Full Length Research Paper

The relationship between succulence and shoot biomass differences according to nutritional status in *Jatropha curcas* L.

Maicon Wandermaz dos Santos[1], Camila Figueiredo da Silva[1], Marcel Giovanni Costa França[2], Everaldo Zonta[1] and Roberto Oscar Pereyra Rossiello[1]*

[1]Departamento de Solos, Rodovia BR 465, Universidade Federal Rural do Rio de Janeiro, Km 7, Seropédica, Rio de Janeiro, CEP: 23.851-970, Brasil.
[2]Departamento de Botânica, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, Pampulha, Belo Horizonte, Minas Gerais, CEP: 31270-901, Brasil.

Diverse types of studies have examined the application of *Jatropha curcas* L. as a source of biofuel. Mineral nutrition levels modify the patterns of crops' growth and productivity, as well as the expression of morphophysiological traits of adaptive value. This study investigated the effects of nutrient solution concentration on biomass partition patterns and morphological attributes linked to water content in organs of *J. curcas*. Selected seedlings of accession 842 were cultivated in full experimental nutritive solution, and in solutions diluted to half concentration and a quarter concentration, all adjusted to pH 6.0. After 28 days under controlled conditions, plants were harvested and measured for height, leaf area and fresh and dry mass of leaves, petioles, stems, roots and total mass. From these data, specific leaf mass, leaf succulence and stem water content levels were calculated. The results indicated that according to increased nutritive solution concentration, plant shoots had up to a two-fold increase in height, and that a decrease in these concentrations caused drastic root and total dry mass reduction. At full concentration, there was a tendency towards dry mass allocation in roots. Comparatively, leaf traits were very sensitive to nutritional level without affecting leaf succulence. Contrastingly, relative to stems, these values significantly increased according to increased nutritive concentration. It could be concluded that beyond its productive importance, the nutritional level available to these plants exerts a positive influence on tissue water contents of succulent stems, whose ecophysiological importance demand additional studies.

key words: Leaf area, relative concentration of nutritive solution, specific leaf dry mass, stem succulence.

INTRODUCTION

Among the oleaginous plants grown with bioenergy purposes, *Jatropha curcas* L., a shrubby species of the Euphorbiaceae family, has received considerable attention as a possible raw material for biodiesel

*Corresponding author. E-mail: rossielo@terra.com.br

Figure 1. Partial view of *J. curcas* plants in the growth room: seedlings of access 852 (from Petrolina, Pernambuco State, Brazil) grown in plastic pots containing Hoagland and Arnon nutritive solution (1950), at three levels of dilution, with five repetitions.

production (Jongschaap et al., 2009). This use is based on a high potential of oil accumulation in the seeds (27-40%) and for being a perennial non-edible species, thus not competing with food crops for agricultural lands (Achten et al., 2008). Originating in Central America, and widely distributed in tropical and subtropical regions, the species has been celebrated for its rusticity, evidenced by its adaptation to diverse edapho-climatic conditions (Makkar and Becker, 2009; Divakara et al., 2010). However, *J. curcas* can still be considered a semi-wild species, in process of domestication and without defined cultivars (King et al., 2009), where many physiological and agronomic aspects remain open to investigation (Achten et al., 2010).

A structural property of *J. curcas* is the succulence of its stem tissues (Maes et al., 2009), a characteristic present in many species of the Euphorbiaceae family (Lüttge, 2008; Mwine and Van Damme, 2011). Generally, tissue succulence is associated with the occurrence of Crassulacean acid photosynthetic metabolism (CAM) or intermediate C_3/CAM in leaves or stems (Virzo de Santo et al., 1983; Martin et al., 1990; Hastilestari et al., 2013). In leaves, the succulence is related to the capacity for water storage by leaf area unit (Mantovani, 1999), while in stems, it can be approached by its water content, according to Maes et al. (2009).

Among the determinants of plant productivity, knowledge of nutritional requirements is essential for the proper formulation of crop fertilization practices. In this respect, various aspects of mineral nutrition of *J. curcas* have been focused in recent years (Laviola and Dias, 2008; Fernandes et al., 2013; Freiberger et al., 2014). Beyond its direct contribution to the formation of total biomass and its distribution between organs during the growth cycle of the plant, mineral nutrition level influences the expression of important morphological attributes for the adaptation of the species to diverse environmental conditions (McDonald et al., 1996; Illenseer and Paulilo, 2002). However, in respect to mineral nutrition of *J. curcas*, available information relative to both types of influences is quite limited.

For these reasons, our working hypothesis was that the nutritional level available for the initial vegetative growth of *J. curcas* exerts combined influences on biomass production and distribution as well as on morphological traits linked to tissues' water content.

MATERIALS AND METHODS

The experiment was conducted in the Department of Soils of the Federal Rural University of Rio de Janeiro (UFRRJ), Brazil (22°45'48"S; 43°41'23"W), in controlled environmental conditions. Mature seeds of the accession 842, from the UFRRJ *Jatropha* Germoplasm Bank, originally collected in Petrolina, Pernambuco State, Brazil (09°23'55"S; 40°30'03"W) were superficially disinfected (NaClO, 2%, 2 min) and submitted to germination in a greenhouse, using plastic trays filled with autoclaved sand (101.3 kPa; 120°C; 60 min) as substrate.

Initially, the seeds were embedded with distilled water and, after 10 days, were supplied with Hoagland and Arnon solution (1950) diluted to 10%. After complete germination and emergence, seedlings of uniform size, visually free of diseases, were transferred to pots of 3.0 dm^3 (two plants pot^{-1}), containing the experimental solutions (treatments): Hoagland and Arnon full solution, equivalent to Relative Concentration (RC) =1.0; solution diluted to half concentration (RC = 0.5); or solution diluted to a quarter of original concentration (RC = 0.25), with the pH adjusted to 6.0 ± 0.1. The pots remained under pre-programmed environmental conditions (photosynthetic irradiance: 450 µmol m^{-2} s^{-1}; photoperiod: 12 h; day/night air temperature: 28/24°C), placed according to an entirely randomized experimental design with five replications (Figure 1).

The solutions were changed at 7-day intervals and, during this period, the volume of water lost by seedling transpiration was

restored with an equal volume of nutritive solution, according to each treatment. During the experimental period, stem height (taken as the distance between the base of the stem and the extremity of the terminal bud in the main branch) and principal root length were measured repeatedly. After 28 days, plants were harvested and fractionated into leaf (L), petiole (P), stem (S) and root (R). Subsequently, these fractions were weighed to obtain the respective fresh masses (LFM, PFM, SFM and RFM), and as soon as possible placed for drying in a forced air oven at 65°C until constant mass, to obtain the corresponding dry masses (LDM, PDM, SDM and RDM). Leaf area (LA) was determined through digital analysis of images obtained with an HP scanner at 200 dpi resolution, and processed with the software SIARCS® 3.0 (Integrated System for Roots and Soil Coverage Analysis developed by Embrapa - Agricultural Instrumentation, Brazil). From these data, the following traits were calculated: Root and stem elongation rate (ER, mm day^{-1}) and specific leaf mass (DML LA^{-1}), leaf succulence from the expression LS = (LFM - LDM) LA^{-1} (Evans, 1972; Moreira et al., 2009), and stem water content (SWC, %), calculated as: 100* [1- (DMS FMS^{-1})]. The results obtained were submitted to variance analysis, treatments being discriminated by test F (P ≤ 0.05), and the means compared by Tukey test (P = 0.05).

RESULTS AND DISCUSSION

At the end of the growth period, plants differed significantly in height (F= 15.13; P = 0.0005), since stem elongation rate of plants grown in the full solution was 2.2 fold higher than those of plants grown in the more diluted solutions (3.82; 2.8 and 1.73 mm day^{-1} for RC = 1.0, 0.5 and 0.25, respectively). In roots, the pattern was slightly different since there was no significant difference in the root elongation rate (RER) of plants grown in RC = 1.0 or 0.5 (6.28 vs. 6.14 mm day^{-1}). However, in RC = 0.25, the RER was drastically reduced (2.89 mm day^{-1}).

In relation to total dry mass production (TDM), the data indicate that *J. curcas* plants significantly reduced their production (36.2%) in RC = 0.25 (Figure 2A). This result confirms recent information indicating that although *J. curcas* can adapt its growth to nutrient-poor soils (Divakara et al., 2010), it responds positively to fertilization practices in terms of production of dry mass and seeds (Yong et al., 2010; Lima et al., 2011; Prates et al., 2012; Freiberger et al., 2014). In terms of TDM distribution, there was a tendency towards greater allocation in roots at RC = 1, since the root shoot^{-1} relationship varied from 0.145 to 0.132 g g^{-1} when the RC of the solution passed from 1.0 to 0.25 without, however, reaching statistical significance (P > 0.05).

In comparison to dry mass accumulation, leaf area (LA) production was more sensitive to nutritional level once, when RC = 0.25 the LA per plant was just 32.5% of that obtained from RC = 1 (Figure 2B). Experiments with *J. curcas* plants of diverse origins, cultivated in nutritive solution or solid substrate, in controlled environments or greenhouses, have shown positive results from the application of increasing supply of nitrogen and phosphate fertilizers regarding chlorophyll contents, photosynthetic assimilation and leaf area (Yong et al.,

2010; Lima et al., 2011; Prates et al., 2012). Thus, collectively, these previous studies support the present data by showing the stimulating effects of mineral nutrition on key biomass formation processes as light absorption and carbon assimilation.

Table 1 presents data relative to the distribution of fresh and dry mass between organs of shoots and roots. In relation to the effects of nutritive solution RC on fresh mass of various organs, the greatest contrasts were observed between RC = 0.25 and RC = 1.0, including significant reductions to the order of 70% for petioles (PFM) and roots (RFM); 52% for leaves (LFM) and 45% for stems (SFM). In all cases, the values corresponding to RC = 0.5 indicated intermediate reductions which reached statistical significance (P < 0.05) in the case of roots and petioles (Table 1). When data were expressed on a dry mass (DM) basis, there was an important modification in the reduction patterns induced by dilution of the nutrient solution: significant effects were only restricted to the leaf and petiole fractions (Table 1). However, the relative contribution of each fraction to total mass was affected by nutritional level (Figure 2*A*), particularly in stems, in which the ratio SDM TDM^{-1} varied from 0.436 to 0.36, when RC passed from 0.25 to 1.0. Correlatively, in leaves, the ratio LDM TDM^{-1} was inverted, varying from 0.39 to 0.432 in the same conditions.

Figure 3A presents the relationship FM DM^{-1} for leaves and stems. In leaves, this relationship remained stable in relation to RC values (4.30 - 4.68 g g^{-1}), reducing significantly only in RC = 0.25. In stems, the amplitude of this relationship was much greater, increasing 48% (from 5.48 to 8.11 g g^{-1}, P < 0.05), when RC changed from 0.25 to 1.0. Figure 3B presents data relative to specific leaf mass (SLM) showing decreasing values, statistically differentiated, from RC = 0.25 to the full solution (71.6; 48.3 and 39.4 g m^{-2} for RC = 0.25; 0.5 and 1.0, respectively). Maes et al. (2009), studied responses of *J. curcas* plants of 114 days in age to water deficit, obtaining a value of 183 cm^2 g^{-1} for specific leaf area (SLA), equivalent to SLM = 54.6 g m^{-2}, a value of the same magnitude as those presented here. Differences in SLM between and within species are due to variations in leaf density and/or thickness (Niinemets, 1999). It is interesting to observe that various studies have verified that leaf thickness increases are associated with decreasing levels of soil fertility (Hassiotou et al., 2010), a situation simulated in the present work by dilution of the original solution. It has been suggested that in these conditions, increases in leaf thickness are a compensatory mechanism for smaller leaf areas, in order to maintain leaf hydration levels (Mantovani, 1999). Contrastingly, greater values of SLM are associated with greater dilution (Figure 3B).

This suggests that the adaptive characteristics of *J. curcas* plants to their nutritional environments for growth have early expression at the seedling stage. SLM values
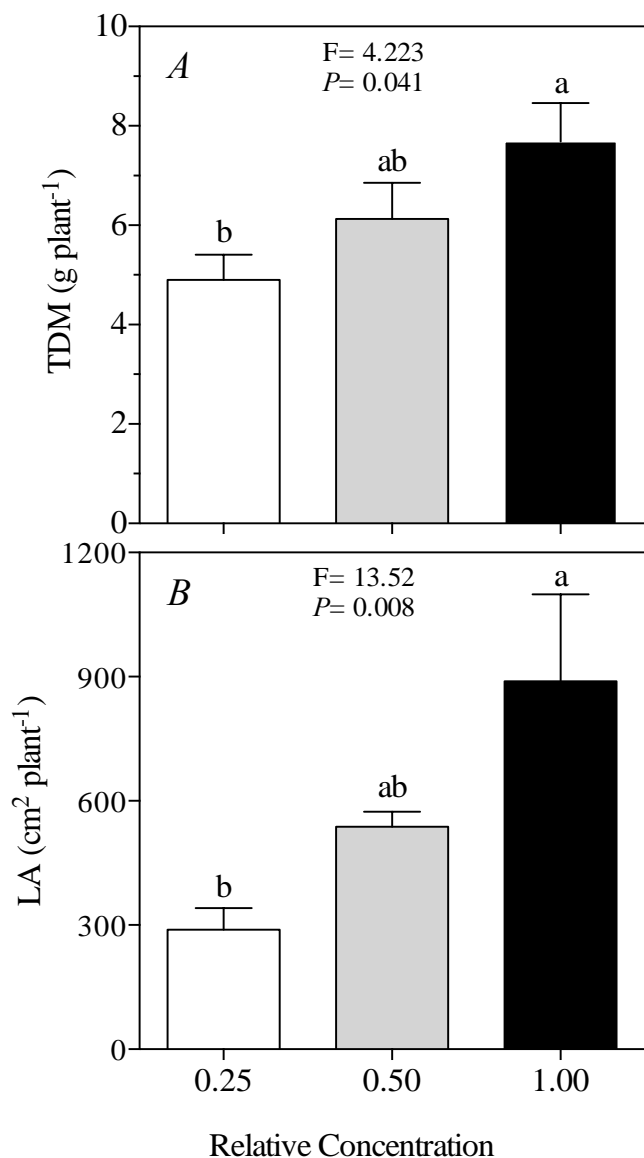
Figure 2. *A*. Total dry mass (TDM); *B*. Leaf area (LA), of *J. curcas* seedlings, grown for 28 days in three levels of relative concentration (RC) of nutritive solution. Values of RC correspond to full solution (1.0) or diluted to half (0.5) or quarter (0.25) of the original nutrient concentrations. Columns with the same lower-case letter on top do not differ significantly (Tukey, P < 0.05). Vertical bars indicate the standard error of means.

resulted inversely related with the corresponding DM FM^{-1} relationships (r = - 0.707; P = 0.032), but this did not affect leaf succulence levels, which oscillated, non significantly, between 140 - 190 g H_2O m^{-2}, with a tendency to increase in RC = 0.25 (Figure 4). These values can be considered low if compared with those reported by Mantovani (1999), and particularly with certain epiphytic bromeliad species with very succulent leaves, in the range of 650 - 850 g H_2O m^{-2} (Reyes-García et al., 2012).

In relation to stem water content levels (Figure 5), the result was very different, since these responded in a linear, positive form to crescent RC values (SWC = 80.43(± 0.74) + 7.48 (± 1.12) RC; r^2 = 0.773; n = 15). By fresh mass unit, stems of plants grown in RC = 1 contained about 6% more water than those cultivated in RC = 0.25 (SWC = 87.6 vs. 81.7%, respectively), while those in RC = 0.5 had an intermediate value. These differences in SWC between treatments are of considerable magnitude, which could be demonstrated by an estimate of its succulence, in approximate terms. Assuming that fresh mass value of an organ can be used as a proxy for their volume (Garnier et al., 1999) and considering its cylindrical morphology, stem succulence for RC = 0.25 corresponded to 1895 ± 60 g H_2O m^{-2}, while in RC = 1 this estimate was 2306 ± 144 g H_2O m^{-2}. These values are between ten and fifteen times greater than those corresponding in leaves (Figure 4). Thus, although the succulence of stems could be a structural characteristic in *J. curcas* (Maes et al., 2009), their water storage capacity by volume or surface area unit is determined by nutritional status available to plants (Figure 5).

Anatomical and morphological traits of shrub species with succulent stems have received research attention in recent years. These succulent stems are differentiated in an outer green photosynthetically active chorenchyma and an internal water storing hydrenchyma (Lüttge, 2008). Cell walls of water storage tissues have a lower modulus of elasticity than those of the chlorenchyma, so that they can absorb and release more water with small changes in turgor potential (Lüttge, 2008). In the cells of the peripheral stem chlorenchyma, that have thin walls and a large central vacuole (Cushman and Bohnert, 1997), water inflow should be favored by increases in the availability of inorganic solutes that regulate osmotic potential, as K^+, Cl^- and NO_3^- (Jones, 1980; Rodrigues et al., 2013). This could contribute to explaining the positive association observed between external nutrient concentration and water capacitance in stem tissues (Figure 5). In fact, in other plant species, a close correlation was previously observed between osmotic pressure increases (or decreases in osmotic potential) and succulence parameters (Lüttge, 2008).It has been suggested that *J. curcas* has the ability to combine C_3/CAM photosynthesis in succulent stems, while leaves are capable of altering their water use efficiency, changing their C_3 metabolism for CAM (Jongschaap et al., 2009). In *Euphorbia tirucalli*, a drought tolerant species with potential as a biofuel source, photosynthetic pathways include C_3 metabolism in non-succulent leaves and CAM in succulent stems (Hastilestari et al., 2013). Nevertheless, in the case of *J. curcas*, this strategy still needs experimental verification. Succulence is a plant characteristic with clear ecophysiological implications (Mantovani, 1999; Mwine and Van Damme, 2011), which in *J. curcas* plants, until now, has been mainly explored in

Table 1. Dry and fresh mass of leaves (L), petioles (P), stem (S) and roots (R), of *J. curcas* seedlings, grown for 28 days in three levels of relative concentration (RC) of nutritive solution.

RC	Fresh mass (g plant^{-1})			
	L	P	S	R
0.25	7.06[b]*	1.88[b]	11.72[b]	3.63[b]
0.50	10.96[ab]	3.40[b]	16.40[ab]	7.20[b]
1.00	14.64[a]	6.01[a]	21.35[a]	11.11[a]
C.V. (%)	21.9	31.4	21.6	27.9
	Dry mass(gplant^{-1})			
	L	P	S	R
0.25	1.93[b]	0.28[b]	2.16[a]	0.58[a]
0.50	2.58[ab]	0.35[b]	2.48[a]	0.72[a]
1.00	3.16[a]	0.56[a]	2.66[a]	0.93[a]
C.V. (%)	24.7	32.8	21.4	27.0

*Means following the same letter do not differ between them by Tukey test at 5%. C.V. = coefficient of variation.
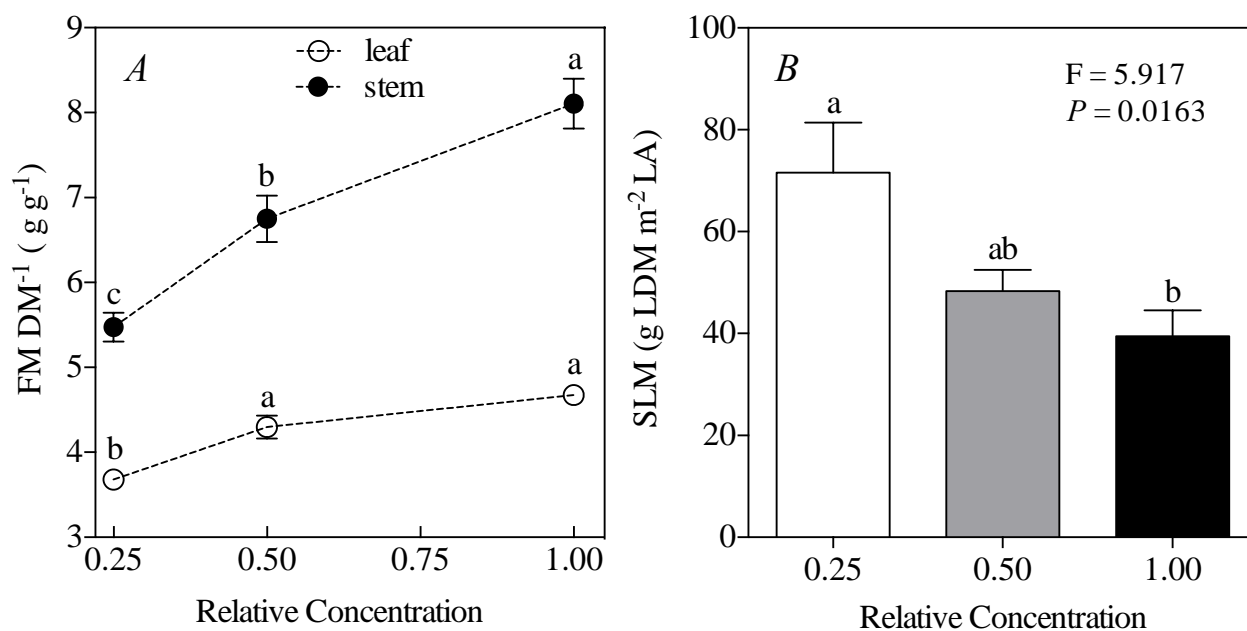

Figure 3. *A*. Fresh mass/dry mass (FM DM^{-1}) ratios; *B*. specific leaf mass (SLM) values of *J. curcas* seedlings, grown for 28 days, in three levels of Relative Concentration (RC) of nutritive solution. Values of RC are the same as Figure 2. Symbols (*A*) or columns (*B*) with the same lower-case letter at the top do not differ significantly (Tukey test P < 0.05). Vertical bars indicate means standard error.

in relation to its adaptation to environments characterized by water deficit or soil salinity (Maes et al., 2009; Arcoverde et al., 2011; Díaz-López et al., 2012; Rodrigues et al., 2013; Sapeta et al., 2013).

Conclusions

Taken together, the present results indicate that there is a potential for the optimization of growth and productivity of *J. curcas* by varying nutritional levels through the application of fertilizers. In particular, the nutrient status of the growth solution of young *J. curcas* plants exerts a direct influence on the production of assimilatory leaf area, as well as on accumulation and allocation of total biomass between different plant organs. At the same time, although nutritional levels do not alter leaf succulence levels, they directly affect the water storage capacity in stems.
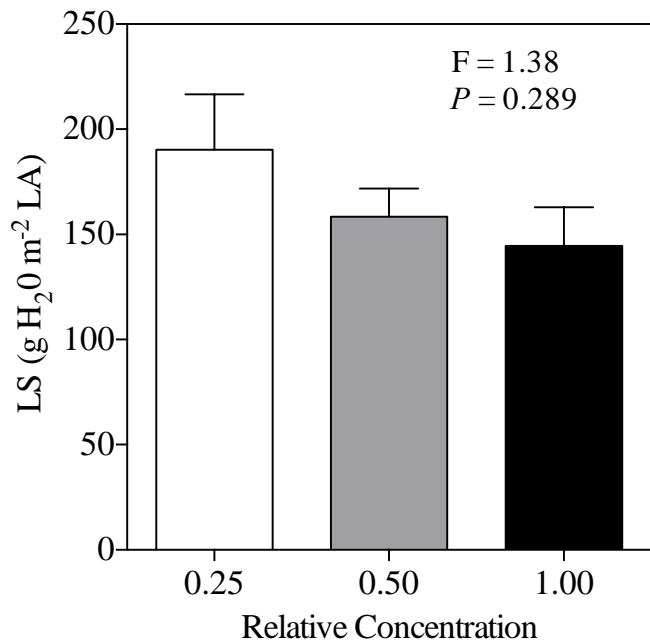
Figure 4. Succulence of fully expanded leaf (LS) of *J. curcas* seedlings, grown for 28 days in three levels of Relative Concentration (RC) of nutritive solution. Vertical bars indicate means standard error.
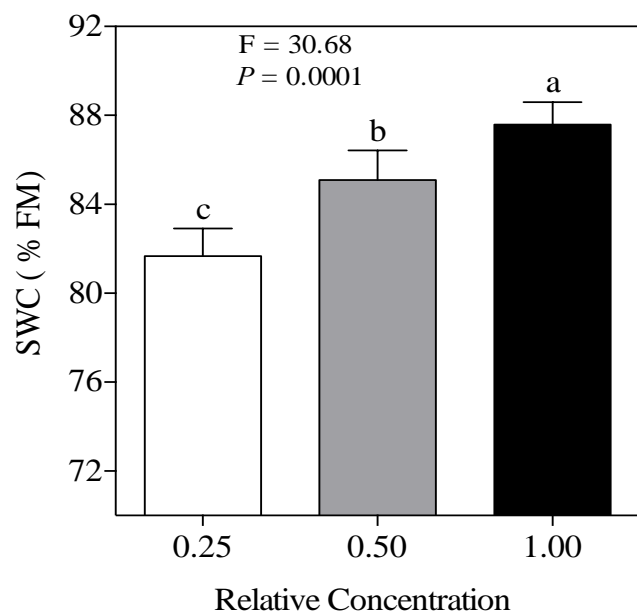

Figure 5. Stem water content (SWC, % FM) of *J. curcas* seedlings, grown for 28 days in three levels of relative concentration (RC) of nutritive solution. Different lower-case letters, at the top of columns, indicate significant differences (Tukey, $P < 0.05$). Vertical bars indicate means standard error.

Conflict of Interests

The authors have not declared any conflict of interests.

REFERENCES

Achten WMJ, Nielsen LR, Aerts R, Lengkeek AG, Kjaer ED, Trabucco A, Hansen JK, Maes WH, Graudal L, Akinnifesi FK, Muys B (2010). Towards domestication of *Jatropha curcas*. Biofuels 1(1):97-107. doi:10.4155/bfs.09.4.

Achten WMJ, Verchot L, Franken YJ, Mathijs E, Singh VP, Aerts R, Muys B (2008). *Jatropha* bio-diesel production and use. Biomass Bioenerg. 32(12):1063-1084. doi:10.1016/j.biombioe.2008.03.003.

Arcoverde GB, Rodrigues BM, Pompelli MF, Santos MG (2011). Water relations and some aspects of leaf metabolism of *Jatropha curcas* young plants under two water deficit levels and recovery. Braz. J. Plant Physiol. 23:123-130. doi.org/10.1590/S1677-04202011000200004.

Cushman JC, Bohnert HJ (1997). Molecular genetics of Crassulacean Acid Metabolism. Plant Physiol. 113(3):667-676.

Díaz-López L, Gimeno V, Lidón V, Simón I, Martínez V, García-Sánchez F (2012). The tolerance of *Jatropha curcas* seedlings to NaCl: An ecophysiological analysis. Plant Physiol. Biochem. 54:34-42. doi:10.1016/j.plaphy.2012.02.005.

Divakara BN, Upadhyaya HD, Wani SP, Laxmipathi Gowda CL (2010). Biology and genetic improvement of *Jatropha curcas* L.: A review. Appl. Energ. 87(3):732-742. doi:10.1016/j.apenergy.2009.07.013.

Evans GC (1972). The quantitative analysis of plant growth. Oxford: Blackwell, P 734.

Fernandes JD, Chaves LHG, Dantas JP, Silva JRP (2013). Fenology and production of *Jatropha* when grown with different sources of fertilization. Rev. Ciên. Agron. 44(2):339-346. doi.org/10.1590/S1806-66902013000200017.

Freiberger MB, Guerrini IA, Castoldi G, Ivetta LG (2014). Phosphorus fertilization on the early growth and nutrition of physic nut seedlings. Rev. Bras. Ciên. Solo 38(1):232-239. doi.org/10.1590/S0100-06832014000100023.

Garnier E, Salager JL, Laurent G, Sonié L (1999). Relationships between photosynthesis, nitrogen and leaf structure in 14 grass species and their dependence of the basis of expression. New Phytol. 143:119-129. doi:10.1046/j.1469-8137.1999.00426.x

Hassiotou F, Renton M, Ludwig M, Evans JR, Veneklaas EJ (2010). Photosynthesis at an extreme end of the leaf trait spectrum: how does it relate to high leaf dry mass per area and associated structural parameters? J. Exp. Bot. 61:3015-3028. doi.org/10.1093/jxb/erq128.

Hastilestari BR, Mudersbach M, Tomala F, Vogt H, Biskupek-Korell B, Van Damme P, Guretzki S, Papenbrock J (2013). *Euphorbia tirucalli* L. Comprehensive characterization of a drought tolerant plant with a potential as biofuel source. PLoS ONE 8:e63501. doi:10.1371/journal.pone.0063501

Hoagland DR, Arnon DI (1950). The water culture method for growing plants without soil - Circ 347, Berkeley: The College of Agriculture of University of California, P 34.

Illenseer R, Paulilo MTS (2002). Growth and nutrient use efficiency in *Euterpe edulis* Mart. seedlings under two levels of irradiance, nitrogen and phosphorus. Acta Bot. Bras. 16(4):385-394. doi.org/10.1590/S0102-33062002000400002.

Jones MM (1980). Turgor maintenance by osmotic adjustment: a review and evaluation. In: Turner NC and Kramer PJ. Adaptation of plants to water and high temperature stress. New York: Wiley Interscience, pp. 87-103.

Jongschaap REE, Blesgraaf RAR, Bogaard TA, van Loo EN, Savenije HHG (2009). The water footprint of bioenergy from *Jatropha curcas* L. Proc. Nat. Acad. Sci. 106:E92. doi:10.1073/pnas.0907272106.

King AJ, He W, Cuevas JA, Freudenberger M, Ramiaramanana D, Graham IA (2009). Potential of *Jatropha curcas* as a source of renewable oil and animal feed. J. Exp. Bot. 60(10):2897-2905. doi:10.1093/jxb/erp025.

Laviola BG, Dias LAS (2008). Nutrient concentration in *Jatropha curcas* L. leaves and fruits and estimated extraction at harvest. Rev. Bras. Ciên. Solo 32(5):1969-1975. doi.org/10.1590/S0100-06832008000500018 .

Lima RLS de, Severino LS, Gheyi HR, Sofiatti V, Arriel NHC (2011). Phosphorus fertilization on growth and contents of macronutrients in *Jatropha curcas* seedlings. Rev. Ciên. Agron. 42(4):950-956. doi.org/10.1590/S1806-66902011000400017.

Lüttge U (2008). Stem CAM in arborescent succulents. Trees 22(2):139-148. doi:10.1007/s00468-007-0198-z.

Maes WH, Achten WMJ, Reubens B, Raes D, Samson R, Muys B (2009). Plant–water relationships and growth strategies of *Jatropha curcas* L. seedlings under different levels of drought stress. J. Arid Environ. 73(10):877-884. doi:10.1016/j.jaridenv.2009.04.013.

Makkar HPS, Becker K (2009). *Jatropha curcas*, a promising crop for the generation of biodiesel and value-added coproducts. Eur. J. Lipid Sci. Technol. 111(8):773-787. doi:10.1002/ejlt.200800244.

Mantovani A (1999). A method to improve leaf succulence quantification. Braz. Arch. Biol. Technol. 42(1):9-14. doi.org/10.1590/S1516-89131999000100002.

Martin CE, Loeschen VS, Coke LB (1990). Crassulacean acid metabolism in selected terrestrial succulents in southeastern Jamaica, including two species in the Commelinaceae. Oecologia 84(1):99-102. doi:10.1007/BF00665601.

McDonald AJ, Ericsson T, Larsson CM (1996). Plant nutrition, dry matter gain and partitioning at the whole-plant level. J. Exp. Bot. 47:1245-1253. doi:10.1093/jxb/47.

Moreira ASFP, Lemos Filho JP, Zotz G, Isaias RMS (2009). Anatomy and photosynthetic parameters of roots and leaves of two shade-adapted orchids, *Dichaea cogniauxiana* Shltr. and *Epidendrum secundum* Jacq. Flora 204(8):604-611. doi:10.1016/j.flora.2008.08.003.

Mwine JT, Van Damme P (2011). Why do Euphorbiaceae tick as medicinal plants? A review of Euphorbiaceae family and its medicinal features. J. Med. Plant Res. 5(5):652-662. doi.org/journal/JMPR/article-abstract/E2D4CC218726.

Niinemets Ü (1999). Components of leaf dry mass per area —thickness and density— alter leaf photosynthetic capacity in inverse directions in woody plants. New Phytol. 144(1):35-47. doi:10.1046/j.1469-8137.1999.00466.x.

Prates FBS, Lucas C dos SG, Sampaio RA, Brandão Júnior D da S, Fernandes LA, Junio GRZ (2012). Growth of *Jatropha* seedlings in response to single superphosphate and rock-flour fertilization. Rev. Ciên. Agron. 43(2):207-213. doi.org/10.1590/S1806-66902012000200001.

Reyes-García C, Mejia-Chang M, Griffiths H (2012). High but not dry: diverse epiphytic bromeliad adaptations to exposure within a seasonally dry tropical forest community. New Phytol. 193(3):745-754. doi:10.1111/j.1469-8137.2011.03946.x.

Rodrigues CRF, Silva EN, Ferreira-Silva SL, Voigt EL, Viégas RA, Silveira JAG (2013). High K^+ supply avoids Na^+ toxicity and improves photosynthesis by allowing favorable K^+: Na^+ ratios through the inhibition of Na^+ uptake and transport to the shoots of *Jatropha curcas* plants. J. Plant Nut. Soil. Sci. 176(2):157-164. doi:10.1002/jpln.201200230.

Sapeta H, Costa JM, Lourenço T, Maroco J, Linde PV, Oliveira MM (2013). Drought stress response in *Jatropha curcas*: Growth and physiology. Environ. Exp. Bot. 85:76-84. doi:10.1016/j.envexpbot.2012.08.012.

Virzo de Santo A, Alfani A, Russo G, Fioretto A (1983). Relationship between CAM and succulence in some species of *Vitaceae* and *Piperaceae*. Bot. Gaz. 144(3):342-346. http://www.jstor.org/stable/2474430.

Yong JWH, Ng YF, Chen AYL (2010). Effect of fertilizer application on photosynthesis and oil yield of *Jatropha curcas* L. Photosynthetica 48(2):208-218. doi:10.1007/s11099-010-0026-3.