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Gas exchange and carbon metabolism in leaves of crabwood (*Carapa guianensis* Aubl.) in three mechanisms and suspension of water stress

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Abstract

Crabwood or Andiroba (in Brazil) is an arboreal species with variations in their physiological processes from soil and climatic conditions induced, such as lack or excess water. The objective of this study was to evaluate the effects of drought and flooding in gas exchange, abscisic acid, starch, total soluble carbohydrates, sucrose in Andiroba leaves with seven months of age and resilience of these young plants after cessation of stress. The experiment was conducted in a greenhouse. The experimental design was completely randomized in a factorial 3x5 (three water conditions: control, water deficit and flooding and 5 periods reviewed. 0, 10, 20, 30 and suspension of water stress after 72h) with 5 repetitions, totaling 75 sample units. Significant decreases were observed in water potential, stomatal conductance, transpiration and starch content, and significant increase in abscisic acid (ABA) content, total soluble carbohydrates and sucrose, with significant values on the 30th day of the experiment. After the water stress, the plants failed to recover the initial values of all variables, recovering only the sucrose levels. Andiroba is satisfactorily tolerant to water stress imposed in this experiment, but does not show a rapid recovery after the suspension of water stress, with higher sensitivity to water stress.

Keywords: Drought; Flooding; Osmoregulator; Physiological processes; Carbohydrate content.
Abbreviations: DM_ dry matter; FM_ fres matter; GLU_ glutamine; MPa_ megapascal.

Introduction

Carapa guianensis Aubl. is one of the species with great potential in logging and non-timber in Amazon, with your usual name Andiroba (Tonini *et al*. 2009). Beyond that, the Andiroba has promising potential to aclimate to ambiental changes provided in a near future for most of the Amazon region (Camargo and Marenco 2012). The selection of species tolerant to water stress is of fundamental importance to the success of forestry, in areas under severe hydro condition, since the growth and development of plants are affected by biotic and abiotic factors, among them the temperature and the water content in soil (Streck 2002). In regions with different climate and soil characteristics, have been used measurements of gas exchange in forest plantations to evaluate primary productivity answers of these species on the diurnal and seasonal variations (Waring and Landsberg 2011). The main control mechanism of gas exchange is the stomatal movement in higher plants. For most species, stomatal closure occurs after reductions in soil water availability (Taiz and Zeiger 2013). When submitted to flooding, promotes the reduction in transpiration rates, decreases their energetic performance and reproduce metabolic signals of different types, in response to decreased oxygen levels, changing your growth and anatomy, aiming their survival (Bailey-Serres and Voesenek 2008). As a defense mechanism of water stress, plants generally promote the increase of total soluble carbohydrates for maintenance of growth, as well as being osmoregulators, in other words, holds the water for a longer time within the plant tissue (Freitas 2014). Resulting in a larger distribution of species with good adaptability and morphological differences, as is the case of *Carapa guianensis* Aubl (Pitman *et al*. 2001). Among these peculiarities, water is a major factor that regulates the growth and survival of seedlings (Tobe *et al*. 2005). From the principle of multidisciplinary, studies in Plant Physiology have contributed a lot in the evolutionary process of Forestry, becoming an indispensable tool for understanding the physiological processes of tree species and the interactions of plants with the environment. Thus, this study area may help in the selection of promising species with greater capacity, through the development of 12 physiological descriptors chips that classify as tolerant and adapted to the various factors of environmental stress (Nascimento, 2013). Andiroba is a tree species with variations in their physiological processes from induced soil and water conditions, as lack or excess water. Therefore, the objective of this study was evaluated the effects of drought and flooding in gas exchange and carbon metabolism in leaves of Andiroba and recovery after the period of stress.

Results

The predawn water potential (Ψ_{am}) of plants maintained under drought and flooding was significantly reduced with increasing number of days, however, after suspension of water stress the plant could not recover immediately (Fig. 1). The values for the plants under deficit were -0.48; -0.89; -1.94, -3.46 and -0.95 MPa, for the plants under flooding the values are -0.47, -0.68, -1.07, -2.85 and -0.77 MPa in evaluation times 0, 10, 20, 30 and suspension of water stress after 72 h, respectively. These results suggest that the decreased of Ψ_{am} in plants under water deficiency relates to the time that the young plants are not receiving water. The plants with water deficiency show a higher reduction of water potential in relation of flooded plants, showing a smaller decline in 30th day of experiment established. The plants submitted to flooding showed a recovery of 85.24%, when compared with control plants, occurred only 72h after the suspension of water stress. The contents of abscisic acid (ABA) in andiroba leaves significantly increased with water stress time, compared to the control plants (Fig. 2). The ABA values in irrigated plants were from 48 to 50.14 ng g^{-1} MS. Plants under drought had values from 51.89 to 221 ng g^{-1} MS and the plants under flooding with 52.16 to 193.16 ng g^{-1} MS in the evaluation points 0 to 30 days. The recovery for both treatments was not effective, because for the plants subjected to water stress the young plants showed a recovery of 80.35% and for the plants under flooding the recovery was 51.04% when compared with the control plants. Another variable who also significantly reduced was the stomatal conductance (g_s) with values form 1050 to 1028; 1109 to 495; 1110 to 229 mmol m^{-2} s^{-1} for the control plants, water deficit and flooded, respectively (Fig. 3). The suspension of water stress in 72h, was not enough for the plants might recover their initial stomatal conductance, when compared with control plants, reaching a recovery of 42.66% for plants under water deficit and of 13.03% for the plants under flooding. The reduction of g_s also caused a decrease in transpiration rate, with values from 18.21 to 16.4; 17.83 to 6.88; 16.64 to 6.0 mmol m^{-2} s^{-1} to control plants, water deficit and flooded respectively (Fig. 4). The most representative values were in 30th day of experiment, both in plants under drought as under flooding. This reduction ally with the low water potential made them unable to recover the initial transpiration activity when suspended the stresses imposed. The recovery for both treatments was slow, because for the plants under water deficit, the recovery was 24.11%, and for the plants under flooding the recovery was 4.24%. The starch contents were decreased when subjected to water stress, although the time of 10 days did not differ statistically between plants under flooding and plants irrigated daily. The lowest concentrations occur in plants with water deficit in 30th day, with 0.597 mmol of GLU/g^{-1} residual (Fig. 5). After the suspension of water stress, the percentage recovery was 31.74% for plants under water stress and 23.93% for flooded plants, not recovering the initial concentration. Referring to the total soluble carbohydrates, the results showed a significant increase for plants, promoting significant increase in the content of this substance in relation to water regimes and times of stress, as shown in Fig. 6. The values obtained for the control plants at time 0, 10, 20 and 30 days, respectively, were 105; 111; 110; 115 µmol g^{-1} DM (dry matter), plants under water stress 108; 118; 153; 184 µmol.g^{-1} DM and plants flooded 106; 109; 143; 147 µmol g^{-1} MS with statistical difference after 20 days of stress. After the suspension of drought, extreme values reached a maximum stress time, declined reaching a recovery rate of 29.11% for the plants with water stress and 23.81% in flooded plants, not resuming its initial concentration (E0), after three days of suspension of stress.

The sucrose concentration increased with the development of water stress time, significant amount were presented at the 30th day of stress (Fig. 7). With 13.01 to 13.45 (control plants), from 13.9 to 16.6 (plants under drought stress) and from 13.21 to 15.61 (plants under flooding) µmolg^{-1} MS. Statistically different after 10 days of experiment.

Discussion

The decrease in the water potential is possibly due to increased tension in the xylematics vessels, as more negative the Ψ_{am} is, bigger is the force required for the plant absorbs the water of soil to be transported to the aerial part. This transport may be injured depending on the degree of severity in the water deficiency. In *C. guianensis* Aubl, the transport after the stress was partially injured, because when it is rehydrated, the species do not recover their initial potential that was between -0.48 MPa, getting a recovery of 82.29%.

In the plants subjected to flooding, the decrease in water potential is related to the low concentration of O_2 despite the roots are completely submerged in water in the leaves tissue. Meanwhile, according to Oliveira Neto (2010), this decrease should have promoted a behavior change in plant metabolism, such as, the oxidate phosphorylation for phosphorylation of ADP to ATP in reactions that occur exclusively in glicolysis and fermentation, causing with that the synthesis capacity also changes of 36 ATP, when aerobic respiration, for only 2 ATP through fermentation. The plants subjected to flooding have shown a recovery of 85.24%, when compared to the control plants, past just 72 h after the cessation of water stress. According to Kim and Lieth (2003), a very important aspect in studies of stress and recovery of the ''status'' leave water is the speed of imposition of water deficiency and your duration, which may involve different responses in varieties of the same species. The slow induction of water stress, with low leave water potential values, reached before the rehydration, can enable an a bigger production and abscisic acid accumulation in leaves, allowing the storage cell turgor by maintaining low values of stomatal conductance. Species with greater ability to maintain turgor, under conditions of moderate water deficit, are more apt to support periods of water deficit (Nascimento 2009). According with Pimentel (2004), in a moderate water deficit occurs a reduction in stomatal opening, and consequently in transpiration, there is also a reduction in photosynthetic activity, by the decreasing of availability of CO_2. Another response to an increase in abscisic acid in the leafs, in conditions of low soil water availability occur an outstanding increase of the reason root/aerial part, which, together with the effect of ABA on stomatal closure, helps the plant to face the water stress (Souza 2012), decreasing the photosynthetic capacity, which results in a less starch accumulation, may signal the need for increased levels of sucrose and carbohydrates. Close results of this work were founded by Nascimento et al. (2011), when evaluating the photosynthetic recovery in young plants of *Hymenaea courbaril* L. under water deficit and posterior irrigation, found that after 11 days without irrigation, occurred the stomatal closure, significantly affecting all the studied variables. Among these, the water relations were the ones that best express the injuries promoted by drought, standing out the water potential, which showed considerable reductions. The same occurred regarding gas exchange, transpiration rate and stomatal

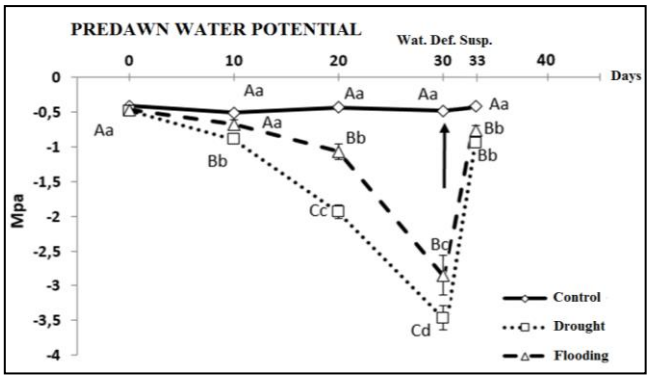

Fig 1. Predawn water potential in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show differences between the collection days of the same treatment compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

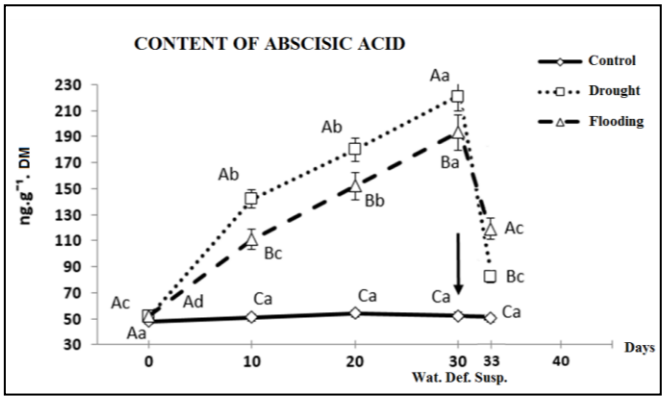

Fig 2. Content of abscisic acid in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show differences between the collection days of the same treatment compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

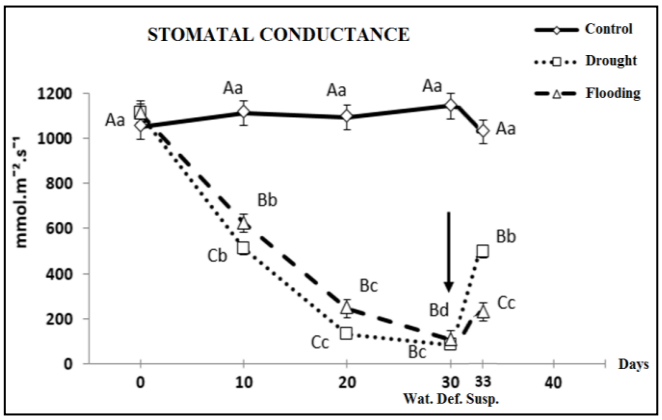

Fig 3. Stomatal condutance in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show differences between the collection days of the same treatment compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

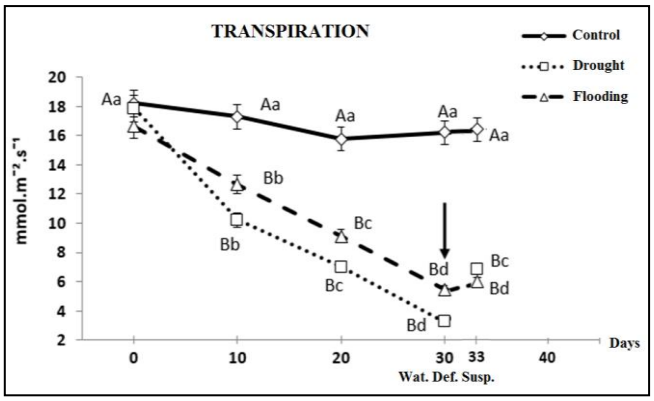

Fig 4. Transpiration in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show differences between the collection days of the same treatment compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

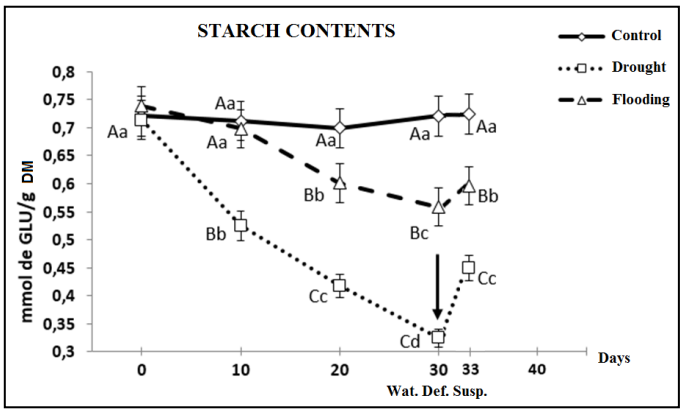

Fig 5. Starch contents in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show statistical differences between the collection days of a same treatment, compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

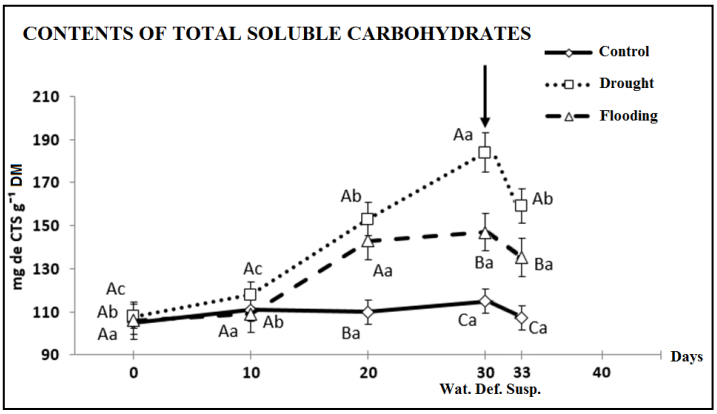

Fig 6. Contents of total soluble carbohydrates in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show statistical differences between the collection days of a same treatment, compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

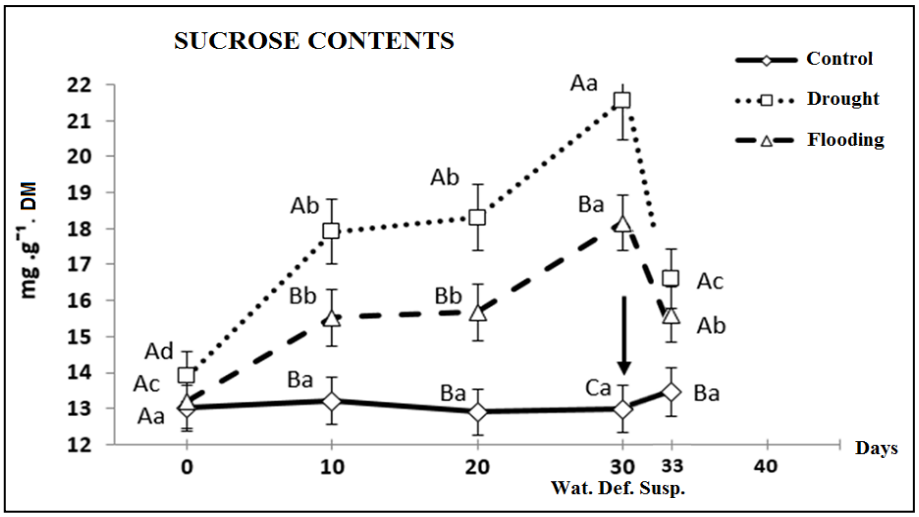

Fig 7. Sucrose contents in young plants of crabwood subjected to water deficit and flooding. Capital letters show statistical differences between the treatments and the lowercase letters show statistical differences between the collection days of a same treatment, compared by Tukey's test at 5% of probability. Bars represent the standard deviation of the means. The arrow indicates the suspension time of the stress.

conductance. The plants reirrigation promoted the stomatal reopening, after five days, recovering all the variables (Nascimento et al. 2011).

The decreasing of g_s is one of the first responses to environmental stress, however if this condition continues for a long period, the mechanisms evolved are more complicated than simply a reduction in g_s, resulting in biochemical limitations in the photosynthesis rate and plant growth (Centrito et al. 2003). Albuquerque et al. (2013), studying African mahogany plants, also observed a reduction in stomatal condutance in plants under conditions of water deficit and rehydration. The reduction of transpiration possibly occurs due to stomatal closure, which is promoted by the increase of biosynthesis or redistribution of ABA, regulating hormone of stomatal closure in stressed plants. Similar results were found by Fu et al. (2010), when studied plants of poplar or aspen (*P. euphratica e P. Russkii)* which is a tree of Salicaceae family, the results reflected to stomatal closure and to low leave transpiration.

This reduction is probably linked to starch degradation by the α and β – amylase enzymes, favoring the formation of new sugars, like sucrose. These results corroborate with the work of Paula et al. (2013), involving Brazilian mahogany plants (*Swietenia macrophylla* King) in two sampling periods, dry and rainy, where occurred a reduction of 30% in average of starch contents in leaves analyzed during the dry season compared with the analyzed during the rainy season. These results may be explained by the fact that the water stress affect the utilization of carbohydrates by changing basically the efficiency with which assimilates are converted to the development of new parts of the plant.

This increase for both stresses can be probably related to the increased activity of enzymes that act in the process of breaking of starch, where the formed and transported sugars can be in the form of sucrose. Levels of the compound also changed during the experimental time, evidenced by the increase in differentiated 30th day of water stress, returning to decrease only three days of water stress suspension, with percentage recovery rate of 57.96% and 49.51% for plants under water deficit and flooded respectively an increase in the concentration of sucrose in leaves of bean plants-atanã (*Parkia giganto* carp Ducke) under water stress in the soil.

Materials and methods

Location and growth conditions

The experiment was conducted in a greenhouse at the Federal Rural University of Amazonia, Capitão Poço, PA. Before the beginning of treatment, all plants were placed below sombrite 50%, irrigated daily during one month to keep them at field capacity and acclimatization (Fernandez and Sykes 1968). Conditioning 200 mL of macro and micronutrients every 15 days until the beginning of the experiment, in the form of nutrient solution (Hoagland and Arnon 1950), modified at Biodiversity Studies in Higher Plants Laboratory (EBPS), UFRA.

Plant materials

Young plants of Andiroba from seeds were provided by AIMEX (Association of timber exporting industries in the state of Pará) with four months old, were placed in plastic pots with capacity for 20L. The substrate used was formed by dystrophic yellow latosol, cattle manure in a proportion of 3:1, respectively.

Management of plants

The plants were subjected to three water regimes: irrigated (control), water deficit (total suspension of irrigation at the beginning of the experiment) and flooding (kept a sheet of 5 cm of water above ground) at an interval of thirty days. After the thirty-day period, water stress was suspended, the plants under water stress were rehydrated and plants under flooding were taken of it. During the experimental period, the "control plant" were watered daily to replace water lost, being made individually for each pot, taking into account the daily weighings assembly (pot + plant + soil).

Experimental design

The experimental design was completely randomized in a factorial 3x5 (three water conditions: control, water and flooding deficit and 5 periods reviewed. 0, 10, 20, 30 and

suspension of water stress after 72h) with 5 repetitions, totaling 75 sample units. The potential water was determined between 4:30 and 5:30 a.m., through of a pressure bump type Scholander (m670, Pms Instrument Co, Albany, USA), as described by Pinheiro et al. (2007). As samples, mature and fully expanded leaflets were selected since the second or third pair mature leaf from the apex, taken with the aid of a razor blade, between 9:00 and 11:00 a.m., packed in moistened polyethylene bags and transported on ice to the laboratory for analysis, in a maximum time of 60 min, and immediately frozen (about -20ºC) for biochemical analysis in the future. After sample collect, all the plants were irrigated in the late afternoon and, in the following predawn, 12h later the continuation of irrigation, the water potential was redetermined, gas exchange was evaluated and leaf samples collected, as described above, in order to verify recovery capacity of the plant after ceased the stress.

Statistical analysis

The variance analysis was applied to the results and when there was a significant difference, the averages were compared by the Tukey's test at 5% significance. Beyond that, the standard deviations were calculated for each treatment, and the statistical analysis made by the program (SAS-institute 1996).

Biochemical analysis

Determining abscisic acid

Described by Ross et al. (2004), with some modifications. 50 mg of dried leaf tissues in a forced air circulation glasshouse, were macerated in liquid N with Polivinil Polipirolidona 100% (PVPP). Then, was placed in 1,5 mL of solvent extraction (acetone/H_2O/acetic acid: 80/19/1). The extract was transferred to another tube. The mortar was washed with 500 µL of solvent extraction (acetone/H_2O/acetic acid: 80/19/1) and transferred to the same tube, adding 40 mg of (-) -5, 8', 8', 8', -d_4-ABA deuterated. The supernatant was, next, transferred to the injector via.

The analysis was made by liquid chromatography coupled to mass spectrometry in ionization mode negative electrospray (HPLC/MS/ESI-). The detection and quantification of ABA in the samples were made by multiple reaction monitoring (MRM) via mass specific transition selecting of the molecule of interest (for ABA, 263 → 153 and, for ABA d4, 267 → 156).

Determining starch concentrations

The method for obtaining the starch concentrations were according Dubois et al. (1956). Were made two ethanolic extractions of 50 mg of the dry mass of leaves, using 5.0 mL of 80% ethanol, for 30 min at 80ºC, for the first extraction. And with 5.0 mL of 30% $HClO_4$ for 30 min at 25ºC, for the second extraction. After the extractions, was centrifuged at 2,000 rpm for 10 min and collected the supernatants. These get being united and measured for the volume to 10 mL with distilled water to obtain a total extract. In the test tubes were placed 100 mL of supernatant + 400 mL of distilled water and shaking in vortex, adding 0.5 mL of 5% phenol and shaking in the vortex, after that was uniformly added at once in the center of the tube, with graduated pipette, 2.5 mL of concentrated H_2SO_4 and shaken the tubes in vortex again, and taken after 20 min of rest to spectrophotometer at 490 nm.

Total soluble carbohydrates (TSC)

The total soluble carbohydrates content was determinated according the colorimetric method described by Dubois et al. (1956), modified as follows: Vegetable samples were homogenized in 5 mL of distilled water and the resulting homogenized was incubated at 100ºC, for 30 min. After centrifugation at 700 g, for 10 min, the supernatant was collected and the extraction procedure was repeated twice. The supernatants were combined and homogenized and, of the resulting final extract, an aliquot of 20 µL was sampled for the remaining steps. Each aliquot received 480 µL of deionized water and, after stirring for 15 min, were added 500 µL of 5% phenol and 2.5 mL of concentrated sulfuric acid to each sample. After Strong stirring for 20 min, the reading was realized by a spectrophotometer (GenesysTM10 series, Thermo Electron Co, Wisconsin, USA) at 490 nm.

Determination of sucrose

For determination of sucrose, the Van Handel method (1968) suffered some changes. The samples were macerated in 1.5 mL of MCW (methanol; chloroform; water 12: 5: 3, v/v/v) and stirred for 20 min. The homogenate was centrifuged at 500 g, for 30 min, in ambient temperature. After collection of the supernatant, the extraction process was repeated twice in a row, gathering the supernatants and determining its final volume. After shaking, heating at 100ºC for 10 min and cooling in ice bath, a volume of 3.0 mL of 0.2% anthrone soluction (in sulfuric acid) was added to each tube. The mixture was stirred and heated again at 40ºC for 20 min and, after cooling, the reading was realized at 620 nm by a spectrophotometer (GenesysTM10 series, Thermo Electron Co, Wisconsin, USA).

Determination of gas exchange

The stomatal conductance to water vapor (g_s) and the transpiration rate (E) were determined by an portable porometer of dynamics balance (mod. LI 1600, LiCor, Nebraska, USA). The measurements were made at 9:00 a.m. As samples, mature leaflets and completely expanded were selected from leaves of second or third pair counted starting from the apex. After gas exchange, leaf samples were collected and immediately taken to a forced air circulation glasshouse at 65ºC until the drought for the flour preparation.

Conclusion

The suspension of irrigation, as well as drowning for 30 days was enough to change and cause a decrease in metabolic pathways of young plants of Andiroba, reducing water potential, transpiration rate, stomatal conductance and starch, but increasing levels of total soluble carbohydrates, sucrose and ABA. The water stress suspension time was not enough for the resumption of the initial values of all variables. Andiroba is satisfactorily tolerant to water stress showed a rapid partial recovery after cessation of water stress, with higher sensitivity to water stress.

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