RESEARCH ARTICLE

ECOPHYSIOLOGICAL AND BIOCHEMICAL RESPONSES IN YOUNG *EUTERPE OLERACEA* MART PLANTS SUBMITTED TO WATER STRESS

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ABSTRACT

The objective of this study was to assess the ecophysiological aspects and metabolic responses of carbon and nitrogen in açaí (*Euterpe oleracea* Mart.) plants submitted to water stress. The experiment was conducted in a greenhouse at Universidade Federal Rural da Amazônia in the Brazilian city of Belém, State of Pará. The experimental design was completely randomized in two water conditions (control and water stress), with 5 repetitions, fully 30 experimental units, where each plant was an experimental unit. The treatments assessment was done at 0, 4, 8, 12 and 16 days of imposing water stress. The parameters analyzed were: water potential, gas exchange, hydraulic conductivity, vapor pressure deficit, carbohydrate concentrations, sucrose, ammonium and free proline, amino acids and total soluble proteins, glycine betaine. The suspension of irrigation for 15 days in young plants of *Euterpe oleracea* Mart. showed significant changes in all parameters, limiting perspiration, reducing the water potential and stomatal conductance, hydraulic conductivity and fluctuations in the VPD (Vapor Pressure Deficit), the free ammonia concentration and total soluble protein but increased carbohydrate concentrations and total soluble amino acids, sucrose, glycine betaine and proline. These changes have shown that açaí saplings show sensitivity to water stress, adjusting osmotically though.

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INTRODUCTION

The Amazon rain forest covers a large number of palm trees, totaling 200-250 species, which constitute the greater heterogeneity of palm trees in Brazil, with 35 of the 42 genera and about 150 of 193-208 species recognized for the country (LORENZI *et al.*, 2010). Among these, the *Euterpe oleracea* Mart. palm tree stands out due to its economic, social, cultural and environmental importance.

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Belonging to the *Arecaceae* family, it has a geographical distribution that runs through the Antilles to South America, especially in regions with tropical forests, and is popularly known as açaí-do-pará; açaí-de-touceira and juçara (OLIVEIRA *et al.*, 2011). In all, the process of deforestation has increased the frequency of events that cause water stress in plants, and this fact is probably associated with climate change resulting from phenomena related to global warming (HOERLING *et al.*, 2012). Current studies indicate that tropical forests are sensitive to temperature rise, increased droughts and changes in water availability in the soil (CLARK *et al.*, 2010). Because of these facts, many are the answers when the plants are subjected to water stress, and stomatal closure has been the first process to be affected, such as the net

assimilation rate of CO_2. As well as gas exchanges and stomatal conductance (gs) and transpiration (E) (SURESH *et al.*, 2010). Lack of water also presents morphological and physiological changes, such as hydraulic conductivity ofroots, and modification of carbon metabolism enzymes activity (RIBEIRO *et al.*, 2013). However, answers in favor of stressful conditions such as accumulation of metabolites or osmoprotective substances can be understood as a mechanism of plant resistance to stressful environments. Metabolic changes that lead to the accumulation of organic solutes such as glycine betaine, proline, soluble amino acids and soluble sugars have been increasingly frequent in studies on water stress conditions (FARHAD *et al.*, 2011). These solutes are concentrated in large quantities in low water potential conditions, protecting cells against dehydration and contributing to the osmotic adjustment (ZHOU; YU, 2010). Proline has been an extensively studied solute. Because it acts as a mediator of the osmotic adjustment, in integrity and protection of the plasma membrane, and as carbon and nitrogen source (HEMAPRABHA *et al.*, 2013). Therefore, the aim of this study was to assess the ecophysiological aspects and metabolic responses of carbon and nitrogen in açaí (*Euterpe oleracea* Mart.) plants submitted to water stress.

MATERIALS AND METHODS

Experimental conditions

The experiment was conducted in a greenhouse at Universidade Federal Rural da Amazônia in the city of Belém, State of Pará, Brazil (01° 28' S 48° 29' W).

Plant material, Substrate, pots and plant nutrition

The plants were propagated by seeds, acquired at Associação das Indústrias Exportadoras de Madeira do Estado do Pará (Wood Exporters Industry Association of the Brazilian State of Pará) (AIMEX), and acclimated in a greenhouse for a period of 6 months for ambiance. The substrate used was average textured yellow latosol. The pots used were in polyethylene in the dimensions 0.30 m x 0.30 m (height x diameter) and capacity of 10 kg. Corrections of macro and micronutrients soil levels and soil pH were done by means of the results of the soil chemical analysis held in the soil laboratory at Embrapa Amazônia Oriental (Embrapa Eastern Amazon), applying 600 mL of a complete nutrient solution (HOAGLAND; ARNON, 1950), divided in 3 months, for every month for 200 mL of complete nutrient solution before beginning the experiment.

Experimental design and treatments

The experimental design was completely randomized in two water conditions (control and water stress), with 5 repetitions, fully 30 experimental units, where each plant was an experimental unit. The treatments assessment was done at 0, 4, 8, 12 and 16 days of imposing water stress, and control plants were daily irrigated an average of 300 mL of water to compensate for evapotranspiration losses.

Leaf water potential and gas exchange

The water potential (Ψam) was measured between 4:30 pm and 5:30 pm using an pressure pump type Schölander (m670, Pms Instrument Co., Albany, USA) (PINHEIRO *et al.* 2007). The stomatal conductance (gs) and transpiration rate (*E*) were evaluated using a steady-state porometer (LICOR AM-300, model 1600, Nebraska, USA), in conditions of light and CO_2 environments, between 09:30 and 10:30 h in all of the plants in the experiment (COSTA and MARENCO, 2007).From the data of stomatal conductance, pressure deficit of water vapor (PDWV) and water potential to time, the hydraulic conductivity (KL) was calculated using the equation KL = (gs PDWV x) / (Yam - Yx) (HUBBARD *et al.*, 1999; DONOVAN *et al.*, 2000).

Leaf sample preparation

The leaves were harvested and placed in a 70ºC oven with forced air circulation at 96 h. The dried leaves were ground, and the powder was stored in a glass container in the dark at 15ºC until biochemical analysis were performed in the laboratory of Biodiversity Studies in Higher Plants (BSHP).

Total soluble carbohydrates

To determine the quantity of total soluble carbohydrates, 20 mg of leaf powder was incubated with 2.0 μL of 80% ethanol at 95°C for 20 min and centrifuged for 5 min at 5.0 g and 20°C. The supernatant was then removed, and the quantification of the total soluble carbohydrates was performed in reactions containing 1.250 μL of 100% H_2SO_4, 70 μL of 15% phenol, 580 μL H_2O, and 100 μL of extract for a total volume of 2.0 μL. Measurements were taken at 490 nm (DUBOIS *et al.*, 1956) using glucose (Sigma chemicals, São Paulo, Brasil) as a standard.

Sucrose

The determination of sucrose was carried out with 50 mg of leaf powder incubated with 1.5 mL of solution MCW (methanol, chloroform and water) in the proportion of 12:5:3 (v/v) at 20°C by 30 minutes under agitation, centrifuged at 10,000 *g* for 10 minutes at 20ºC and the supernatant was removed. The sucrose quantification was carried out at 620 nm, in agreement with Van Handel (1968), using sucrose (Sigma Chemicals) as standard.

Free ammonium

Free ammonium was determined with 50 mg of leaf dry matter powder incubated with 5 ml of sterile distilled water at 100°C for 30 min, after the homogenized mixture was centrifuged at 2.000 *g* for 5 min at 20°C and the supernatant was removed. The quantification of free ammonium was carried out at 625 nm in accordance with Weatherburn (1967), with $(NH_4)_2SO_4$ (Sigma Chemical) as standard.

Total soluble amino acids

Determination of amino acids was performed using 50 mg of leaf dry matter powder, and incubated with 5 mL of sterile distilled water at 100°C by 30 minutes. After incubation, the homogenized was centrifuged at 2.000 *g* for 5 minutes at 20ºC and supernatant was removed.

Quantification of the total soluble amino acids was carried out at 570 nm according to Peoples *et al.* (1989), and L-asparagine + L-glutamine (Sigma Chemicals) was used as standard.

Total soluble proteins

Determination of the total soluble proteins was carried out with 100 mg of powder, incubated with 5 mL of extraction buffer (Tris-HCl at 25 mM and pH 7.6). This was homogenized and kept in agitation for 2 h, and centrifuged to 2.000 *g* for 10 minutes at 20ºC. Quantification of the total soluble proteins was carried out at 595 nm in accordance with Bradford (1976), with albumin bovine (Sigma Chemicals) as standard.

Glycine betaine

The glycinebetaine was determined with 25 mg of leaf dry matter powder, which it was incubated with 2 mL of sterile distilled water at 25°C by 4 h and under agitation, after the homogenized was centrifuged to 10.000 g by 10 min at 25°C and the supernatant was removed. The glycinebetaine quantification was carried out at 365 nm according to Grieve and Grattan (1983), in which was utilized glycinebetaine (Sigma Chemicals) as standard.

Free proline

Determination of free proline were performed using 50 mg of leaf dry matter powder, and incubated with 5 mL of sterile distilled water at 100ºC for 30 min. After incubation, the homogenized was centrifuged at 2,000 *g* for 5 min at 20ºC and supernatant was removed. The quantification of free proline was performed after measuring the absorbance at 520 nm according to Bates *et al.* (1973) based on L-proline (Sigma Chemicals) as standard.

Statistical analyzes

The data were submitted to variance analysis and when significant differences occurred the Tukey's test at 5% level of error probability was applied. The standard errors were calculated in all evaluated points. The statistical analysis was carried out with the SAS software (Statistical Analysis System, 2008).

RESULTS AND DISCUSSION

Water potential (Ψam), hydraulic conductivity, VPD

As observed in (Fig 1A), the water potential values decreased over the experiment days in plants under water stress, with values of (-2.6 MPa) when compared to the control plants (-1.40 MPa), representing a decrease of 85.71%. The hydraulic conductivity in plants under water stress markedly decreased during the experiment (Fig 1B). Obtaining final values of 0.02 mmole m^{-2} s^{-1} MPa. In percentage terms this drop represented 90% when compared to the control plants 0.2 mmole m^{-2} s^{-1} MPa. Considering the means observed for AT (air temperature), LT (leaf temperature) and RH, it was observed that VPDLA (Vapor Pressure Deficit between Leaf and Atmosphere) ranged from 0.64 kPa to 2.20 kPa (Fig. 1C),

presenting maximum values at times of higher AT and LT (Fig 2A and Fig 2B) and lower RH (Fig 2C).
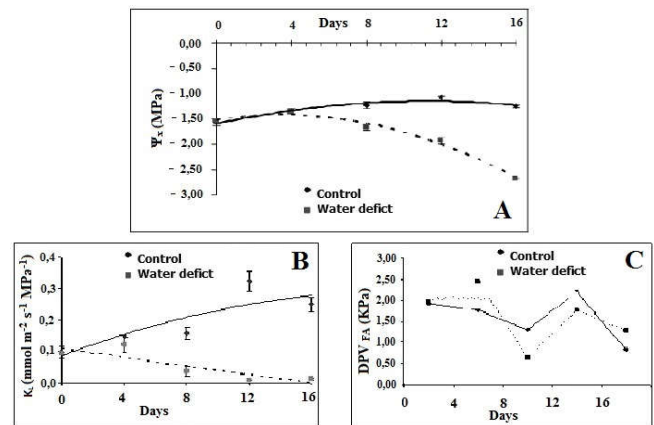

Fig 1.Water potential (A), hydraulic conductivity (B), VPD(C) in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means

With decreasing soil water availability, loss of turgidity is probably occurring, resulting in decrease in leaf water potential and consequently stomatal closure and decreased transpiration, and these factors interfere in the photosynthetic process in order to adapt to drought conditions (GE *et al*. 2012). Similar results were found by Husem (2010) when working with T*ectona grandis Linn. f.* Under irrigation suspension for 20 days, there was a 50% reduction in water content compared to plants subjected to water availability. According to Peçanha (2008), in woody plants, atmospheric conditions that favor high transpiration rates have an important influence on leaf water potential due to the low hydraulic conductivity of the root system. Since soil with low water content leads to a lower hydraulic conductivity (Fig 1B) of the root system, directly interfering in the water supply to the plant shoot (FIGUEIREDO *et al*., 2014). The values shown by the water potential and stomatal conductance variables according to Fig. 1A and 3B show the degree of interference of low levels of hydraulic conductivity in plants under water stress. In the work developed by Martins & Augusto (2012) with the species of cacao, açaí and peach-palm, they found opposite results, noting when, in saturated soil, hydraulic conductivity was positively correlated.

Air temperature, leaf temperature, relative humidity, photosynthetically active radiation (PAR)

As observed in Fig 2A and Fig 2B, the temperature values (of air and leaf) have fluctuated over the days of the experiment on average from 31.70 °C to 36.23 °C and from 31.90 °C to 36.3 °C, respectively. The average relative humidity ranged from 58% to 86% (Fig 2C). The PAR ranged from 830 mmole m^{-2}.s^{-1} to 1254.13 mole m^{-2}.s^{-1}, and the highest values were recorded on the 16th day and the lowest ones on the 12th day (Fig 2D). Increasing VPD can be explained by the absence of an adequate supply of water in which occurs stomatal closure, which reduces perspiration, decreases the leaf cooling capacity
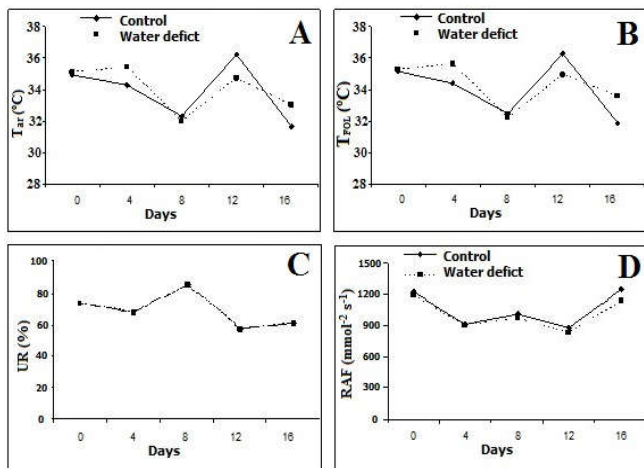
Fig 2.Air temperature (A), leaf temperature (B), relative humidity (C), photosynthetically active radiation (PAR) (D)in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means.

and increases the temperature of this organ and since the leaf keeps getting light, it causes an increase in VPD (leaf-air), leading to reduced photosynthesis (ARAÚJO *et al*., 2010). The loss of water through the leaves is generally determined by VPD (leaf-air) (Silva *et al*. 2013).Schwider *et al*. (2013), working with eucalyptus clones, have found that on days when the air temperature is higher, the vapor pressure deficit of air was higher.

Transpiration and stomatal conductance

For perspiration of açaí palm leaves, a decrease was observed throughout the experiment (Fig 3A) and this behavior is similar to that of stomatal conductance gs (Fig 3B). Leaf transpiration of the control plants showed values ranging from 1.96 μmole.m^{-2}.s^{-1}to 5.57 μmole.m^{-2}.s^{-1}, reaching the maximum on the 16th day of the experiment. As for the plants subjected to water stress, they had values ranging from 0.20 μmole.m^{-2}.s^{-1}to 1.98 μmole.m^{-2}.s^{-1}, corresponding to a percentage of 64.45%. The means of E did not differ statistically between treatments at the beginning of the experiment, while on the other days the differences were statistically significant (Fig 3A).
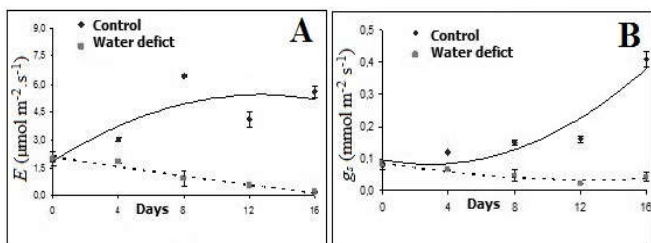

Fig 3. Transpiration (A) and stomatal conductance (B) in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means

The gs rates of irrigated plants did not differ significantly at the beginning of the experiment, showing a mean value of 0.08 mole m^{-2}.s^{-1}, having on the course of the days substantial increases until reaching their maximum on the 16th day (0.41 mole m^{-2}.s^{-1}). A reverse trend was observed for the plants under water stress, where the gs was maximum on the 1st day of the experiment (0.08 mole m^{-2}.s^{-1}), significantly reducing on the other days (0.04 mole m^{-2}.s^{-1}), which corresponded to a percentage of 50%.

According to Rivas *et al*. (2013), stomatal closure causes a greater reduction of H_2O flowing out of the leaves than in the CO_2 flowing to the chloroplasts, decreasing the transpiration rate further than the photosynthetic rate. The decrease of E is caused by the drop in gs rates as a result of stomatal closure in the treatment under water stress due to high vapor pressure deficit during the day. Oliveira (2014) has also noted that E rates had followed the reduction of gs for the two species of palm trees studied, *Syagrus coronata* and *Acrocomia aculeata*.

Concentrations of total soluble carbohydrates and sucrose

The results revealed a significant increase of 21.62% in total soluble carbohydrates concentrations of plants subjected to water stress (Fig 4A). The values obtained for the plants under water stress was 0.74 mmole of Glu/g DM, while for the control plants it was of 0.58 mmole of Glu/g DM.The figures shown for the sucrose concentrations (Fig 4B) in plants under water stress were 28,5μmole.g^{-1} DM, representing an increase of 33.33% when compared to the control plants (19.0 μmole.g^{-1} DM).
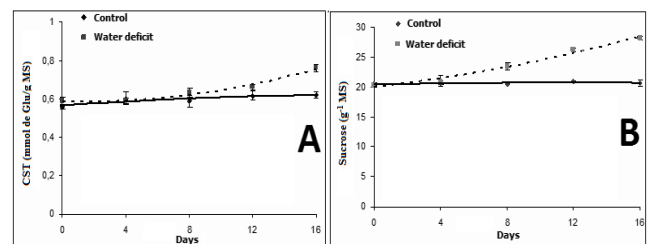

Fig 4.Total soluble carbohydrates(A), sucrose (B), in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means

In plants under water stress, accumulation of total soluble carbohydrates can occur in leaves, for carbohydrates govern the fixing rate of CO_2 and/or the synthesis or hydrolysis of starch, confirming the decrease in starch content found in this work (GORAI *et al*., 2010). Lisar *et al*. (2012) claim that under water stress, some of the carbohydrates arranged in the cytoplasm are used in the activation of drought tolerance mechanisms, regardless of the mechanism in question. However, this increase in soluble carbohydrates depends on the species, the species genotype, the drought level and duration, developmental stage, as well as the experimental conditions (MOSTAJERAN RAHIMI-EICHI, 2009; YOUSFI *et al*., 2010). Also, soluble sugars are sources of carbon and energy in cells and they are important signaling molecules with significant roles in stress tolerance mechanisms in plants via

osmotic adjustment (MOSTAJERAN and RAHIMI-EICHI, 2009). In other words, plants invest more in protection mechanisms to stress than in growth when subjected to water stress. This corroborates the results observed by Rivas *et al.* (2013), which showed increases in the concentration of carbohydrates in *Moringa oleifera* leaves under water stress of 10 days. The possible reduction of starch concentrations in leaves with water stress under action of α and β-amylase enzymes partly explains the sucrose increases (Fig 4B), because the starch degradation is converted into carbohydrates and one of those carbohydrates is sucrose. The decrease in the photosynthetic process because of low levels of gas exchanges probably decreased the activity of the C3 cycle because of non-absorption of CO_2, resulting in low energy levels for the plants and one of the plants strategies was to degrade the reserve starch into sucrose to keep cellular activity. Work developed by Paula *et al.* (2013) with mahogany plants has found an increase of 118.06% sucrose in plants analyzed in the period under water stress compared to plants analyzed in the rainy season.

Concentrations of free ammonium, total soluble amino acids and proteins

The results showed a significant reduction of 51.85% in the free ammonium concentrations in plants subjected to water stress (Fig 5A). The values obtained for the plants under water stress was 13 mmole g^{-1} of NH_4^+/Kg of DM, while for the control plants it was of 27 mmole g^{-1} of NH_4^+/Kg of DM. The total soluble amino acids content in açaí plants ranged from 203.1 μmole.g^{-1} DM and 227.64 μmole.g^{-1} DM in the control plants, while in the plants under water stress it ranged between 217.68 μmole.g^{-1} DM and 267.96 μmole.g^{-1} DM. The total soluble amino acids levels were higher in plants with water stress on the last day of the experiment with 17,71% (Fig 5B). The results showed a significant reduction of 46.06% in total soluble protein concentrations in plants subjected to water stress (Fig 5C). The values obtained for the plants under water stress was 14.4 mg protein/g DM, while for the control plants they were of 26.7 mg protein/g DM.
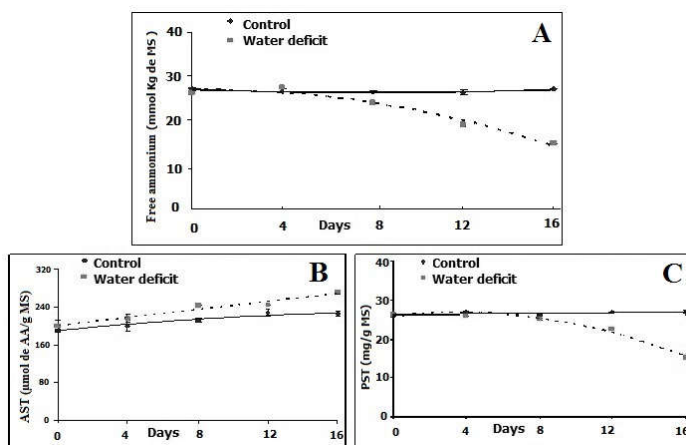

Fig 5.Concentrations of free ammonium (A), total soluble amino acids (B) and total soluble proteins (C)in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means

The reduction of ammonium levels can probably be explained due to the high activity of the enzyme system GS/GOGAT where glutamine synthesis (GS) catalyzes the reaction of ammonia and glutamate, producing glutamine, and the glutamate synthase enzyme (GOGAT) is responsible for the glutamine reaction with 2-oxoglutarate, generating two glutamate molecules. Given these statements, a methodology that measures the activity of enzymes GS/GOGAT or glutamate dehydrogenase (GDH) is necessary, which is an alternative route from which is catalyzed the reversible reaction that synthesizes or deaminates glutamate, prevailing the formation of ammonium and 2-oxoglutarate to actually be able to corroborate the reason for the low ammonium concentrations, as emphasized by Carvalho (2012). Pereira *et al.* (2013) found no significant differences for ammonium concentrations when working with two pepper cultivars under water stress and progressive combinations of silicon. Where to cultivate Vermelho gigante (Giant Red) showed higher concentrations compared to cultivar Ikeda.

The increase of amino acids in plants takes place primarily by degradation of proteins. The reduction in soil water probably increased the synthesis of proteolytic enzymes which have the role of degrading the proteins by breaking peptide bonds, yielding amino acids. This likely change in proteolytic enzymes is beneficial for the species under study, because by increasing the levels of this amino acid it makes possible to maintain the leaf water potential and the plant defense to dehydration (SOUSA *et al.*, 2015). Corroborating Amorim *et al.* (2011), when analyzing the contents of this organic solute in leaves of *Anacardium occidentale*, they have also found that non-irrigated plants had an increase of 57.7% in amino acid levels in response to water stress. Water stress reduced protein levels due to its metabolism being affected in these conditions, where the biosynthesis process of this substance is one of the first paralyzed metabolic events after the perception of water stress (MARAGHNI *et al.*, 2011); this occurs after the stomata are closed and there is the beginning of proteolysis, causing an increase in the content of free amino acids (Fig 5B) and of proline (Fig 6B), with consequent decrease in protein concentration (Fig 5C), as a defense, plants alter their metabolic behavior to fit osmotically (TURKAN, 2011).Paula *et al.* (2011), studying the development of mahogany (*Swietenia macrophylla* King), have obtained a reduction in protein levels in plants subjected to water stress.

Concentrations of glycine-betaine, proline

The results showed an increase of glycine betaine content in plants under water stress, compared to control plants. For plants under water stress concentrations of 45 mg/g DM and control plants of 26 mg/g DM were found, representing an increase of 42.22% in plants under water stress when compared to control plants (Fig 6A).There was an increase for proline concentrations in plants under water stress from the 8th day compared to control plants (Fig 6B). Under these conditions, proline accumulation reached values of 5.2 μmole g^{-1} at the end of the experiment, whereas for irrigated plants the proline concentration remained in constant values throughout the experiment; in percentage terms, there was an increase of 30%.
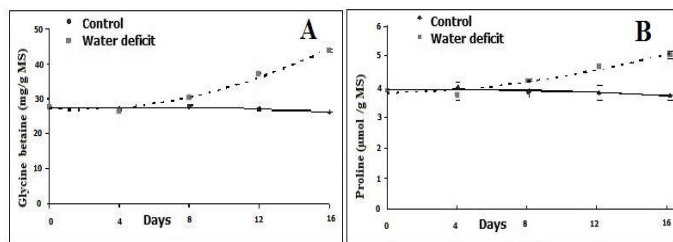
Fig 6. Concentration of Glycine Betaine (A) and Proline free (B)in leaves of young plants of *Euterpe oleracea* mart submitted during 16 days under water stress. The letters a and b show statistically significant differences between treatments were compared by Tukey test at 5% probability. The bars represent the standard deviations of the means

This significant increase in glycine betaine is caused by the accumulation of compatible solutes that are not deleterious to cell metabolism and by increasing the osmotic pressure inside the cells to maintain water absorption and cell turgidity pressure, which causes continuity of the physiological processes, even at lower levels (MARIJUAN& BOSCH, 2013). Glycine betaine is involved in osmotic adjustment, protection of cellular structures and antioxidant protection (SILVA *et al*., 2010). Consequently, the accumulation of that solute may have contributed, at least in part, for the protection of plants against the adverse conditions of osmotic potential in soil (Sousa *et al*., 2012). Corroborating the work in question, Sousa *et al*. (2012) have observed an increase in glycine concentration in *Jatropha curcas* plants under 35 days of water stress.

Proline is considered a key osmolyte for the osmotic adjustment of plants under abiotic stresses, acting as compatible solute, accumulating in the cells, with an osmoprotective role of membrane integrity against the deleterious effects caused by reactive oxygen species (ROS), preventing denaturation of proteins and preserving the structure of some enzymes (GIANNAKOULA *et al*., 2008). Similar results were found by Pereira *et al*. (2012), working with different cultivars of peanut under water stress conditions, where all plants increased in proline concentrations, while the more sensitive cultivar presented the accumulation in the range of 36%.

Conclusion

Euterpe oleracea Mart. young plants subjected to 16 days of water stress showed significant changes in all parameters, limiting perspiration, reducing the water potential and stomatal conductance, hydraulic conductivity and fluctuations in the VPD, in free ammonia concentrations and total soluble proteins, but increased carbohydrate concentrations and total soluble amino acids, sucrose, glycine betaine and proline. These changes have shown that açaí saplings show sensitivity to water stress, adjusting osmotically though.

Acknowledgment

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