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Flooding avoidance *Triplaris gardneriana* Wedd. (Polygonaceae): growth and morpho-anatomical aspects

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ABSTRACT. The aim of this study was to analyze the effect of flooding in *Triplaris gardneriana* Wedd, cultivated in drained soil (control) and in flooded condition. The experiment was developed in a greenhouse, using plants with 90 days after the emergency. The response to treatment was evaluated at 0, 30, 60 and 90 days. Growth measurements were made, such as biomass allocation, relative growth rate (RGR). Adventitious roots were not measured only observed, as well as the development of hypertrophied lenticels. The RGR was continuously reduced along the 90 days in flooding conditions for the roots, stem and leaves, compared to control. The flooding of the substrate caused alterations such as: increasing of the cortex width and diameter of the central cylinder of root and increasing the diameter of the vessel element of the root and stem. Results show that *T. gardneriana* remains under stress when submitted to flooding. Therefore, the production of structures as lenticels, aerenchyma and adventitious roots, structures related to the avoidance of this type of stress, were key factors for the maintenance and survival of *T. gardneriana*.

Keywords: Pantanal, hypoxia, RGR, flooding.

Evitação do alagamento em *Triplaris gardneriana* Wedd. (Polygonaceae): crescimento e aspectos morfo-anatômicos

RESUMO. O objetivo deste trabalho foi analisar o efeito do alagamento em *Triplaris gardneriana* Wedd, cultivadas em condições de solo drenado (controle) e solo alagado. O experimento foi desenvolvido em casa de vegetação, utilizando-se plantas com 90 dias após a emergência. As respostas ao tratamento foram avaliadas para os períodos de 0, 30, 60 e 90 dias. Foram feitas medidas de crescimento, como alocação de biomassa, taxa de crescimento relativo (TCR). Raízes adventícias não foram medidas, apenas observadas, assim como o desenvolvimento de lenticelas hipertrofiadas. A TCR foi continuamente reduzida durante os 90 dias em condições de inundação para as raízes, o caule e as folhas em relação ao controle. O alagamento do substrato provocou alterações anatômicas como aumento da largura do córtex e do diâmetro do cilindro central da raiz e aumento do diâmetro dos elementos de vaso do caule e da raiz. Nossos resultados indicam que *T. gardneriana* permanece em estresse quando submetida a inundações. No entanto, a produção de estruturas relacionadas à evitação deste tipo de estresse foi chave para a manutenção e sobrevivência de *T. gardneriana*.

Palavras-chave: Pantanal, hipoxia, TCR, alagamento.

Introduction

The flooding process can be a high stress factor, playing a limiting role in the distribution of the arboreal vegetation (Lüttge, 1997), once the excess of water interferes in the vigor and growth of the non-adapted plants (Crawford, 1992; Schueler & Holanda, 2000).

The restrictions to plant development induced by flooding result from the low availability of oxygen in the roots, causing changes in the metabolism and concentration of phytotoxins, besides the increase of anaerobic decomposition of the organic matter and the availability of potentially toxic mineral substances (Schluter & Crawford, 2001; Visser, Voesenek, Vartapetian, & Jackson, 2003; Bailey-Serres & Voesenek, 2008).

Thus, the wetlands are occupied by plants tolerant to variable periods of flooding, because these plants compensate the anaerobic conditions of the soil by developing protection mechanisms, reducing the harmful effects in conditions of hypoxia and anoxia (Benz, Rhode, & Cruzan, 2007). Such mechanisms consist in morphological (Parolin et al. 2004) and physiological adaptations (Armstrong, Brandle, & Jackson, 1994).

However, the sensitivity to flooding can vary with the type, duration and intensity of the stress, as well as the stage of development of the plant. Even just considering the tropical plants, there is great diversity of responses in arboreal species to the seasonal flooding of the soil (Parolin et al. 2004; Duarte et al. 2005; Ferreira, Piedade, Junk, & Parolin, 2007).

The specie of the family Polygonaceae, *Triplaris gardneriana* Weed is a tree commonly found in Pantanal, Center-West of Brazil, subject to regular and intense flooding, and which remains partially submerged most of the year (Damasceno-Junior, Semir, Santos, & Leitão-Filho, 2005). These flooding conditions expose *T. gardneriana* species to distinct microhabitats with a greater period of flooding, resulting in a high tolerance degree to this condition.

Once that *T. gardneriana* is distributed in natural and seasonally flooded areas of Pantanal, our hypothesis is that the flooded soil induces responses that enable this specie to tolerate and/or avoid the stress imposed by flooding. This study evaluated whether: (1) Seedlings of *T. gardneriana* kept in water saturation conditions of the soil survive and present changes in growth; (2) Plants of *T. gardneriana* kept in flooded soil produce structures related to the stress avoidance to hypoxia. By understanding the adaptive mechanisms of plants, we enrich the knowledge on the strategies of plants to flooding, particularly at a phase of seedlings/saplings, critical stage for the establishment of plants (Junk, 1993).

Material and methods

Plant material and treatments

Seeds of *T. gardneriana* were collected in 15 matrixes approximately 10 km apart, in order to avoid the collection of seeds from a single population, sub-region of Abobral and Miranda (19°30'S, 57°04'W), Mato Grosso do Sul, Brazil. The fruits from the distinct matrixes were homogenized to obtain a single lot, and the seeds were set to germinate in Styrofoam trays containing organic soil (60% pinus bark, 15% fine grade vermiculite, 15% superfine grade and 10% humus).

A total of 90 plants were used and transferred at 10 days and around 3 cm tall to plastic vases of 3.5 liters (one plant per vase) containing organic soil, with no addition of fertilizers. After a period of 30 days acclimatization in a greenhouse, the experiment started, in a totally random design, with 45 plants kept in flooded soil and 45 control plants in drained soil. The plants flooded for 90 days were kept with a 2 cm water level above ground, and the control plants were irrigated by aspersion twice a day.

Plant growth

At 0, 30, 60 and 90 days after the flooding of the soil, the number of new leaves were counted and length of the stem was measured with the aid of a measuring tape and the diameter of the stem in the region of the lap with a digital caliper. For the study of plant growth and development, ten control plants and ten plants flooded were separated in roots, stem and leaf and were used in the beginning of the experiment and after 30, 60 and 90 days of flooding. These organs were dried in an oven at 70°C for 72 hours, time enough to reach constant weight. Each part of the plant was weighed in a semi-analytical scale, and the total biomass was calculated by the sum of the mentioned biomass categories. From this value, the relative growth rate (RGR) was calculated according to the procedures indicated by Benincasa (2003).

The leaf area (LA) of the first completely expanded leaf was obtained after 30, 60 and 90 days of the treatments. The LA was obtained through photography from a digital camera, Sony brand model W110, using a millimeter sheet as measurement referential. The images were processed using the program Sigma Scan Pro v. 5.0, Jandel Scientific (1991). From the values of LA and the dry mass of leaves, the specific leaf area (SLA) was obtained according to the formula described by Benincasa (2003).

Anatomy

For the anatomical study, five plants were separated from each treatment, fixated in FAA 50 (Johansen, 1940) at 90 days experiment. Free hand transversal cuts were made in the root and lap of the stem with the aid of a steel blade, the sections were clarified in sodium hypochlorite 20%, stained with safranin/astra blue (Kraus & Arduin, 1997), and fixed in glycerin 50% (Johansen, 1940).

The sections were analyzed in a light microscope and with the aid of a micrometric ocular the stem's cortex and the cortex of the pivoting root were analyzed. Thus, we obtained the width of the cortex, diameter central cylinder and the diameter of the vessel elements. The differential qualitative anatomical characters, obtained for the control and flooded plants were documented in a Leica DC 300F system of microscope image capture.

Statistical analysis

ANOVA was used to establish variance and the comparison between medium values used Tukey's test at 5% of probability. Statistical analyses were performed in R version 3.0.2 (R Development Core Team, 2013).

Results

Plants of *T. gardneriana* survived the 90 days of experiment and exhibited a considerable tolerance to flooding. There were no significant differences between plants growth with 0, 30 and 90 days of flooding ($p > 0.05$). The length of the stem and diameter of the stem's base and the number of leaves were greater in the control individuals (Table 1).

Table I. Means (± standard deviation) for *Triplaris gardneriana*, comparing control and flooded plants in three successive months. *p < 0.05 (n = 10).

Days	Treatment	Growth(cm)	Stem diameter (mm)	N°. of leaves
0	-	4.04 ± 0.80	1.19 ± 0.07	4.85 ± 0.65
30	Control	12.15 ± 3.12	3.45 ± 0.50	9.25 ± 0.69
	Flooded	5.14 ± 1.53***	1.99 ± 0.97***	6.9 ± 1.18
60	Control	20.03 ± 4.34	4.71 ± 0,29	9.25 ± 2.03
	Flooded	7.39 ± 3.86***	2.25 ± 0.90***	5.95 ± 2.71
90	Control	20.05 ± 6.71	5.37 ± 0.86	9.55 ± 2.72
	Flooded	7.79 ± 3.83***	2.33 ± 0.98***	5.9 ± 2.73

Triplaris gardneriana presented chlorosis at 30 days of flooding. The RGR was lower in flooding conditions, presenting significantly lower values ($p < 0.05$) for the root, stem and leaves (Table 2).

Table 2. Mean ± standard deviation of the relative growth rate (RGR) of the root, stem and leaves of *Triplaris gardneriana*. Numbers followed by equal letters in the columns showed no statistical differences (Tukey 5%), *n* = 10.

Days	Treatment	Root	Stem	Leaves
30	Control	0.01 ± 0.006 a	0.008 ± 0.003 a	0.192 ± 0.60 a
	Flooded	0.001 ± 0.002 b	0.001 ± 0.001 b	0.026 ± 0.01 b
60	Control	0.028 ± 0.009 a	0.018 ± 0.007 a	0.06 ± 0.05 a
	Flooded	0.001 ± 0.001 b	0.001 ± 0.010 b	0.000 ± 0.00 b
90	Control	0.03 ± 0.013 a	0.018 ± 0.008 a	2.02 ± 6.06 a
	Flooded	0.001 ± 0.002 b	0.001 ± 0.002 b	0.0001 ± 0.05 b

Compared to the control plants, the values of LA were significantly inferior in the flooded plants after 30 and 90 days of flooding (Figure 1). The flooding for 30 and 90 days induced increase in the SLA in plants of *T. gardneriana* (Figure 1) kept in flooded soil when compared to the control plants.

There were changes in the percentage of dry biomass of *T. gardneriana* kept under flooding (Figure 2). The flooded plants of *T. gardneriana* invested 35% of biomass in leaves, 33% roots and 32% stem; and the control plants invested 29% in leaves, 25% in stem and 46% in roots.

Flooding induced the formation of adventitious roots, longitudinal fissures and hypertrophy of lenticels with a mass of spongy tissue in the lap region after 10 days of flooding in *T. gardneriana* (Figure 3).

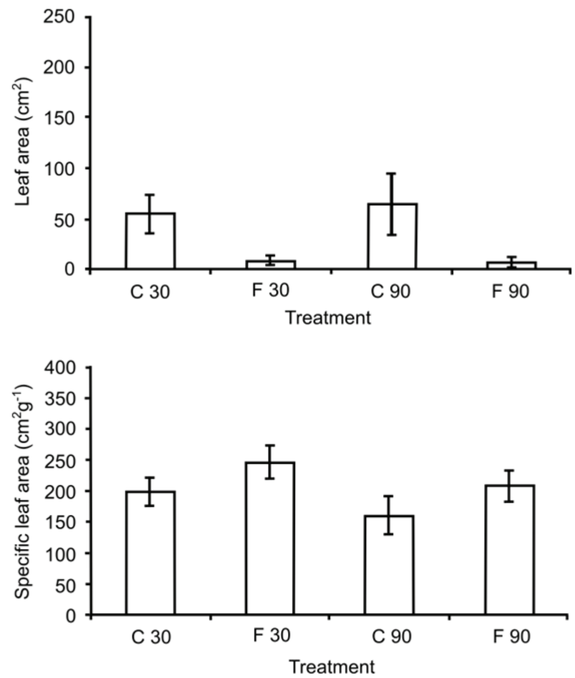

Figure 1. Means of leaf area ($p < 0.001$, n = 10) and specific leaf area ($p < 0.05$, *n* = 10) of *Triplaris gardneriana* under control (C) and flooded plants (F) at 30 and 90 days.

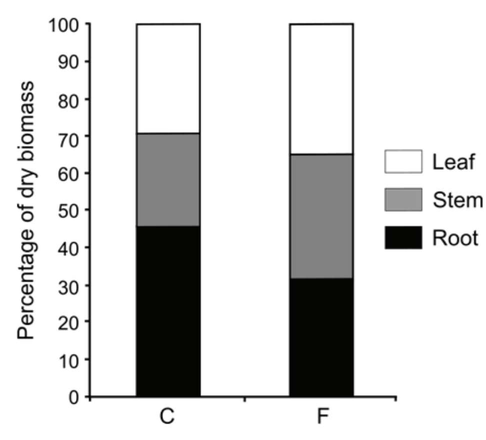

Figure 2. Percentage of dry biomass of the vegetative organs in the control plants (C) and flooded plants (F) of *Triplaris gardneriana* at 90 days of the experiment.

In the parenchyma cells of roots in plants kept in flooded soil, there was a decrease in the starch reserve (data not shown). The analysis of the transversal sections of the stem and root of *T. gardneriana* showed that the flooding of the substrate induced the decrease of some anatomical structures (Table 3) such as: width of the cortex and diameter of the central cylinder of root and diameter of the vessel element of root and stem.

Figure 3. *Triplaris gardneriana* after 90 days of experiment. (A) *T. gardneriana* grown in drained soil. (B) *T. gardneriana* grown in flooded soil, with development of hypertrophied lenticels (arrow 1) and adventitious roots (arrow 2)

Table 3. Mean ± standard deviation of anatomical traits of the main root and the stem of *Triplaris gardneriana* grown in drained soil – control plant (C) and flooded soil (F) for 90 days. The t test was applied at a level of 5% probability (n = 5).

Anatomical traits (μm)	C	F
Width of the root cortex	860 ± 100 a	400 ± 90 b
Width of the stem cortex	840 ± 120 a	810 ± 140 a
Diameter central cylinder of the root	1760 ± 120 a	960 ± 60 b
Diameter central cylinder of the stem	2110 ± 240 a	2040 ± 190 a
Diameter elements of vessel of the root	33.75 ± 2.5 a	25 ± 0.75 b
Diameter elements of vessel of the stem	37.5 ± 2.5 a	23.75 ± 2.75 b

Discussion

Although our results indicate that the *T. gardneriana* plants are capable of surviving for considerable periods of flooding, such condition seems to be prejudicial to the development. Flooding reduced the growth of the plants studied in all of the morphological variables measured, which can be a reflection of oxygen reduction for the roots, preventing the plants from absorbing water and nutrients and from synthesizing hormones as cytokines (Jackson, 1993).

The results of LA and SLA indicate increase in thickness of leaves in detriment of the expansion of the leaf area in the flooded plants. These responses can be important for the water economy of the plant (Batista, Medri, Bianchini, Medri, & Pimenta, 2008). Some studies pointed water deficit in flooded plants due to the lower water absorption caused by modifications in permeability of membranes in the cells of the roots, in consequence of the hypoxic environment, resulting in lower water conductivity in the roots (Else, Coupland, Dutton, & Jackson, 2001). The duration of flooding affected the biomass of the leaf, stem and root of the flooded plants, since it slowed the productivity in response to the flooding, compromising the growth of vegetative organs. According to Lobo and Joly (1995) the species tolerant to flooding have the capacity of maintaining biomass of the aerial part during the flooding period, as seen for *T. gardneriana* during the 90 days of experiment. However, flooding is a condition of stress for these species, since there was a deviation from the optimum (Larcher, 2004), indicated by the significantly different values between the control and flooded plants.

The decrease in RGR of the leaf, root and stem of *T. gardneriana* kept in flooded soil may be showing the lowest quantity of energy available, and this decrease is caused by the deviation in the metabolic pathways of glucose to fermentation pathways, which results in the reduction of energy levels (Crawford & Braendle, 1996). That may lead to the loss of biomass, as response to the reduction in availability of carbohydrates due to change from aerobic to anaerobic respiration, which is energetically less efficient than the aerobic route (Crawford & Braendle, 1996).

The formation of adventitious roots, aerenchyma and hypertrophied lenticels is strongly associated with the survival of *T. gardneriana*. Such responses are common in species tolerant to flooding of the soil (Parolin, 2001) and described as enablers of oxygen transportation to the roots, contributing to the recovery and maintenance of aerobic respiration in flooded plants (Ferreira, Piedade, Franco, & Junk, 2009; Suralta & Yamauchi, 2008; Colmer, 2003; Finlayson, 2005). In addition, hypertrophied lenticels can enable the elimination of potentially toxic components produced during anaerobiosis, such as ethylene, ethanol and acetaldehyde (Kozlowski, 1997). Similar responses were reported for several aquatic species or the ones that live in flooded areas, such as *Myriophyllum spicatum* (Xie, Ren, & Li, 2007), *Himatanthus sucuuba* (Ferreira et al., 2009) and *Calophyllum brasiliense* (Oliveira & Joly, 2010). According to Armstrong (1968) the capacity presented by several species of surviving under such conditions depends partially or totally on the capacity of production and on the activity of these structures.

Triplaris gardneriana showed lower quantity of starch in flood plants. According to Kolb et al., (1998) the decrease in starch reserves of the cortical parenchyma during flooding can be related to the large demands of carbohydrates required for the development of the observed morpho-anatomical structures, in addition to the need of maintaining the anaerobic metabolism, which demands high energy rate (Koslowski, 1997; Crawford & Brandle, 1996). Species such as *Lithraea molleoides* (Medri et al., 2007) and *Guibourtia hymenifolia* (Santiago &

Paoli, 2007) have also presented lower quantity of starch reserve in plants kept in flooded soil.

The lower diameter of the vessel elements of the main root and stem in flooded plants of *T. gardneriana* can be related to the process of avoiding embolism and ensuring the water flow, once the flooding can reduce the absorption of water by the plant (Coutts, 1981).

Conclusion

The survival of the plants during the 90 days experiment is an indication of the maintenance of the minimal metabolic rate, resulting in the survival of the plants. The results show faster responses to flooding for the species *T. gardneriana*, as it is demonstrated with the production of lenticels and adventitious roots at 10 days of experiment, with a greater biomass and growth. These responses can be related to the plant's distribution in the field since they occupy areas with longer flooding. Therefore, this species present adaptive mechanism that characterizes its local distribution, with greater exposure to flooding, although the energy production generated is larger during the normoxia period.

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