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Tolerance to waterlogging in young *Euterpe oleracea* plants

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Abstract

This study investigated whether gas exchange and the present content of antioxidant compounds can contribute to the survival of *Euterpe oleracea* plants in environments of frequent waterlogging. A factorial randomised, experimental design included two distinct water conditions (waterlogging and control) and five evaluation times (0, 6, 12, 18, and 24 d). Gas-exchange parameters, leaf temperature, electrolyte leakage, and contents of antioxidant compounds were measured. Waterlogging did not promote significant alterations in net photosynthetic rate and transpiration, and stomatal conductance was reduced only after 18 d. Malondialdehyde and glutathione contents did not significantly change during waterlogging. Additionally, electrolyte leakage was significant only after 18 d of waterlogging. Thus, this study revealed that maintenance in gas exchange and antioxidant compounds might contribute to the survival of *E. oleracea* plants in environments exposed to waterlogging.

Additional key words: abiotic stress; açaí palm; ascorbate; glutathione; photosynthesis; submergence.

Introduction

E. oleracea (Mart.), an Amazonian palm, is of economic importance due to the production of energy drinks, which are produced from its fruit and stem, respectively (Rogez 2000, Bobbio *et al.* 2002). The fruits contain high amounts of lipids and minerals, such as K, Ca, and Mg (Menezes *et al.* 2008, Yuyama *et al.* 2011). Additionally, a study conducted by Bobbio *et al.* (2000) revealed that the fruit is the important source of anthocyanins. Brazil is the main producer of *Euterpe oleracea* and is also an important consumer and exporter of the products derived from this palm (Rogez 2000).

Flooding promotes typical alterations in the biochemistry, physiology, anatomy, and morphology of plants (Fante *et al.* 2010, Henriquel *et al.* 2010, Cortezi and Colli 2011, Alves *et al.* 2012). The main problem of soil flooding is the limited oxygen available to root systems. Water soil saturation eliminates the spaces previously occupied by air, which limits root respiration (Drew 1997, Bailey-Serres and Voesenek 2008). Other effects on root systems include increased porosity (Przywara and Stepniewski 1999) and biomass loss (Mielke *et al.* 2003).

Stomata closure is frequently observed in waterlogged plants and is associated with decreased water conductivity in the roots (Davies and Flore 1986). Additionally, gas exchange declines (Dias-Filho 2002, Bertolde *et al.* 2012), thereby it affects negatively net photosynthesis (Liao and Lin 2001) and transpiration (Du *et al.* 2012). However, when exposed to waterlogging, species, such as *Zea mays* (de Souza *et al.* 2009) and *Oryza sativa* (Nishiuchi *et al.* 2012), exhibit morpho-anatomic modifications that promote the survival of these plants under hypoxic or anoxic conditions (Armstrong *et al.* 1994).

Plants exposed to waterlogging may be damaged at the cellular level, mainly when increased production of reactive oxygen species (ROS) occurs. ROS at high concentrations can modify the structures and functions of organelles like chloroplasts, and cause irreversible metabolic dysfunctions leading to cell death (Pereira *et al.* 2010).

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Abbreviations: ASC – ascorbate; C_i – intercellular CO_2 concentration; CT – control; DWT – days after waterlogging; *E* – transpiration rate; EL – electrolyte leakage; g_s – stomatal conductance to water vapor; GSH – glutathione; MDA – malondialdehyde; PEPC – phospho*enol*pyruvate carboxylase; P_N – net photosynthetic rate; P_N/C_i –instantaneous carboxylation efficiency; ROS – reactive oxygen species; Rubisco – ribulose-1,5-bisphosphate carboxylase/oxygenase; RuBP – ribulose-1,5-bisphosphate; TBA – thiobarbituric acid; T_L – leaf temperature; WT – waterlogging treatment; WUE – water-use efficiency.

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The antioxidant system of plants includes enzymes and nonenzymatic compounds, such as ascorbate and glutathione, both of which contribute to ROS elimination.

In the Amazonian forest, trees and other plants are exposed to partial or total submersion for up to seven months of each year (Junk 1989). The species that are able to survive there possess waterlogging tolerance mechanisms. A study of Menezes Neto *et al*. (1995) reported modifications to anaerobic metabolism, but the number of investigations on physiological responses and antioxidant systems remains limited. Our study aimed to investigate whether gas exchange and antioxidant compounds can contribute to the survival of *E. oleracea* in environments with frequent waterlogging.

Materials and methods

Location and growth conditions: The experiment was performed on the Campus of Paragominas of the Universidade Federal Rural da Amazônia, Paragominas city, Brazil (2º55'S and 47º34'W) in a greenhouse without an environment control. The minimum, maximum, and median temperatures were 22, 37, and 26º C, respectively (Fig. 1). The relative humidity during the experimental period varied between 65 and 93%. During the measurement period (12:00 h), the photosynthetically active radiation varied between 451 and 1,453 µmol(photon) m^{-2} s^{-1}.

Plants: Seeds of *E. oleracea* (Mart.) were germinated in 8-L pots (0.25 m high, 0.20 m in a diameter) equipped with holes for water drainage. The pots were filled with *Plantmax*® substrate (*Buschle & Lepper*, Brazil), and the plants were irrigated daily with 1 L of distilled water. After 100 d, seedlings of similar appearance and size were selected. Subsequently, 120-d-old seedlings received 0.2 L of nutrient solution (Hoagland and Arnon 1950), with this solution being applied at regular intervals (every 30 d) until the plant age of 12 months.

Experimental design: The experiment employed a factorial randomised design with two distinct water conditions (waterlogging and control, being described as WT and CT, respectively) and five evaluation times (0, 6, 12, 18, and 24 d), making a total of 10 measurements. The experiment was assembled with 5 replicates in a total of 50 experimental units, with one plant in each unit.

Waterlogging treatment and harvest: All plants were grown until the age of 12 months as described above. Subsequently, the plants were submerged in water for 24 consecutive days during WT. The water level was maintained at 5 cm above the root collar and it was adjusted as necessary. To implement WT, large 25-L pots were used (0.30 m height and diameter) without drainage holes. The young plants were repotted into the larger pots and then WT was initiated. Plants subjected to CT were watered daily with distilled water. Parameters associated with gas exchange were measured during each evaluation period. Additionally, the leaves in the middle of the plant were harvested and frozen in liquid nitrogen, being stored at –20°C for subsequent biochemical determinations.

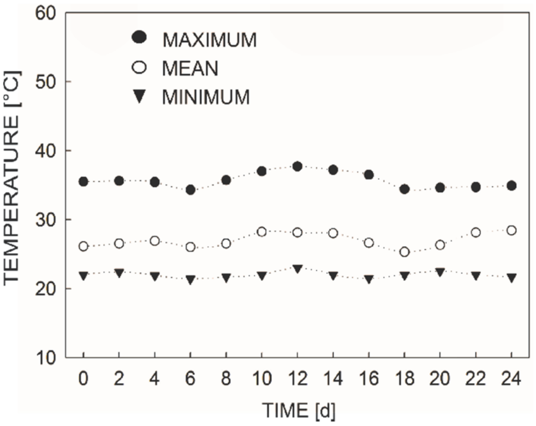

Fig. 1. Maximum, mean, and minimum temperatures during the experimental period.

Leaf gas exchange: Stomatal conductance (g_s), intercellular CO$_2$ concentration (C_i), net photosynthetic rate (P_N), transpiration rate (E), and leaf temperature (T_L) were evaluated using an infrared gas analyser (*ADC Bioscientific*, *model LCPro*$^+$, England). These parameters were measured at the adaxial surface of fully expanded leaves, localised in the middle region of the plant. The water-use efficiency (WUE) was estimated according to Ma *et al*. (2004), and the instantaneous carboxylation efficiency (P_N/C_i) was calculated using the formula described by Aragão *et al*. (2012). Gas exchange was evaluated in all plants between 9:00 and 12:00 h. The irradiance was maintained at 800 µmol m^{-2} s^{-1} during the measurements.

Electrolyte leakage (EL) was measured using the method described by Gong *et al*. (1998) with minor modifications. Fresh leaves (200 mg) were cut into 1-cm-long pieces and placed in containers containing 8 mL of distilled deionised water. The containers were incubated in a water bath at 40°C for 30 min, and the initial electrical conductivity of the medium (EC$_1$) was measured using a conductivity meter (*QUIMIS*, *model Q795A*, Brazil). The samples were boiled at 95°C for 20 min to release all electrolytes. After the samples were cooled, the final electrical conductivity (EC$_2$) was measured (Gong *et al*. 1998). The percentage of EL was calculated using the formula EL (%) = EC$_1$/EC$_2$ × 100.

Sample preparation: Samples for analysis of malondialdehyde (MDA), ascorbate (ASC), and glutathione (GSH) were extracted as described by Wu *et al.* (2006). The extraction mixture was prepared by homogenising 500 mg of fresh leaf matter in 5 mL of 5% (w/v) trichloroacetic acid. Subsequently, the samples were centrifuged at 15,000 × *g* for 15 min at 3°C, and the supernatants were collected.

MDA content was determined by mixing 0.5 mL of supernatant and 1 mL of the reaction mixture containing 0.5% (w/v) thiobarbituric acid (TBA) in 20% trichloroacetic acid. This mixture was incubated in boiling water at 95°C for 20 min, and the reaction was stopped by placing the reaction containers in an ice bath. The samples were then centrifuged (*Marconi*, *model MA1805*, Brazil) at 10,000 × *g* for 10 min prior to measurement of the absorbance at 532 nm. The value for nonspecific absorption at 600 nm was subtracted using a spectrophotometer (*Femto*, *model 700 plus*, Brazil). The amount of MDA–TBA complex (red pigment) was calculated using an extinction coefficient of 155 $\mathrm{mM^{-1}\ cm^{-1}}$, as reported by Cakmak and Horst (1991)

ASC: The assay mixture for ASC detection contained 0.2 mL of supernatant and 1.8 mL of reaction mixture described by Cakmak and Marschner (1992) with minor changes. The reaction mixture was prepared in 100 mM phosphate buffer (pH 7.6) and it was composed of 0.4 mL of 10% trichloroacetic acid, 0.4 mL of 44% orthophosphoric acid, 0.4 mL of 4% 2,2'-dipyridyl in 70% ethyl alcohol, and 0.2 mL of 3% $\mathrm{FeCl_3}$. This mixture was incubated at 40°C for 40 min, and the resulting color intensity was measured at 525 nm.

GSH: 0.2 mL of supernatant, 1.8 mL of reaction mixture containing 100 mM phosphate buffer (pH 7.6), and 0.6 mM 2-nitrobenzoic acid were combined, and the absorbance was measured at 412 nm (Wu *et al.* 2006).

Statistics: The data were subjected to variance analysis, and significant differences between means were determined using the *F* test at the 5% error probability level (Steel *et al.* 2006). The standard deviations were calculated for each treatment at all evaluation points. A correlation analysis was performed using the *Pearson*'s parametric method. The statistical analyses were performed using *SAS* software.

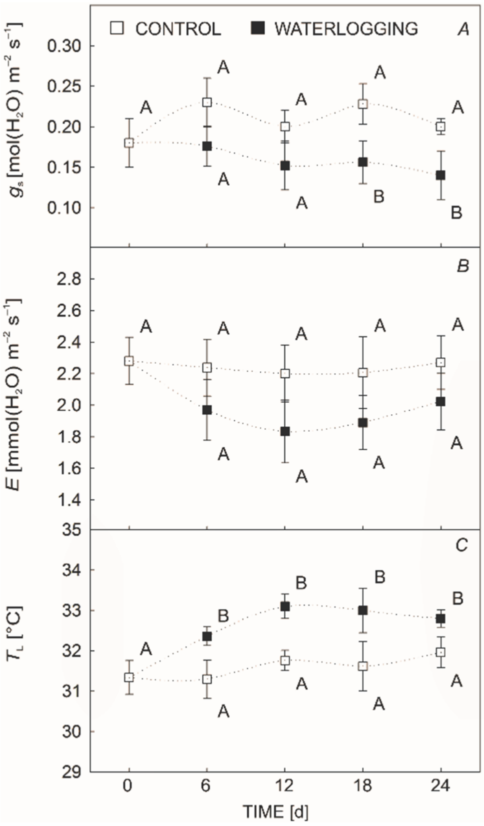

Fig. 2. *A*: Stomatal conductance (g_{s}), *B*: transpiration rate (*E*), and *C*: leaf temperature (T_{L}) in young *Euterpe oleracea* plants subjected to waterlogging. *The same letters* show insignificant differences at *F*-test ($P<0.05$) to each time. Means ± SD, $n = 5$.

Results

***g*s, *E*, and *T*L**: g_{s} was reduced due to WT, although a significant effect was observed only after 18 and 24 days after waterlogging (DWT) (Fig. 2*A*). Compared with CT, the greatest decrease of approximately 31% was observed on 18 DWT. Although the differences in the g_{s} were significant, WT induced only insignificant decrease in *E*, and the difference was more intense on 12 DWT (Fig. 2*B*). WT promoted a significant increase in the T_{L} from 6 to 24 DWT (Fig. 2*C*). The greatest difference in this parameter was observed after 18 DWT, being 4%, compared with CT.

***P*N, *C*i, WUE, and *P*N/*C*i**: WT did not promote any significant alteration in P_{N}. However, WT reduced P_{N} by approximately 16–19% starting 6 to 24 DWT, respectively, compared with CT (Fig. 3*A*). C_{i} in plants was not significantly different under WT compared with CT. The reductions observed on all days were approximately 4% (Fig. 3*B*). WT resulted in variable WUE; the insignificant increase was observed after 6 DWT, and the insignificant decrease was observed on 12 until 24 DWT (Fig. 3*C*) relative to the CT plants. The difference was approximately 8%, being observed on 12 DWT. In contrast, the $P_{\mathrm{N}}/C_{\mathrm{i}}$ was not affected by WT. Additionally, decrease of about 18% appeared on 18 DWT compared with the CT (Fig. 3*D*).

EL and MDA, GSH and ASC contents: EL increased significantly during 18 and 24 DWT. The greatest increase (9%) relative to the CT was observed on 18 DWT (Fig. 4*A*). The MDA content was not affected by WT (Fig. 4*B*). The greatest increase was observed on the 24 DWT (approximately 15% greater than that of the CT). The content of ASC decreased by WT and this decrease was significant from the 6 DWT; the greatest difference (18%) compared with the CT was observed after 12 DWT (Fig. 4*C*).

WT did not affect the GSH contents (Fig. 4*D*). The most intense decrease (8%) relative to the CT plants was observed after 24 DWT.

Discussion

A decrease in g_s induced by WT is associated with decreased water absorption and also due to a reduction in the length of the contact surfaces of the root system. In other words, WT decreases root aeration. Consequently, the tissue suffers fermentation and reduced water transport into the root (Kozlowski 1997). Additionally, a decrease in g_s is one of the first responses of plants to WT (Dat *et al.* 2006). Decreased g_s in WT plants was also reported in *Cecropia pachystachya* by Batista *et al.* (2008).

The observed decline in *E* of WT plants could be attributed to a decreased assimilation of water into the plants, as WT reduces the oxygen availability (Wegner 2010) and hydraulic conductivity in root systems (Islam and McDonald 2004). The decrease in *E* is also related to stomata closure, which is observed after WT (Reis *et al.* 2007). Our results were consistent with those of Martinazzo *et al.* (2013), who studied *Prunus salicina* subjected to WT.

The increase in T_L could be explained by the decrease in *E*, as WT decreases water absorption *via* the roots and it consequently affects negatively plant thermoregulation (Jones 1998). Martínez-Alcántara *et al.* (2012) reported a decrease in the amount of root matter in waterlogged *Citrus*.

The only insignificant decline in P_N suggested that *E. oleracea* is tolerant to WT and that the observed decrease was associated with reduced g_s; consequently, the supply of CO_2 for P_N was limited. Medri *et al.* (2012) suggest the decrease in P_N as a response to oxygen deficiency in flooded soil. Similar results consistent with those of the present study were reported by Calbo *et al.* (1998) in *Mauritia vinifera*.

In the present study, C_i decreased by WT in *E. oleracea*, although the change was not significant. This effect was probably linked to the lower g_s and consequently limited CO_2 availability. Naeem *et al.* (2010) reported similar results for this parameter in *Brassica napus* exposed to salt stress.

An increase in WUE is observed in plants subjected to mild or moderate stress, which indicates a strong decrease in *E*. Conversely, a decrease in this parameter was associated with decreased $P_{N,}$ because the efficiency of water use is proportional to P_N. Similar results have been presented by Leiblein and Lösch (2011) in *Ambrosia artemisiifolia* subjected to WT.

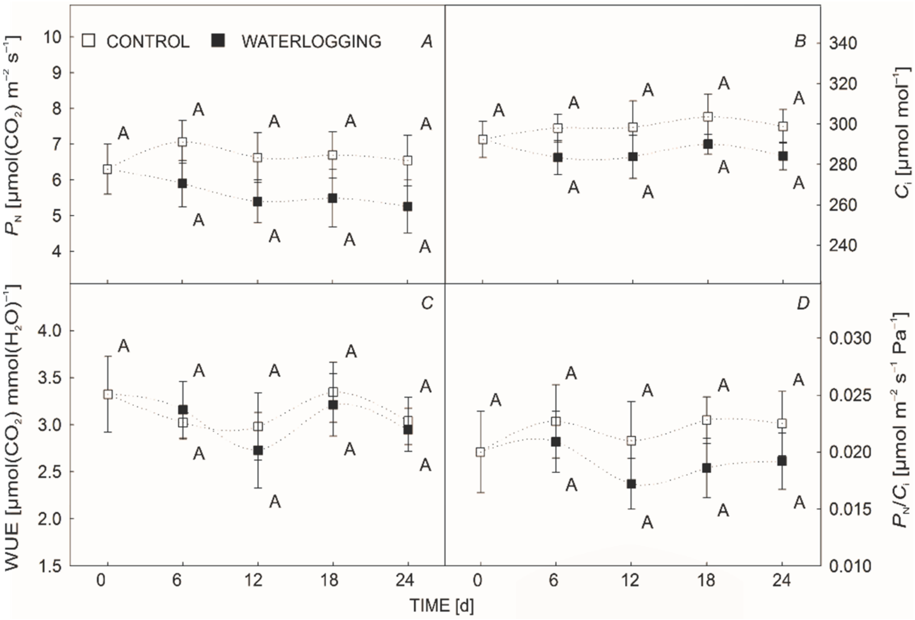

Fig. 3. *A*: Net photosynthetic rate (P_N), *B*: intercellular CO_2 concentration (C_i), *C*: water-use efficiency (WUE), and *D*: carboxylation instantaneous efficiency (P_N/C_i) in young *Euterpe oleracea* plants subjected to waterlogging. *The same letters* show insignificant differences in *F*-test ($P<0.05$) at each time. Means ± SD, $n = 5$.

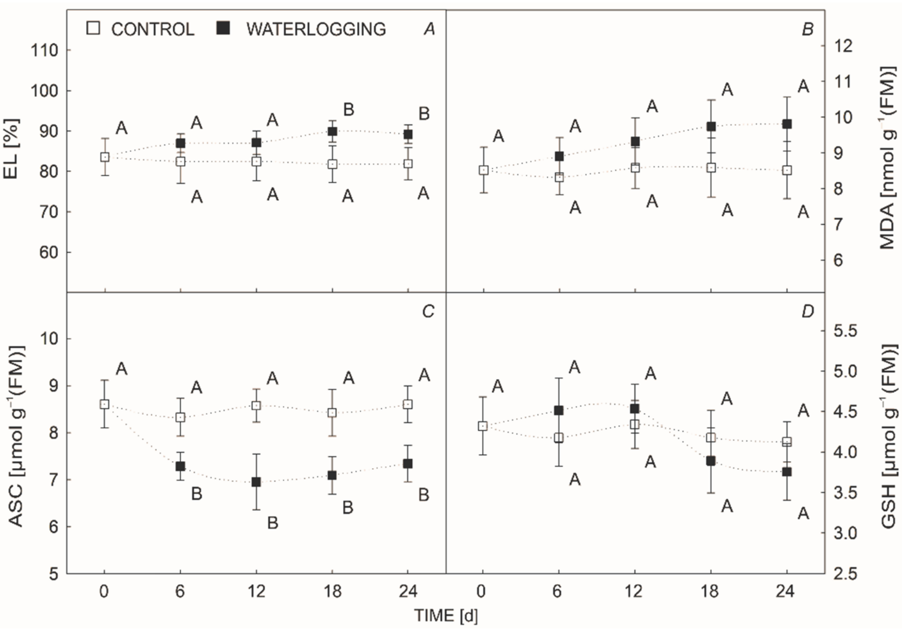

Fig. 4. Electrolyte leakage (*A*), malondialdehyde (*B*), ascorbate (*C*), and glutathione (*D*) in young *Euterpe oleracea* plants subjected to waterlogging. The same letters show insignificant differences in *F*-test ($P<0.05$) at each time. Means ± SD, $n = 5$.

The slight reduction in P_N/C_i might be associated with the finding that plants subjected to WT show low gas exchange (Liao and Lin 2001), resulting in decreased CO_2 availability and probably decreased enzyme activity, including ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phospho*enol*pyruvate carboxylase (PEPC) activity. These enzymes are responsible for the assimilation of CO_2, due to reaction with ribulose-1,5-bisphosphate (RuBP), which forms various carbon skeletons. Consistently with the present study, Grisi (2010) reported a decrease in P_N/C_i of *Schinus terebinthifolius* under water-saturated conditions.

Plants subjected to WT enhanced significantly EL only during 18 and 24 DWT, suggesting that this species is tolerant to WT. Increased EL occurs due to the rupture or increased permeability of membranes. Similar results have been reported by Leul and Zhou (1999) in *B. napus* subjected to WT.

The increase in MDA contents was observed in the WT plants. Generally, they produce free radicals and ROS, which react with unsaturated fatty acids resulting in the degradation of membrane structures and cellular damage (Lopes *et al.* 2005) with a consequent increase of lipid peroxidation. Similar results were reported by Jamei *et al.* (2009), who investigated the effects of WT in *Zea mays* plants.

WT decreased the content of ASC. It could be attributed to a low activity of L-galactono-1,4-lactone dehydrogenase, which catalyses the last step of ASC biosynthesis *via* the L-galactose pathway (Davey *et al.* 1999). ASC is the most abundant, nonenzymatic, water-soluble antioxidant, capable of removing ROS produced by oxidative stress during WT (Alhagdow *et al.* 2007). Similar reductions in ASC contents were also observed in *Citrus* roots (Arbona *et al.* 2008).

WT promoted insignificant variations in GSH contents, indicating that *E. oleracea* was tolerant to WT. The increase evident until the 12 DWT was associated with stress induced by flooding (May *et al.* 1998, Potters *et al.* 2002). However, the decrease observed after the 12 DWT suggested that the effects of stress decreased, and the survival capacity of this species increased during WT. GSH biosynthesis is a frequent response of plants exposed to abiotic stresses (Kocsy *et al.* 2001, Sofo *et al.* 2005). Hossain *et al.* (2009) described fluctuations in GSH contents in *Citrus* plants subjected to WT.

Conclusion: WT did not promote significant changes in the rates of net P_N and E, and g_s was reduced only after 18 days. No significant differences in the contents of the antioxidant compounds malondialdehyde and glutathione were observed during WT. In addition, EL was significant after 18 DWT. Therefore, this study revealed that maintenance in gas exchange and the action of antioxidant compounds contributed to the survival of *Euterpe oleracea* plants in environments exposed to waterlogging.

References

Alhagdow, M., Mounet, F., Gilbert, L. *et al.*: Silencing of the mitochondrial ascorbate synthesizing enzyme L-galactono-1,4-lactone dehydrogenase affects plant and fruit development in tomato. – Plant Physiol. **145**: 1408-1422, 2007.

Alves, G.A.R., Santos Filho, B.G., Lobato, A.K.S. *et al*.: Water relations, nitrogen compounds and enzyme activities in leaf and root of young Yellow Lapacho (*Tabebuia serratifolia*) plants subjected to flooding. – Plant Omics J. **5**: 216-222, 2012.

Aragão, R.M., Silva, E.N., Vieira, C.F., Silveira, J.A.G.: High supply of NO_3^- mitigates salinity effects through an enhancement in the efficiency of photosystem II and CO_2 assimilation in *Jatropha curcas* plants. – Acta Physiol. Plant. **34**: 2135-2143, 2012.

Arbona, V., Hossain, Z., López-Climent, M.F., Pérez-Clemente, R.M., Gómez-Cadenas, A.: Antioxidant enzymatic activity is linked to waterlogging stress tolerance in citrus. – Physiol. Plantarum **132**: 452–466, 2008.

Armstrong, W., Brändle, R., Jackson, M.B.: Mechanisms of flood tolerance in plants. – Acta Bot. Neerl. **43**: 307-358, 1994.

Bailey-Serres, J., Voesenek, L.A.C.J.: Flooding stress: acclimations and genetic diversity. – Ann. Rev. Plant Biol. **59**: 313–339, 2008.

Batista, C.U.N., Medri, M.E., Bianchini, E., Medri, C., Pimenta, J.A.: [Flood tolerance in *Cecropia pachystachya* Trec.(Cecropiaceae): ecophysiological and morpho-anatomical aspects.] – Acta Bot. Bras. **22**: 91-98, 2008. [In Portuguese]

Bertolde, F.Z., Almeida, A.-A.F., Pirovani, C.P. *et al*.: Physiological and biochemical responses of *Theobrama cacao* L. genotypes to flooding. – Photosynthetica **50**: 447-457, 2012.

Bobbio, F.O., Bobbio, P.A., Oliveira, P.A., Fadelli, S.: Stability and stabilization of the anthocynins from *Euterpe oleracea* Mart. – Acta Aliment. **31**: 371-377, 2002.

Bobbio, F.O., Druzian, J.I., Abrão, P.A., Bobbio, P.A.; Fadelli, S.: [Identification and quantification of the anthocyanins from the fruit of açai (*Euterpe oleracea*) Mart.] – Ciênc. Tecnol. Aliment. **20**: 388-390, 2000. [In Portuguese]

Cakmak, I., Horst, W.J.: Effect of aluminum on lipid peroxidation, superoxide dismutase, catalase, and peroxidase activities in root tips of soybean (*Glycine max*). – Physiol. Plantarum **83**: 463-468, 1991.

Cakmak, I., Marschner, H.: Magnesium deficiency and high light intensity enhance activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase in bean leaves. – Plant Physiol. **98**: 1222-1227, 1992.

Calbo, M.E.R., Moraes, J.A.P.V., Calbo, A.G.: [Growth, stomatal conductance, photosynthesis and porosity of flooded *Mauritia vinifera* plants.] – Rev. Bras. Fisiol. Veg. **10**: 51-58, 1998. [In Portuguese]

Cortezi, D.G., Colli, S.: [Effect of flooding and application of plant growth regulators on sprouting of *Guazuma ulmifolia* (Malvaceae) and *Sesbania virgata* (Fabaceae).] – Rev. Bras. Bot. **34**: 423-430, 2011. [In Portuguese]

Dat, J.F., Folzer, H., Parent, C., Badot, P.-M., Capelli, N.: Hypoxia stress: Current understanding and perspectives. – In: da Silva, J.A.T. (ed.): Floriculture, Ornamental and Plant Biotechnology: Advances and Tropical Issues. Volume III. Pp. 183-193. Global Science Books, Isleworth 2006.

Davey, M.W., Gilot, C., Persiau, G. *et al*.: Ascorbate biosynthesis in Arabidopsis cell suspension culture. – Plant Physiol. **121**: 535-543, 1999.

Davies, F.S., Flore, J.A.: Flooding, gas exchange and hydraulic conductivity of highbush blueberry. – Physiol. Plantarum **67**: 545-551, 1986.

de Souza, T.C., de Castro, E.M., Pereira, F.J., Parentoni, S.N., Magalhães, P.C.: Morpho-anatomical characterization of root in recurrent selection cycles for flood tolerance of maize (*Zea Mays* L.). – Plant Soil Environ. **55**: 504-510, 2009

Dias-Filho, M.B.: Tolerance to flooding in five *Brachiaria brizantha* accessions. – Pesqui. Agropecu. Bras. **37**: 439-447, 2002.

Drew, M.C.: Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. – Annu. Rev. Plant Physiol. Plant Mol. Biol. **48**: 223-250, 1997.

Du, K., Xu, L., Wu, H., Tu, B.L., Zheng, B.: Ecophysiological and morphological adaptation to soil flooding of two poplar clones differing in flood-tolerance. – Flora **207**: 96-106, 2012.

Fante, C.A., Alves, J.D., Goulart, P.F.P., Deuner, S., Silveira, N.M.: [Physiological responses in soybean cultivars submitted to flooding at different stages.] – Bragantia **69**: 253-261, 2010. [In Portuguese]

Gimeno, V., Syvertsen, J.P., Simón, I. *et al*.: Physiological and morphological responses to flooding with fresh or saline water in *Jatropha curcas*. – Environ. Exp. Bot. **78**: 47-55, 2012.

Gong, M., Li, Y.J., Chen, S.Z.: Abscisic acid-induced thermotolerance in maize seedlings is mediated by calcium and associated with antioxidant systems. – J. Plant Physiol. **153**: 488-496, 1998.

Grisi, F.A.: [Physiological aspects of aroeira (*Schinus terebinthifolikus* Raddi) under different levels of water saturation in protected environment and ciliar area in process of recuperation.] – PhD Dissertation, Universidade Federal do Paraná, Curitiba 2010. [In Portuguese.]

Henriquel, P.C., Alves, J.D., Goulart, P.F.P. *et al*.: [Physiological and anatomical characteristics of Sibipiruna plants under hipoxia.] – Cienc. Rural **40**: 70-76, 2010. [In Portuguese]

Hoagland, D.R., Arnon, D.I.: The Water Culture Method for Growing Plants without Soil. – California Agricultural Experiment Station, Berkeley 1950.

Hossain, Z., López-Climent, M.F., Arbona, V., Pérez-Clemente, R.M., Gómez-Cadenas, A.: Modulation of the antioxidant system in citrus under waterlogging and subsequent drainage. – J. Plant Physiol. **166**: 1391-1404, 2009.

Islam, M.A., Macdonald, S.E.: Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. – Trees-Struct. Funct. **18**: 35-42, 2004.

Jamei, R., Heidari, R., Khara, J., Zare, S.: Hypoxia induced changes in the lipid peroxidation, membrane permeability, reactive oxygen species generation, and antioxidative response systems in *Zea mays* leaves. – Turk. J. Biol. **33**: 45-52, 2009.

Jones, H.G.: Stomatal control of photosynthesis and transpiration. – J. Exp. Bot. **49**: 387-398, 1998.

Junk, W.J.: Flood tolerance and tree distribution in Central Amazonian floodplains. – In: Holm-Nielsen, L.B., Nielsen, I.C., Balslev, H. (ed.): Tropical Forests: Botanical Dynamics, Speciation and Diversity. Pp. 47-64, Academic Press, Salt Lake City 1989.

Kocsy, G., Ballmoos, P., Rüegsegger, A. *et al*.: Increasing the glutathione content in a chilling-sensitive maize genotype using safeners increased protection against chilling-induced injury. – Plant Physiol. **127**: 1147-1156, 2001.

Kozlowski, T.T.: Responses of Woody plants to flooding and salinity. – Tree Physiol. Monogr. **1**: 1-29, 1997.

Leiblein, M.C., Lösch, R.: Biomass development and CO_2 gas exchange of *Ambrosia artemisiifolia* L. under different soil moisture conditions. – Flora **206**: 511-516, 2011.

Leul, M., Zhou, W.J.: Alleviation of waterlogging damage in winter rape by uniconazole application: Effects on enzyme activity, lipid peroxidation, and membrane integrity. – J. Plant Growth Regul. **18**: 9-14, 1999.

Liao, C.T., Lin, C.H.: Physiological adaption of crop plants to flooding stress. – P. Natl. Sci. Council **25**: 148-157, 2001.

Lopes, M.J.C., de Souza, I.R.P., Magalhães, P.C. *et al*.: [Protein oxidation and lipid peroxidation of several 'Saracura' maize selection cycles under continuous flooding.] – Rev. Bras. Milho Sorgo **4**: 362-373, 2005. [In Portuguese]

Ma, C.C., Gao, Y.B., Guo, H.Y., Wang, J.L.: Photosynthesis, transpiration and water use efficiency of *Caragana microphylla*, *C. intermedia* and *C. korshinskii*. – Photosynthetica **42**: 65–70, 2004.

Martinazzo, E.G., Perboni, A.T., de Oliveira, P.V., Bianchi, V.J., Bacarin, M.A.: [Photosynthetic activity in japanese plum under water deficit and flooding.] – Ciênc. Rural **43**: 35-41, 2013. [In Portuguese]

Martínez-Alcántara, B., Jover, S., Quiñones, A. *et al*.: Flooding affects uptake and distribution of carbon and nitrogen in citrus seedlings. – J. Plant Physiol. **169**: 1150-1157, 2012.

May, M.J., Vernoux, T., Leaver, C., van Montagu, M., Inzé, D.: Glutathione homeostasis in plants: implications for environmental sensing and plant development. – J. Exp. Bot. **49**: 649-667, 1998.

Medri, C., Pimenta, J.A., Ruas, E.A. *et al*: [Soil flooding affects the survival, growth and metabolism of *Aegiphila sellowiana* Cham. (Lamiaceae)?] – Semina: Ciênc. Biol. Saúde **33**: 123-134, 2012. [In Portuguese]

Menezes Neto, M.A., Alves, J.D., Oliveira, L.E.M.: [Anaerobic metabolism in *Euterpe oleracea*. II. Plant tolerance mechanism to anoxia.] – R. Bras. Fisiol. Veg. **7**: 47-51, 1995. [In Portuguese]

Menezes E.M.S., Torres, A.T., Srur, A.U.S.: [Lyophilized açaí pulp (*Euterpe oleracea*, Mart.) nutritional value.] – Acta Amaz. **38**: 311-316, 2008. [In Portuguese]

Mielke, M.S., de Almeida, A.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. – Environ. Exp. Bot. **50**: 221-231, 2003.

Naeem, M.S., Jin, Z.L., Wan, G.L. *et al*.: Aminolevulinic acid improves photosynthetic gas exchange capacity and ion uptake under salinity stress in oilseed rape (*Brassica napus* L.). – Plant Soil **332**: 405-415, 2010.

Nishiuchi, S., Yamauchi, T., Takahashi, H., Kotula, L., Nakazono, M.: Mechanisms for coping with submergence and waterlogging in rice. – Rice **5**: 1-14, 2012.

Pereira, F.J., Magalhães, P.C., de Souza, T.C., Castro, E.M., Alves, J.D.: [Antioxidant system activity and aerenchyma formation in 'Saracura' maize roots.] – Pesqui. Agropecu. Bras. **45**: 450-456, 2010. [In Portuguese]

Potters, G., de Gara, L., Asard, H., Horemans, N.: Ascorbate and glutathione: guardians of the cell cycle, partners in crime? – Plant Physiol. Bioch. **40**: 537-548, 2002.

Przywara, G., Stepniewski, W.: The influence of waterlogging at diferent temperatures on penetration depth and porosity of roots and on stomatal diffusive resistance of pea and maize seedlings. – Acta Physiol. Plant. **21**: 405-411, 1999.

Reis, I.N.R.S., Santos Filho, B.G., Castro, C.V.B., Lameira, C.N., Rossato, V.: [Gas exchange and biomass alocation in young curauá (*Ananas erectifolius* L. B. Smith) plants subjected to waterllonging.] – Rev. Bras. Bioci. **5**: 507-509, 2007. [In Portuguese]

Rogez, H.: [Açaí: Prepare, Composition and Conservation Improvement.]. 288 p. EDUFPA, Belém 2000. [In Portuguese]

Sofo, A., Tuzio, A.C., Dichio, B., Xiloyannis, C.: Influence of water deficit and rewatering on the components of the ascorbate–glutathione cycle in four interspecific *Prunus* hybrids. – Plant Sci. **169**: 403-412, 2005.

Steel, R.G., Torrie, J.H., Dickey, D.A.: Principles and procedures of statistics: a biometrical approach. 666 p. Academic Internet Publishers, Moorpark 2006.

Wegner, L.H.: Oxygen transport in waterlogged plants. – In: Mancuso, S., Shabala, S. (ed.): Waterlogging Signaling and Tolerance in Plants. Pp. 3-19. Springer, New York 2010.

Wu, Q.S., Xia, R.X., Zou, Y.N.: Reactive oxygen metabolism in mycorrhizal and non-mycorrhizal citrus (*Poncirus trifoliata*) seedlings subjected to water stress. – J. Plant Physiol. **163**: 1101-1110, 2006.

Yuyama, L.K.O., Aguiar, J.P.L., Filho, D.F.S. *et al*.: [Physicochemical characterization of acai juice of *Euterpe precatoria* Mart. from different amazonian ecosystems.] – Acta Amaz. **41**: 545-551, 2011. [In Portuguese]