Universidade Federal Rural do Semi-Árido
Pró-Reitoria de Pesquisa e Pós-Graduação
http://periodicos.ufersa.edu.br/index.php/sistema

ISSN 0100-316X (impresso)
ISSN 1983-2125 (online)
http://dx.doi.org/10.1590/1983-21252016v29n409rc

MATTER ACCUMULATION AND PHOTOSYNTHETIC RESPONSES OF MACAW PALM TO CYCLICAL DROUGHT[1]

CLENILSO SEHNEN MOTA[2]*, MARCO ANTONIO OLIVA CANO[3]

ABSTRACT – The objective of this work was to evaluate the plant-water relations, photosynthetic parameters and growth of macaw (*Acrocomia aculeata* (Jacp.) Lodd. ex Mart.) plants, thus, ten plants were subjected to three successive drought and rehydration cycles and ten other plants were irrigated normally as control. The drought cycles consisted of a suspension of irrigation until the net CO_2 assimilation rate (A) reach values lower than 5% of the control, and a rehydration until a plants recover at least 85% of A of the control plants. Reductions in A, stomatal conductance (g_s) and transpiration (E), above 95%, were found with predawn leaf water potential (Ψ_{pd}) of -1.85 MPa. After rehydration, the g_s and E of plants with and without water stress was not different, however, A presented a significant difference. Leaf water potentials below -0.5 MPa reduced the intracellular and atmospheric CO_2 ratio and increased water use efficiency, and values of -1.85 MPa, when both showed an increase and decrease, respectively. The reduction of A and g_s was linear and proportional to Ψ_{pd}. Total dry matter accumulation reduced by 50% in the plants subjected to drought. The cyclic water stress resulted in reduction of gas exchange and matter accumulation in macaw palm plants; a stomatal limitation of A occurred until Ψ_{pd} of -1.85 MPa, and then a non-stomatal limitation.

Keywords: *Acrocomia aculeata.* Photosynthesis. Water use efficiency. Plant-water relations.

RESPOSTAS FOTOSSINTÉTICAS E ACÚMULO DE MASSA EM PLANTAS JOVENS DE MACAÚBA SUBMETIDA AO DÉFICIT HÍDRICO CÍCLICO

RESUMO - Com o objetivo de avaliar as relações hídricas, parâmetros fotossintéticos e crescimento em plantas de macaúba, dez plantas foram submetidas a três ciclos sucessivos de seca/recuperação e outras dez irrigadas normalmente como controle. Cada ciclo consistiu em suspender a irrigação até que a assimilação liquida de CO_2 (A) fosse inferior a 5% em relação às plantas controle, momento esse de retomada da irrigação até que A recuperasse no mínimo 85% em relação ao controle. Reduções de A, condutância estomática (g_s) e transpiração (E), acima de 95%, foram obtidas em Ψ_{am} de -1.85 MPa. Após a reidratação, g_s e E não apresentaram diferenças entre as plantas sem e com deficiência hídrica, diferentemente do que ocorreu com A. Potencial hídrico foliar abaixo de -0,5 MPa promoveu redução da relação entre concentração intercelular e atmosférica de CO_2 e aumento do uso eficiente da água, até valores de -1.85 MPa, quando ambos apresentaram elevação e redução, respectivamente. A redução de A e g_s foi linear e proporcional à de Ψ_{am}. O acúmulo de massa seca total foi reduzida em 50% pela imposição da seca. O estresse hídrico cíclico resultou em redução das trocas gasosas e de acúmulo da massa em macaúba, a limitação estomática de A atuou até Ψ_{am} de -1.85 MPa, quando passou a atuar a não estomática.

Palavras-chave: *Acrocomia aculeata*. Fotossíntese. Eficiência no uso da água. Relações hídricas.

---

*Corresponding author

[1] Received for publication in 02/05/2015; accepted in 06/22/2016.

[2] Instituto Federal Catarinense, Rio do Sul, SC, Brazil; csm.sehnen@gmail.com.
[3] Department of Plant Biology, Universidade Federal de Viçosa, Viçosa, MG, Brazil; godoliva@yahoo.com.br.

INTRODUCTION

Drought is an abiotic stress that affects plants at various levels, from cells and organs to the whole plant (SKIRYCZ; INZÉ, 2010). It is a natural weather phenomenon, which consists of less precipitation than expected for a given period of time (AL-TIMIMI; AL-JIBOORI, 2013). The water stress caused by drought causes different biochemical and physiological responses of plants and is the environmental factor that most affects plant growth and production worldwide.

Stomatal closure is one of the first processes induced by water stress in plants, thus the net CO_2 assimilation rate (A) is directly affected (CHAVES et al., 2009). Decreases in A, as a response to water stress, are observed in palm trees such as *Bactris gasipaes* Kunth (OLIVEIRA et al., 2002), *Euterpe oleracea* Mart. (CALBO; MORAES, 2000), *Cocos nucifera* L. (GOMES et al., 2008) and *Elaeis guineenses* Jacq. (SURESH et al., 2010, 2012). One of the first effects of a decreased A is the reduction of primary productivity, resulting in growth and dry matter accumulation reductions (CHAVES et al., 2009).

Other gas exchange parameters are also reduced in palms as a response to water stress, e.g., stomatal conductance (g_s) and transpiration (E) (GOMES et al., 2008; SURESH et al., 2010, 2012). Stomatal closure is often considered as an early physiological response to drought, resulting in a decreased A, by limiting the CO_2 availability in the leaf mesophyll (CHAVES et al., 2009; VARONE et al., 2012). Galmés et al. (2007) stated that the limitations imposed by a reduced g_s to A are typically followed by a reduction in the atmospheric and intercellular CO_2 concentration ratio (C_i/C_a), suggesting that the photosynthetic apparatus is not affected, but only the C_i was reduced.

The ability that some plants have to recover CO_2 assimilation after a water deficit is essential for prevent or endure a water stress, and establishes the plant resistance to drought (CHAVES et al., 2009; SANTOS et al., 2014). The intensity and duration water stress are crucial factors that affect the photosynthesis recovery speed and extent (MIYASHITA et al., 2005). Analysis on the recovery of the different photosynthetic components after rehydration, considering different water stress intensities, are important for understand the physiological processes during plant rehydration (VARONE et al., 2012), which are essential for develop irrigation programs and improve the crop yield forecast accuracy based on weather data.

Few studies have evaluated the plant recovery phase after a water stress. This period is very significant for more accurately evaluate the plant acclimation capacity, since much of the metabolic damage to plants is expressed at this stage. Therefore, the soil intermittence water availability, due to its continued water losses (evapotranspiration) and intake (precipitation or irrigation), is very important, but often overlooked in studies of resistance and acclimation to drought. The simulation of intermittent periods of soil water availability in field conditions can be achieved from successive drought and rehydration cycles, using large volumes of soil in a greenhouse. Thus, the objective of this work was to evaluate the impact of three consecutive drought and rehydration cycles on the plant-water relations, gas exchange and dry matter accumulation in young macaw palm plants.

MATERIAL AND METHODS

Macaw palm (*Acrocomia aculeata* (Jacp.) Lodd. ex Mart.) seeds were collected from adult, healthy plants, with height ranging from 7 to 10 m, at full production, in Florestal MG (19°53'S, 44° 25'W). The seeds were germinated, and the seedlings were grown to the age of ten months by the company Acrotech Sementes e Reflorestamento Ltda., when they were donated for the experiment. The germination process was according to the methodology described by the Universidade Federal de Viçosa (2009).

The experiment was conducted in a greenhouse at the Federal University of Viçosa (20° 45'S, 42°52'W). The macaw palm seedlings were received on March 19 and transferred to 150 L conical pots with top diameter of 0.7 m, bottom diameter of 0.5 m and height of 0.5 m, filled with a substrate consisted of a mix of soil, sand and cattle manure at volume ratio of 3:1:1. The plants were grown in these pots for nine months. Soil fertilization were performed according to Pimentel et al. (2011). The plants were irrigated daily to maintain soil water content at field capacity (-9 kPa).

Maximum, mean and minimum daily air temperature and solar radiation inside the greenhouse were measured with a nonlinear thermistor and a LI-200SA pyranometer, respectively, both coupled to a LI-1200 Data Set Recorder (Li-Cor Biosciences, USA); and relative air humidity was measured with a thermohygrograph, calibrated with a ventilated wet-bulb psychrometer, throughout the experimental period (December 2008 to April 2009).

Nineteen-month old macaw palm seedlings, with ten replicates per treatment, were subjected to water stress, by suspend their irrigation until the net CO_2 assimilation rate (A) was near zero, which was considered as the maximum stress point (MSP). Then, the plants under water stress were rehydrated until the recovery of A was greater than 85% compared with the plants without water stress (control). Three drought and rehydration cycles were performed. Physiological measurements were performed at intervals of approximately 10 days, in leaflets of the middle region of the second fully expanded leaf, counted from the apex.

Gas exchanges were measured between 8:00h and 11:00h with a LI-6400 photosynthesis portable system (Li-Cor Biosciences, USA). Photosynthetically active radiation (PAR) and temperature of the measuring block were set at 1.500 mmol m^{-2} s^{-1} and 28°C, respectively, using the equipment accessories. PAR was measured with an artificial light source (Blue/Red, model 6400-02B, Li-Cor Biosciences, USA). The readings recorded by the equipment were stable within 3-4 minutes (CV <0.5%).

The different CO_2 concentrations for the response curves to CO_2 (AxC_i), developed from the MSP data, were obtained from cartridges containing 12 g of CO_2, automatically controlled by the LI-6400 CO_2 injector system (6400-01 Li-Cor). The measurements started at 50 mmol mol^{-1}, and were increased to 100, 200, 400, 700, 1.000 and 1.500 mmol CO_2 mol^{-1} of air in the measuring chamber, with intervals of 3-4 minutes. Gas exchange measurements for monitoring water stress showed that the atmospheric CO_2 (C_a) concentration ranged from 380 to 400 mmol mol^{-1}. Intracellular CO_2 (C_i) concentration and the C_i and C_a ratio (C_i/C_a) were calculated based on the net CO_2 assimilation rates (A), stomatal conductance (g_s) and transpiration (E).

Predawn leaf water potential (Ψ_{pd}) was measured at 4h30 in one leaflet per plant, using a Scholander pressure chamber (model Skye SKPM 1400, Skye Instruments LTD., UK). Pressure within the pressure chamber was increased slowly to a rate of 0.016 MPa s^{-1}, with compressed nitrogen. Substrate samples were collected at depth of 0.4 m and its gravimetric moisture was measured after drying at 105°C to constant weight, to determine its matric potential at the maximum stress point. Substrate samples were saturated with water and subjected to different pressures in a Richards' chamber (Richards, 1948), to develop the soil water characteristic curve. Gravimetric humidity values and the van Genuchten equation adjusted to the points of the soil water characteristic curve by using the software SWRC (DOURADO-NETO et al., 2000), were used to assess the matric potential of the substrate in the sample.

Root dry matter production, stem and leaves were quantified separately in plants with and without water stress by the end of the experiment. The roots were washed in running water to remove the substrate adhered to them and dried to a constant weight at 65°C.

The plants were arranged in a completely randomized design with ten repetitions in each treatment (with and without drought stress). Water use efficiency (*WUE*), was evaluated by the ratio of *A* and *E*. The data were subjected to analysis of variance and Tukey's test at significance level of 5% to assess the least significant differences. Statistical analyses were performed using the computer program Statistical Analysis System.

RESULTS AND DISCUSSION

The drought and rehydration cycles (DRC) 1, 2 and 3 lasted for 51, 31 and 31 days, with periods for the recovery of *A* above 85% of 9, 10 and 7 days, respectively. Gomes et al. (2008), observed DRC for *Cocos nucifera* of 44, 35 and 35 days for cycles 1, 2 and 3, respectively. The maximum, mean and minimum air temperature values were higher in cycle 2, and relative humidity in all DRC was similar (Table 1). Solar radiation had the highest intensity in cycle 2 and lowest in cycle 3. Thus, weather conditions may have influenced the recovery period of *A*, since the recovery time was numerically higher in the second cycle compared with the others. Moreover, weather conditions in cycle 2 were more adverse.

Table 1. Maximum (Tmax), minimum (Tmin) and mean (Tmean) air temperature, solar radiation (SR) and relative humidity (RH) inside the greenhouse where young macaw palm plants were cultivated, throughout drought and rehydration cycles.

Cycles	Tmax	Tmin	Tmean	SR	RH
		(°C)		(MJ m^{-2} d^{-1})	(%)
1	30.5b ±0.5	19.6ab ±0.2	23.5b ±0.2	11.7b ±0.6	80.0a ±1.0
2	33.8a ±0.4	20.3a ±0.1	25.2a ±0.2	14.7a ±0.6	76.9a ±1.1
3	30.3b ±0.4	19.3b ±0.3	23.1b ±0.2	9.7c ±0.5	79.7a ±0.7

Means followed by the same letter in the column do not differ by Tukey's test ($p \leq 0.05$).

The matric potential of the substrate of plants under water stress (PUWS) could not be estimated because it exceeded the limit of the methodology used, and thus below -1.5 MPa at the maximum stress point (MSP), i.e. when *A* was near zero. Gravimetric moisture of the substrate of PUWS at the MSP, was similar in the cycles, with average of 14.0%; in matric potential of -1.5 MPa this average was 14.6%, as assessed by the methodology used for develop the soil water characteristic curve.

Plants without water stress (PWWS) had predawn leaf water potential (Ψ_{pd}) average of -0.20 MPa during the experimental period (Figure 1A). The Ψ_{pd} of PUWS decreased progressively from the first evaluation after the irrigation suspension to an average of -1.9 MPa in MSPs, with no significant difference between the averages of the cycles.

Water potential values lower than those found in the present study were found in other palm species subjected to water stress, when *A* was reduced to near zero, such as *Euterpe oleracea* (-2.5 MPa) (CALBO; MORAES, 2000) and *Bactris gasipaes* (-1.9 MPa) (OLIVEIRA et al., 2002), however these authors have not described the evaluation time. Gomes et al. (2010) reported higher values of Ψ_{pd} (-1.2 MPa) in near-zero *A*, in *Cocos nucifera*. A fast recovery of Ψ_{pd} was observed after the rehydration in each cycle, with values similar to those observed in PWWS. Gomes et al. (2008) also reported satisfactory recovery of turgidity after rehydration in *Cocos nucifera*. The higher value of Ψ_{pd} in the first evaluation after irrigation suspension in cycles 2 and 3 shows that the plants had acclimation of Ψ_{pd} in these cycles compared with cycle 1.

The average net CO_2 assimilation rate of the three DRC in PWWS was 14.48 mmol m^{-2} s^{-1} (Figure 1B), and the *A* values were always lower in PUWS, except on day-zero of the experimental period. The average values of g_s and *E* in PWWS, during the three DRC were 0.155 mol m^{-2} s^{-1} and 2.42 mmol m^{-2} s^{-1}, respectively (Figure 1C and 1D). PUWS had g_s and *E* reductions at the beginning of each DRC, but they always recovered in the rehydration periods.

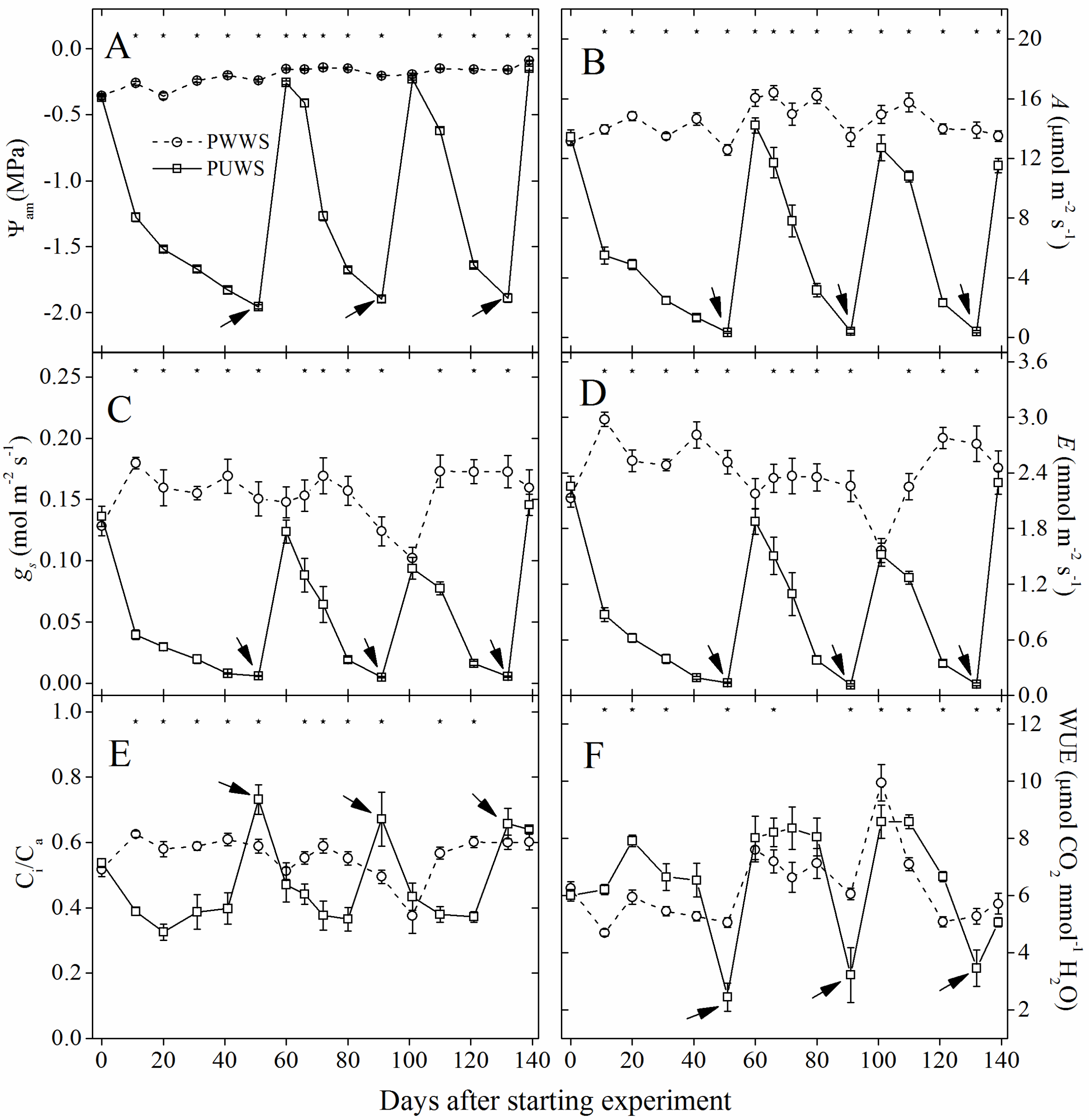

Figure 1. Predawn water potential (Ψ_{pd}; A), photosynthesis (*A*; B), transpiration (*E*; C), stomatal conductance (g_s; D), intercellular and atmospheric CO_2 concentration ratio (C_i/C_a; E) and water use efficiency (*WUE*; F) of young macaw palm plants. Error bars indicate the standard error of the mean. The symbol * indicates a significant difference ($p \leq 0.05$) between plants under water stress (PUWS) and without water stress (PWWS). The arrows indicate the time of rehydration.

The *A*, g_s and *E,* at the MSP, were reduced to less than 5% in PUWS compared with PWWS, with no difference between the averages of the cycles. These reductions caused by water stress were so severe that they became negligible in all cycles. Reductions in *A*, g_s and *E,* at MSP, with similar reduction intensities, were also observed by Gomes et al. (2009) in *Cocos nucifera* and Suresh et al. (2012) in *Elaeis guineensis*. Recovery of g_s and *E* was similar in the three cycles, with similar values in PUWS and PWWS at rehydration. Gomes et al. (2009) subjected *Cocos nucifera* to DRC and also observed g_s and *E* recoveries, but to a lesser extent compared with the results of macaw palm in the present work. The higher values of *A*, g_s and *E* in cycles 2 and 3, compared with cycle 1 in the first evaluation, after irrigation suspension in PUWS, show that they had acclimated.

The atmospheric and intercellular CO_2 concentration ratio (C_i/C_a) of PUWS was different than the C_i/C_a of PWWS, except on day zero, after rehydration and at the MSP of cycle 3 (Figure 1E). *Ci/Ca* was lower in PUWS at most of the experiment time, except at the MSP of cycles 1 and 2, when it was higher. Water use efficiency (*WUE*) was higher in PUWS, except at MSPs compared with PWWS (Figure 1F). The increase of *Ci/Ca* and reduction of *WUE* at MSPs indicates occurrence of a non-stomatal limitation of *A*, and suggests a possible damage in the photosynthetic apparatus, with photooxidative damage and metabolic limitations (MIYASHITA et al., 2005; CHAVES et al., 2009; PINHEIRO; CHAVES, 2011). Stomatal limitation was not reinforced by the absence of response of PUWS to the increase in CO_2 in the measurement chamber (Figure 2). The small increase of *A* in response to the increase in CO_2 concentration in the measuring chamber is probably due to the diffusion of CO_2 through the cuticle. Although this small flow is important, especially when *A* and g_s become negligible, as observed in PUWS (CHAVES et al., 2009).

The reductions of *A* and g_s, based on Ψ_{pd}, were almost linear, but the reduction of g_s starts at a lower value of Ψ_{pd} (Figure 3A and B). Therefore, the reductions of *A* were preceded by a decrease in g_s, which was also observed in *Bactris gasipaes* (OLIVEIRA et al., 2002) and *Mauritia vinifera* (CALBO; MORAIS, 1997). Gomes et al. (2009) found near-zero values of *A* and g_s in Ψ_{pd} of about -1.3Mpa in *Cocos nucifera*. Thus, macaw palm plants were approximately 45% more tolerant to drought than *Cocos nucifera*, considering *A* and g_s, since macaw plants these were zero only at Ψ_{pd} of about -1.85MPa.

The *Ci/Ca* ratio was lower than 0.40 at Ψ_{pd} from -0.5 to -1.85 MPa, and ranged from 0.40 to 0.65 within -0.2 and -0.5 MPa; such range was found in PWWS and PUWS at irrigation time (Figure 3C). The *Ci/Ca* increased and exceeded the value of 0.65 in Ψ_{pd} lower than -1.85 MPa; this increase coincided with the MSP. Similarly, at Ψ_{pd} of -0.2 to -0.5 MPa, the *WUE* was 4.5 and 8.0 μmol CO_2 $mmol^{-1}$ H_2O for PWWS and PUWS, respectively, at irrigation time (Figure 3D). At Ψ_{pd} of -0.5 to -1.85 MPa, the *WUE* increased, ranging from 6 to 9 μmol CO_2 $mmol^{-1}$ H_2O. At Ψ_{pd} below -1.85 MPa, the *WUE* decreased below 4 μmol CO_2 $mmol^{-1}$ H_2O, similarly to the MSPs.

The reduction of *Ci/Ca* and the increase of *WUE* at Ψ_{pd} of -0.5 to -1.85 MPa suggest a stomatal limitation, and the reduction of g_s preceding the reduction of *A* confirms that the stomatal limitation is the factor limiting photosynthesis. The Ψ_{pd} of -1.85 MPa was the limit in which *Ci/Ca* decreases and *WUE* increases, showing that it is the limit for the photosynthetic apparatus activity without damage, despite the reduced *A* and g_s. The *Ci/Ca* increased sharply below this Ψ_{pd} value, indicating that the use of intercellular CO_2 was possibly reduced by photooxidative damage (CHAVES et al., 2009; PINHEIRO; CHAVES, 2011). This photooxidative damage is probably caused by reactive oxygen species (ROS), generated by photochemical, and occurs when the energy dissipation mechanisms are not sufficient to disable these reactive molecules, such as the cycle of xanthophyll and the water-water cycle (PINHEIRO; CHAVES, 2011). Damage to the photochemical are linked to oxidation of chlorophylls and the D1 protein of PSII, such damage, occurring by excess reducing power, are generated by damming upstream of the electron flow. (CHAVES et al., 2009; SANTOS et al., 2014).

The growth of macaw palm plants was affected by the water stress, with reduction in total dry mass by 50% (Figure 4). The smaller dry matter accumulation in PUWS can be attributed, in part, to the reduction of *A*, and the reduction of tissue water potential, thus decreasing expansion and cell division (MULLER et al., 2011).

Roots and leaves were the most affected organs by water stress after the three DRC, both with reduction of 56% in PWWS, and shoot reduced by 48%. Similar result was found by Gomes (2010) in *Cocos nucifera*, with 60 and 48% of reduction for roots and shoots, respectively. The less affected organ by water stress was the stem, with 21% of reduction in PUWS compared with PWWS. The results of dry matter accumulation showed no change in the root/shoot ratio, in contrast to the expected results, because there is often an increase in biomass to the root, under water stress conditions (GLYN BENGOUGH et al., 2011), as observed by Gomes et al. (2010) in *Cocos nucifera* subjected to DRC.

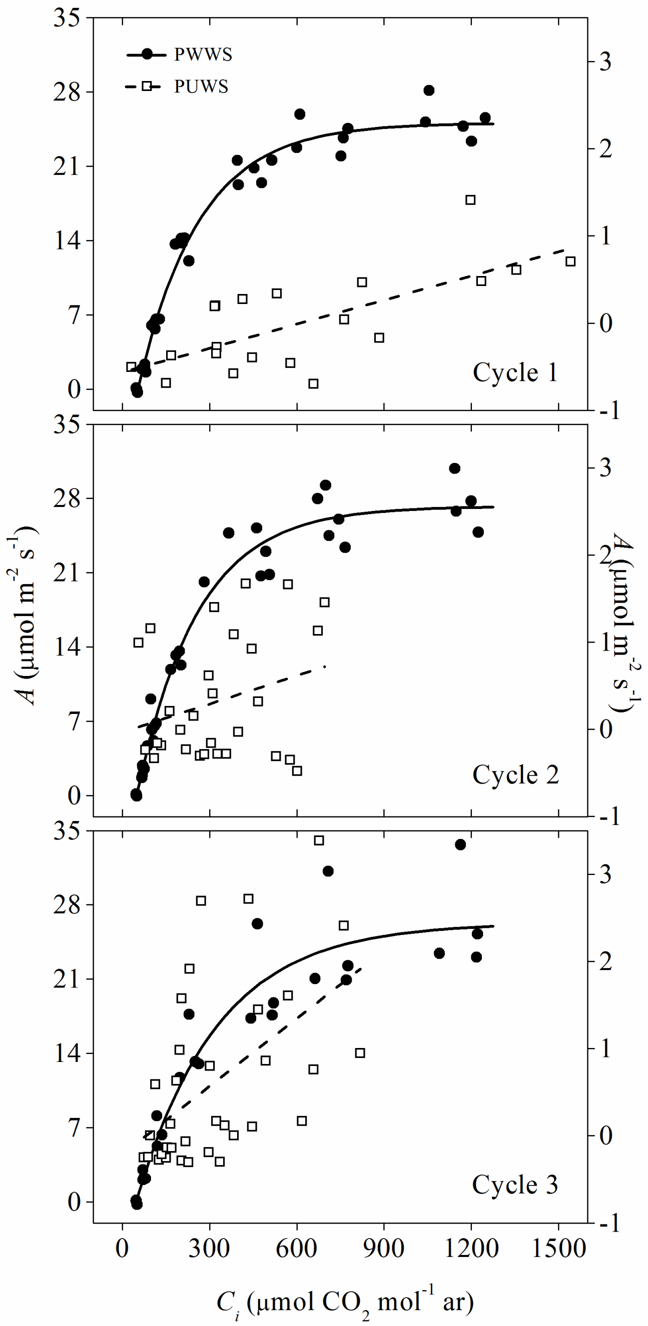

Figure 2. Photosynthetic response curves (*A*) to intercellular CO_2 concentration (C_i), in young macaw palm plants under water stress (PUWS) and without water stress (PWWS).

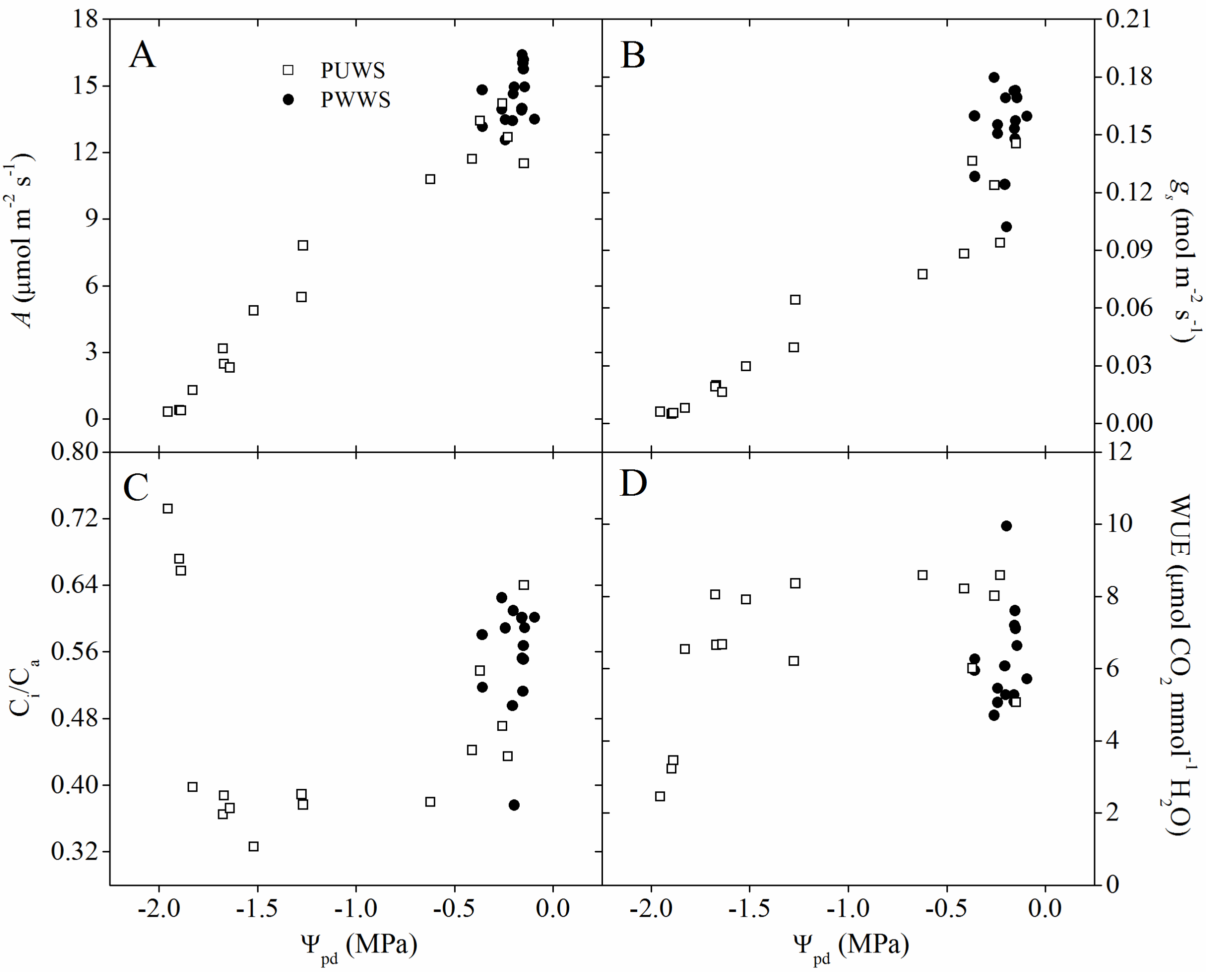

Figure 3. Photosynthesis (A, A), stomatal conductance (g_s, B), intercellular and atmospheric CO$_2$ concentration ratio (C_i/C_a, C) and water use efficiency (WUE, E) based on predawn leaf water potential (Ψ_{pd}) of young macaw palm plants under water stress (PUWS) and without water stress (PWWS).

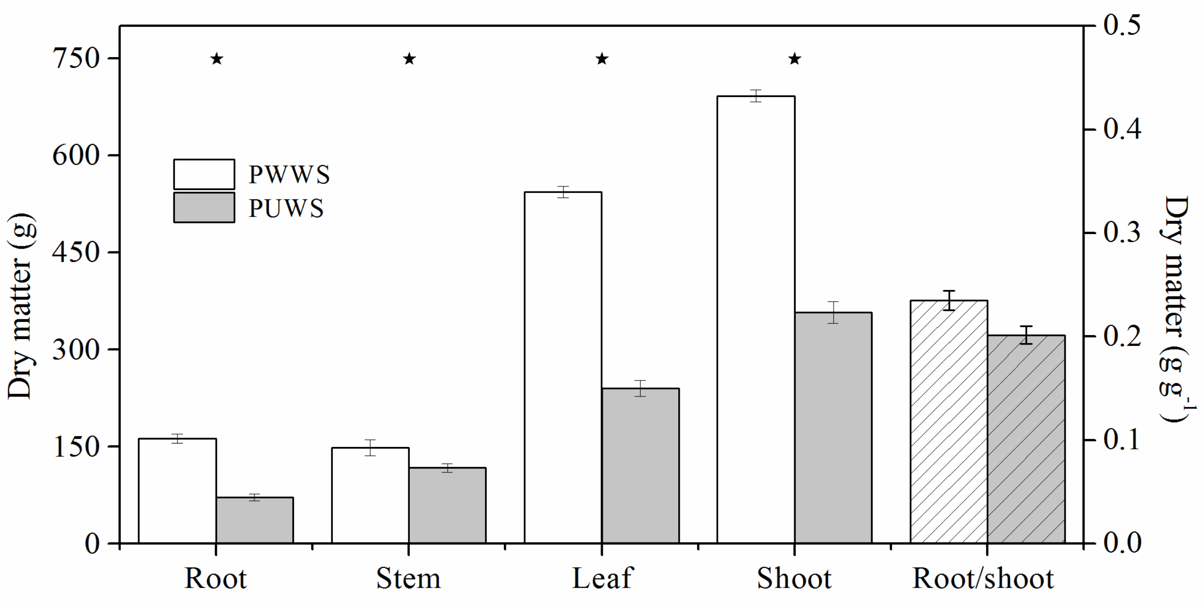

Figure 4. Dry matter in different organs and root/shoot ratio of macaw palm plants. Error bars indicate standard errors of the mean. The symbol * indicates a significant difference (p≤0.05) between plants under water stress (PUWS) and without water stress (PWWS).

CONCLUSIONS

Water restriction in macaw palm causes severe reduction of photosynthesis, however, when applied intermittently can promote acclimation of photosynthesis. Despite the restriction of gas exchange by drought, after rehydration (irrigation), the values recover. The application of water stress with lower leaf water potential (1.85MPa) provides no stomatal limitation of photosynthesis. Water restriction causes severe reduction in dry matter accumulation.

ACKNOWLEDGEMENTS

The authors thank the Fapemig (Minas Gerais State Research Foundation) for partially funding this work.

REFERENCES

AL-TIMIMI, Y. K.; AL-JIBOORI, M. H. Assessment of spatial and temporal drought in Iraq during the period 1980-2010. **International Journal of Energy and Environment**, Najaf, v. 4, n. 2, p. 291-302, 2013.

CALBO, M. E. R.; MORAES, J. A. P. V. Efeitos da deficiência hídrica em plantas de *Euterpe oleracea* (açaí). **Revista Brasileira de Botânica**, São Paulo, v. 23, n. 3, p. 225-230, 2000.

CALBO, M. E. R.; MORAES, J. A. P. V. Fotossíntese, condutância estomática, transpiração e ajustamento osmótico de plantas de buriti submetidas a estresse hídrico. **Revista Brasileira de Fisiologia Vegetal**, Campinas, v. 9, n. 2, p. 117-123, 1997.

CHAVES, M. M.; FLEXAS, J.; PINHEIRO, C. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. **Annals of Botany**, London, v. 103, n. 4, p. 551-560, 2009.

DOURADO-NETO, D. et al. Software to model soil water retention curves (SWRC, version 2.00). **Scientia Agricola**, Piracicaba, v. 57, n. 1, p. 191-192, 2000.

GALMÉS, J.; MEDRANO, H.; FLEXAS, J. Photosynthetic limitations in response to water stress and recovery in Mediterranean plants with different growth forms. **New Phytologist**, Oxford, v. 175, n. 4, p. 81–93, 2007.

GLYN BENGOUGH, A. et al. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. **Journal of Experimental Botany**, Lancaster, v. 62, n. 1, p. 59–68, 2011.

GOMES, F. P. et al. Photosynthetic limitations in leaves of young brazilian green dwarf coconut (*Cocos nucifera* L. '*nana*') palm under well-watered conditions or recovering from drought stress. **Environmental and Experimental Botany**, Amsterdam, v. 62, n. 3, p. 195-204, 2008.

GOMES, F.P. et al. Is abscisic acid involved in the drought reponses of brazilian green dwarf coconut? **Experimental Agriculture**, New York, v. 45, n. 2, p. 189-198, 2009.

GOMES, F. P.et al. Osmotic adjustment, proline accumulation and cell membrane stability in leave of *Cocos nucifera* submitted to drought stress. **Scientia Horticulturae**, Amsterdam, v. 126, n. 3, p. 379-384, 2010.

MIYASHITA, K. et al. Recovery responses of photosynthesis, transpiration, and stomatal conductance in kidney bean following drought stress. **Environmental and Experimental Botany**, Amsterdam, v. 53, n. 2, p. 205-214, 2005.

MULLER, B. et al. Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. **Journal of Experimental Botany**, Lancaster, v. 62, n. 6, p. 1715–1729, 2011.

OLIVEIRA, M. A. J. et al. Fotossíntese, condutância estomática e transpiração em pupunheira sob deficiência hídrica. **Scientia Agricola,** Piracicaba, v. 59, n. 1, p. 59-63, 2002.

PIMENTEL, L. D. et al. Recomendação de adubação e calagem para o cultivo da macaúba: 1a aproximação. **Informe Agropecuário**, Belo Horizonte, v. 32, n. 265, p. 20-31, 2011.

PINHEIRO, C.; CHAVES, M.M. Photosynthesis and drought: can we make metabolic connections from available data? **Journal of Experimental Botany**, Lancaster, v. 62, n. 3, p. 869-882, 2011.

RICHARDS, L. A. Porous plate apparatus for measuring moisture retention and transmission by soils. **Soil Science**, Baltimore, v. 66, n. 2, p. 105–110, 1948.

SANTOS, O. O. et al. Desempenho ecofisiológico de milho, sorgo, e braquiária sob déficit hídrico e reidratação. **Bragantia**, Campinas, v. 73, n. 2, p. 203 -212, 2014.

SKIRYCZ, A.; INZÉ, D. More from less: plant growth under limited water. **Current Opinion in Biotechnology**, London, v. 21, n. 2, p. 197–203, 2010.

SURESH, K. et al. Changes in photosynthetic activity in five common hybrids of oil palm (*Elaeis guineensis* Jacq.) seedling under water deficit. **Photosynthetica**, Praha, v. 50, n. 4, p. 549-556, 2012.

SURESH, K. et al. Gas-exchange characteristics, leaf water potential and chlorophyll a fluorescence in oil palm (*Elaeis guineensis* Jacq.) seedlings under water stress and recovery. **Photosynthetica**, Praha, v. 48, n. 3, p. 430-436, 2010.

Universidade Federal de Viçosa. **Processo de germinação e produção de sementes pré-geminadas de palmeiras do gênero Acrocomia.** Disponível em: https://gru.inpi.gov.br/pePI/servlet/ImagemDocumentoPdfController?CodDiretoria=200&PswdID=ew82p&NumeroID=7f8fdbd8762ec92f6fa7fd5533b854aa2a4e0b906147d250019db1dcf624b8f6&codPedido=744932. Acesso em 10 jun. 2016.

VARONE, L. et al. Stomatal and non-stomatal limitations to photosynthesis in seedlings and saplings of Mediterranean species pre-conditioned and aged in nurseries: Different response to water stress. **Environmental and Experimental Botany**, Amsterdam, v. 75, p. 235-247, 2012.