flooding. In: WILKINSON, R.E. (Org.). **Plant environment interactions**. New York: Dekker, 1994. p. 289-321.

PEZESHKI, S.R.; ANDERSON, P.A. Responses of three bottomland woody species with different flood-tolerance capabilities to various flooding regimes. **Wetland Ecology and Management**, v.4, n.4, p.245-256, 1997.

POTT, A.; OLIVEIRA, A.K.M.; DAMASCENOJUNIOR, G.A.; SILVA, J.S.V. Plant diversity of the Pantanal wetland. **Brazilian Journal of Biology**, v.71, n.1, p.265-273, 2011.

POVH, J.A.; RUBIN FILHO, C.J.; MOURÃO, K.S.M.; PINTO, D.D. Respostas morfológicas e anatômicas de plantas jovens de *Chorisia speciosa* A. St.-Hil. (Bombacaceae) sob condições de alagamento. **Acta Scientiarum Biological Sciences**, v.27, n.3, p.195-202, 2005.

PRESS, M.C.; BROWN, N.D.; BARKER, M.G.; ZIPPERLEN, S.W. Photosynthetic responses to light in tropical rainforest tree seedlings. In. SWQINE, M.D. (Ed.). **Ecology of tropical forest tree seedlings**. Paris/Carnforth: Parthenon, 1996. p.41-58.

REYNA, N.; CORNELIOUS, B.; SHANNON, J.G.; SNELLER, C.H. Evaluation of a QTL for waterlogging tolerance in southern soybean germplasm. **Crop Science**, v.43, n.6, p.2077-2082, 2003.

ROCHA, A.M.S.; MORAES, J.A.P.V. Influência do estresse hídrico sobre as trocas gasosas em plantas jovens envasadas de *Stryphnodendron adstringens* (Mart.) Coville. **Revista Brasileira de Fisiologia**, v.9, n.1, p.43-48, 1997.

SCREMIN-DIAS, E.; LORENZ-LEMKE, A.P.; OLIVEIRA, A.K.M. The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. **Brazilian Journal of Biology**, v.71, n.1, p.275-282, 2011.

SILVA, E.C.;NOGUEIRA, R.J.M.C.; AZEVEDO NETO, A.D.; SANTOS, V.F. Comportamento estomático e potencial de água da folha em três espécies lenhosas cultivadas sob estresse hídrico. **Acta Botanica Brasilica**, v.17, p.231-246, 2003.

SOARES, J.J.; OLIVEIRA, A.K.M. O paratudal do Pantanal de Miranda, Corumbá-MS, Brasil. **Revista Árvore**, v.33, n.2, p.339-347, 2009.

TAIZ, L.; ZEIGER, E. **Plant Physiology**. 5. ed. Sunderland: Sinauer Associates, 2010. 690p.

WALDHOFF, D.; FURCH, B. Leaf morphology and anatomy in eleven tree species from Central Amazonian floodplains (Brazil). **Amazoniana**, v.17, n.1/2, p.79-94, 2002.