Australian Journal of Crop Science AJCS

AJCS 12(04):563-571 (2018) ISSN:1835-2707
doi: 10.21475/ajcs.18.12.04.pne835

Morpho-physiological adaptation of *Jatropha curcas* L. to salinity stress

Polyana Geysa da Silva Cavalcante, Claudiana Moura dos Santos, Humberto Cristiano de Lins Wanderley Filho, João Raphael Lima Avelino, Lauricio Endres*

Laboratory of Plant Physiology, Center of Agricultural Sciences, Federal University of Alagoas, Delza Gitaí Campus, BR 104 Km 85, Rio Largo City – AL, Brazil.

***Corresponding author: lauricioendres@hotmail.com**

Abstract

The aim of the current study is to assess the growth response, biochemical changes, photosynthetic pigments content and gas exchanges of physic nut (*Jatropha curcas*) grown under natural saline conditions. The experiment was arranged in a completely randomized design based on the following soil electrical conductivities: 0.29 dS.m^{-1} (control), 1.76 dS.m^{-1} (moderate salt concentration), 2.61 dS.m^{-1} (high salt concentration), 3.79 dS.m^{-1} (very high salt concentration). Physic nut plants were kept under saline conditions for 19 days in greenhouse. Plant growth analyses were performed on a weekly basis. Plant biomass allocation was quantified at the end of the experiment. Leaf gas exchange, stomatal conductance, Fv/Fm and quantum yield were quantified 102 days after planting. Photosynthetic pigments, amino acids, proline and carbohydrates in fresh leaf tissue were also quantified. The leaf antioxidant enzymes catalase (CAT) and ascorbate peroxidase (APX) were quantified. Although there was no alteration in biomass allocation, the initial growth of *J. curcas* was gradually reduced by increasing salt concentration, which was observed through reduced plant height, stem diameter, and total number of leaves. Soil electrical conductivity 3.79 dS.m^{-1} was lethal to seedlings. Seedlings exposed to salt stress had their photosynthesis, stomatal conductance, transpiration and effective photochemical efficiency reduced, and their catalase and ascorbate peroxidase enzyme activity increased. Amino acids, proline and carbohydrate concentrations increased due to salt stress, whereas there was decrease in the chlorophyll content. *J. curcas* is sensitive to soil salinity at electrical conductivity levels higher than 1.76 dS.m^{-1}. To some extent, salinity effects can be relieved by osmolyte accumulation and by greater antioxidant activity; however, these factors were not sufficient to keep plant growth within normal rates.

Introduction

Salt tolerance is often defined as the plant ability to keep continuous growth under high soluble salt concentrations while cell metabolism remains unchanged (Munns, 2002; Roy et al., 2014). Currently, plant capacity to tolerate saline soil is of great importance, because the number of problems caused by soil salinity increases on a yearly basis. Estimates predict that a large portion of the world's irrigated areas are degraded due to salinization (FAO, 2011; Gupta and Huang, 2014). Salinity can negatively affect plant growth and crop yield, particularly due to the osmotic and toxic effects from saline ions (Niu et al., 1995; Munns and Tester, 2008; Munns, 2010). Saline ions excessively absorbed by plants can lead to ionic toxicity, which is accumulated in the protoplasm. Cell metabolism disturbances affect the photophosphorylation, respiratory chain, nitrogen assimilation and protein metabolism rates (Munns, 2002). Plant response to salinity is a complex phenomenon, so that, several studies have been carried out in order to elucidate the mechanisms used by plants to adapt to salt stress (Munns, 2010; Rahnama et al., 2011; Deinlein et al., 2014; Roy et al., 2014; Gupta and Huang, 2014). The salt-tolerance of a certain species depends on the efficiency of physiological mechanisms that make plants more tolerant to high salt concentrations (Flowers, 2004; Moya et al., 1999; Lacerda et al., 2003).

Jatropha curcas L., known as physic nut (*pinhão-manso* in Brazil), is an oilseed species belonging to Family Euphorbiaceae, native to tropical America (Arruda et al., 2004; Gudeta, 2016). It presents relatively rapid growth and wide geographic distribution due to its strength. This species can grow in tropical wet and dry climate areas, as well as in arid lands or in stony soils. Physic nut seeds have high oil content (ranging from 30% to 50%), depending on the genotype and growing conditions; therefore, the species has high potential to be used in biodiesel production (Arruda et al., 2004; Divakara et al., 2010).

Many studies have reported different plant sensitivity depending on the salt application method (Campos et al., 2012; Díaz-López et al., 2012). Pinheiro et al. (2008) showed decreased leaf dry weight (by 43.7%) and stem dry weight (by 53.5%) in castor bean (*Ricinus communis* L.) grown in soil presenting electrical conductivity (EC) 8.54 dS m^{-1}. De Lima et al. (2015) also found decreased leaf dry weight (by 47.3%) and stem dry weight (by 43.2%) in castor bean 120 days after planting at irrigation water EC 3.9 dS m^{-1}.

The most commonly used method to set the sensitivity to salinity of *J. curcas* is the saline irrigation water (Campos et

al., 2012; Díaz-López et al., 2012; Silva et al., 2013; Hishida et al., 2014; Zhang et al., 2014); however, studies about the physiological responses of *J. curcas* to salinity under natural environment conditions remain scarce. Therefore, the present study was carried out in natural saline soil in order to better understand how *J. curcas* can tolerate saline soils. The aim of the present study was to assess the growth response, and the physiological and biochemical changes recorded in *J. curcas* subjected to natural saline conditions.

Results

Saline stress effect on leaf growth, biomass and area

Plant growth was drastically affected when plants were subjected to very high salt concentrations (soil EC 3.79 dSm^{-1}), which caused 85% plant death 23 DAP; plants grown under moderate and high salinity conditions showed growth suppression compared to that of plants grown in soil with no salt (control treatment) (Fig. 2). Plant height decreased by 26.3% and 45.6%, stem diameter decreased by 21% and 41.3%, and the number of leaves decreased by 18% and 64% under moderate to severe salinity conditions, fact that has contributed to dry matter reduction in physic nut plants (Figure 2). Moderate and high salt concentrations reduced root, stem and leaf biomass, and the specific leaf area (Table I), whereas leaf area was only affected by very high salt concentrations; it presented reduction of approximately 87% (Table I). Biomass allocated to different plant parts and shoot:root ratio were not affected by salinity. Total plant biomass decreased by 37.36 and 90.26%, respectively, under moderate and high salt concentration when it was compared to results shown by plants grown under non-stress conditions.

The effect of saline stress on gas exchanges and on the photochemical efficiency of leaves

Leaf gas exchanges were strongly affected by salinity, which led to consecutive stomatal conductance, transpiration and photosynthesis reduction, even under moderate salinity conditions (Fig. 3A, B and C). Saline stress reduced photosynthetic rates, which presented reduction close to 49% and 72% in the morning and 56% and 88% in the afternoon in plants cultivated under moderate to severe saline conditions, respectively (Figure 3C). The same happened with stomatal conductance and transpiration, which had reduction by 95% in plants cultivated under high salinty conditions when they were compared to plants cultivated in soil with no salt (Figures 3A, B). A similar response was recorded for the effective quantum yield (Fig. 3E); under salinity stress, plants did not show chronic photoinhibition. However, plants showed pronounced dynamic photoinhibition at noon, when soil salinity levels increased (Fig. 3D), which generates the trend of rapid recovery at the end of the day (Fig. 4D). Overall, F_v/F_m remained above 0.7 under all the assessed stress conditions early in the day (Fig. 3D). However, at periods of high sun radiation, plants presented F_v/F_m reduction by 12.4% and 17.8% under moderate to high salinity conditions, respectively. Similarly, effective photosystem II quantum yield (ΦPSII) recorded 24 and 51% reduction under moderate to severe salinity stress, respectively.

Salinity stress resulted in low stomatal conductance, which remained close to zero (Figure 4A); similar response was also recorded for photosynthesis and transpiration (Fig. 4B, C). Stomatal conductance remained practically constant throughout the day in plants grown under non-stress conditions; on the other hand, transpiration rates increased as temperature increased in parallel to VPD increase (Fig. 1F). Moderate salt stress also increased the dynamic photoinhibition, mainly in the afternoon, but it recovered its Fv/Fm at the end of the day. (Figure 4D).

Saline stress effect on the organic solutes and on the antioxidant enzyme

Salinity, even at moderate level, led to reduction in the chlorophyll, carotenoid and soluble protein contents (Fig. 5). Such reduction was remarkable in chlorophill *a,* which presented reduction by 21% and 53% in plants cultivated under moderate to severe salinity conditions, when they were compared to plants grown in soil without salt (Figure 5B). Similar responses were recorded for carotenoids and proteins showing reduction rates above 26% due to salt (Figures 5D, E).

Overall, only high salinity conditions caused amino acids and proline level increase and carbohydrate content reduction (Figure 5). Plants cultivated under high salinity conditions recorded 53% of increase in amino acids level (Figure 5F). The same happened with the proline level, which recorded 45% increase in response to severe saline stress (Figure 5G). Similarly, only severe salt stress led to higher activity of antioxidant enzymes such as ascorbate, peroxidase and catalase, as well as to increase by more than 50% in their activity under such conditions (Fig. 5 I, J).

Discussion

The present study showed that the dry weight reduction in *J. curcas* derived from moderate saline stress, fact that may indicate that growth suppression was primarily caused by the water restriction resulting from the salinity osmotic effect. Hishida et al. (2014) found decreased biomass production in *J. curcas* grown under salt stress. According to these authors, biomass production is strongly reduced in non-halophytic plants, because salt stress results in stomata closure, which reduces CO_2 fixation rates, photosynthetic activity and, consequently, plant growth. Accordingly, De Lima et al. (2015) found negative effect on the growth and productivity of castor beans grown under salt stress, even when the soil was irrigated with water presenting low salinity level.

Early in the morning, the photosystem II maximum quantum yield (Fv/Fm) dropped to lower than 0.7, fact that indicates dynamic photoinhibition in *J. curcas* plants grown under the highest salinity stress level. It probably happened due to the influence of NaCl ions, which can cause significant damages to components in the electron-transport chain (Ashraf and Harris, 2013). The restoration from dynamic photoinhibition in *J. curcas* plants was verified through increase in Fv/Fm at the end of the day. It allowed plants to repair damages caused to the photosynthetic components during salt stress. This recovery of the structural integrity of photosystem II was probably favored by lower irradiance in

Table 1. Leaf area, dry mass of leaves, root and stems, proportion of leaf (%), stem (%), root (%), root / shoot ratio, leaf area ratio (LAR) and specific leaf area (SLA) of Jatropha curcas plants submitted to different concentrations of NaCl control (0 g NaCl Kg-1 of soil), moderate salt stress (1 g NaCl Kg-1 of soil) and high salt stress (2 g NaCl Kg-1 of soil).

Morphological Parameters	Treatments		
	Control	Moderate Stress	Severe Stress
Leaf DM (g)	9.60 A	6.95 B	1.04 C
Stem DM (g)	21.14 A	12.87 B	2.02 C
Root DM (g)	7.03 A	3.84 B	0.62 C
Leaf area (cm^2)	2216.59 A	1856.34 A	296.33 B
% Leaf	25.41 A	29.36 A	28.21 A
% Stem	55.97 A	54.40 A	55.01 A
% Root	18.62 A	16.25 A	16.78 A
Total mass (g)	37.80 A	23.7B	3.70C
Root/Shoot	0.23 A	0.19 A	0.21 A
L A R (cm^2g^{-1})	58.68 A	78.45 A	80.70 A
S L A (cm^2g^{-1})	231.42 B	267.37 A	291.98 A

Means followed by the same letter do not differ at 5% probability by Tukey test.

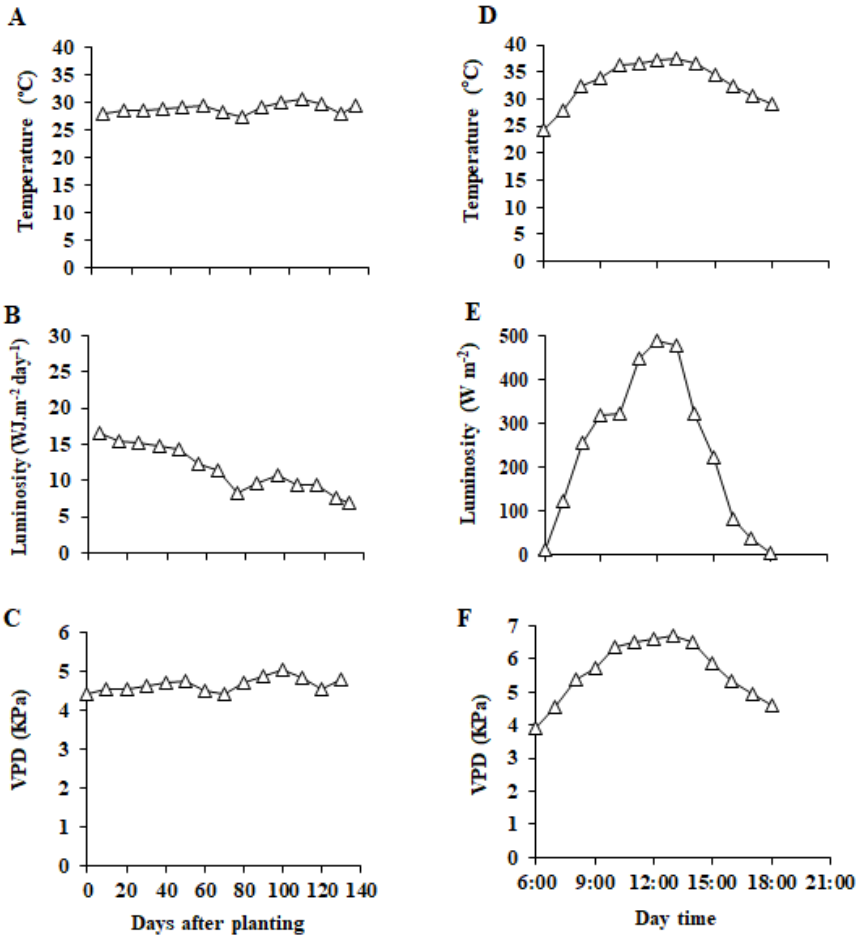

Fig 1. Mean temperature (ºC), luminosity (WJ m-2 day-1) and vapor pressure deficit (KPa) inside the greenhouse (090 27' 57,3" S e 350 49' 57,4" W), at a mean altitude of 127 meters, throughout the experiment and at 102 DAP (A, B e C) e Last day of experiment (D, E e F).

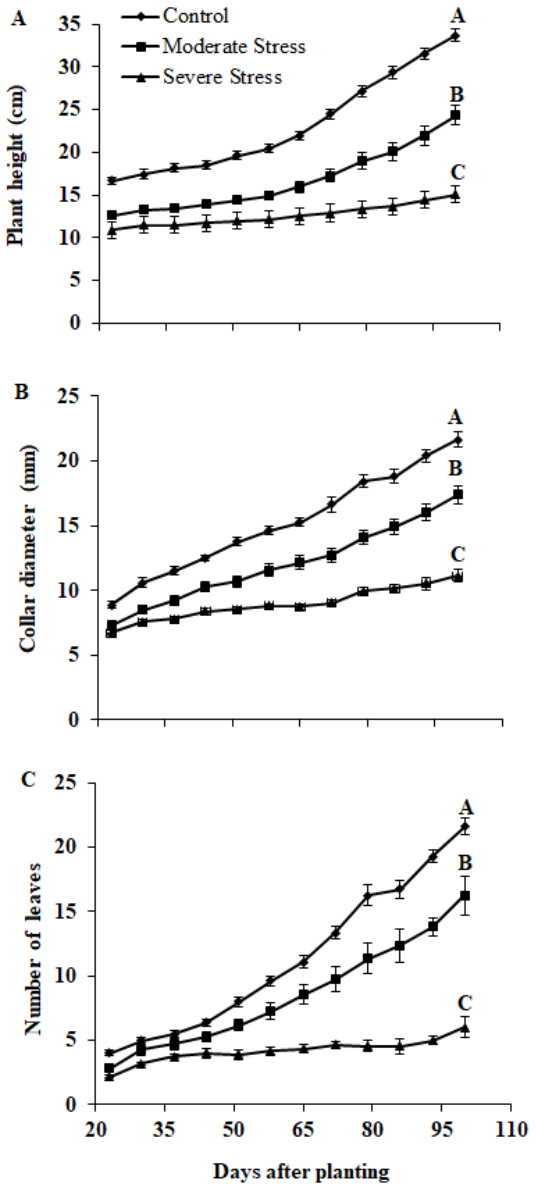

Fig 2. Plant height, cm (A), collect diameter, mm (B) and total leaf number (C) of Jatropha curcas plants submitted to different concentrations of NaCl control (0 g NaCl Kg^{-1} of soil), moderate salt stress (1 g NaCl Kg^{-1} of soil) and high salt stress (2 g NaCl Kg^{-1} of soil). The bars indicate the standard error of the mean. Means followed by the same letter do not differ at 5% probability by Tukey test.

combination with lower temperatures in the afternoon (Powles, 1984); these results were similar to those reported in other studies with *J. curcas* (Hishida et al., 2014). Nevertheless, Silva et al. (2013) demonstrated that saline solution irrigation for 14 days did not change the photochemical efficiency of photosystem II in young *J. curcas* plants.

J. curcas plants also showed decreased effective PSII quantum yield due to salinity increase in consequence of the negative effect of salt stress on the photosynthesis apparatus. Actually, several studies involving different plant species such as *Ricinus communis* L. (Li et al., 2010) and *Mangifera indica* L. (De Lucena et al., 2012) have shown that the PSII effective quantum yield progressively decreases when the salt content in soil solution increases.

Chlorophyll degradation under salt stress may indicate possible damages to the photosynthetic system in *J. curcas* leaves. Campos et al. (2012) also showed decreased total chlorophyll content in *J. curcas* grown under salinity conditions, but no such effect was observed in the carotenoid content. Overall, there is strong evidence that salt stress can reduce chlorophyll concentration, fact that has been attributed either to the decreased recovery ability of the photosynthetic apparatus or to lower chlorophyll synthesis caused by the decreased number of specific enzymes involved in pigment synthesis (Sharma and Hall, 1991; Vajpayee et al., 2000; Meeta et al., 2013).

The salinity–stress tolerance mechanism is known as the ability of plant cells to osmotically adjust and to accumulate organic solutes such as sugars and amino acids (Silveira et al., 2003). Our study showed that moderate salinity levels (EC 1.76 $dS.m^{-1}$) did not affect the amino acid, proline and carbohydrate; they were only affected by higher salt concentrations. However, Campos et al. (2012) found increased osmolyte levels in *J. curcas* plants cultivated in higher salt concentration (EC, 3.5 dS m^{-1}) in the irrigation water. Contradictory results about *J. curcas* seedlings were recorded by Díaz-López et al. (2012), who did not find any contribution from the osmotic adjustment resulting from osmolytes accumulation when plants were under salt stress. They showed that seedlings can tolerate saline irrigation water at EC up to 4 $dS.m^{-1}$. The different responses to osmolytes accumulation in *J. curcas* plants probably derive from the variety of methods used in soil salinization, since most studies focus on using saline irrigation water instead of saline soil.

The lower protein content in salt-stressed of *J. curcas* plants can be attributed to the salt-induced toxic effects caused by protein synthesis decrease and by protein hydrolysis increase (Levitt, 1980). Kumar et al. (2008) also found decreased protein content in *J. curcas* callus under 100 mM of NaCl; their findings corroborate the results in the present study. These results also corroborate other studies, such as that by Campos et al. (2012), who found decreased protein levels in *J. curcas* plants grown under saline conditions.

Higher CAT and APX activity in *J. curcas* plants subjected to extreme salinity conditions can be attributed to the increased levels of reactive oxygen species (ROS) often produced under high salinity condition (Zhang et al., 2016). A remarkable increase in the APX activity was observed in more salt-tolerant *Beta vulgaris* L. (Bor et al., 2003) and *Sesamum indicum* L. cultivars (Koca et al., 2007). Previous studies with *Triticum aestivum* L., *Oriza sativa* L., *Zea mays* L. evidenced that salt-tolerant genotypes had a more efficient antioxidative system (Sairam et al., 2002; Demiral and Turkan, 2005; De Azevedo Neto et al., 2006). According to Sreenivasulu et al. (1999), the increased enzyme activity of APX may play a key role in the tolerance to oxidative stress. The APX and CAT activity in our study remained unchanged under moderate salt stress. Therefore, it seems reasonable to assume that a non-enzymatic antioxidant system may be enough to neutralize ROS produced by the salt stress effects on *J. curcas* under moderate salinity level (Foyer and Noctor, 2003). Accordingly, Mittler (2002) also showed that the CAT activity only increased in tissues presenting the highest H_2O_2 content. The peroxisomal generation of H_2O_2 is favored by

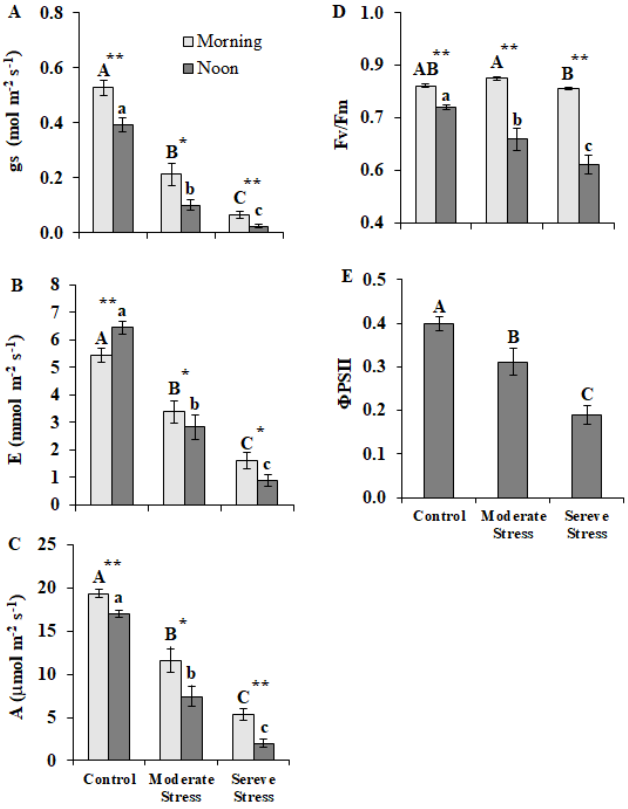

Fig 3. Stomatal conductance, gs (A), transpiration, E (B), photosynthesis, A (C), maximum quantum yield of photosystem II, Fv/Fm (D) and effective quantum yield of the photosystem II, ΦPSII (E) of Jatropha curcas plants submitted to different concentrations of NaCl control (0 g NaCl Kg-1 of soil), moderate salt stress (1 g NaCl Kg-1 of soil) and high salt stress (2 g NaCl Kg^{-1} of soil) in the morning and afternoon. Means followed by the same capital letters or lower case letters do not differ at 5% probability by Tukey test. Means in the same treatment for morning and afternoon followed by ** or * differ at 1% and 5%, respectively, by t-test.

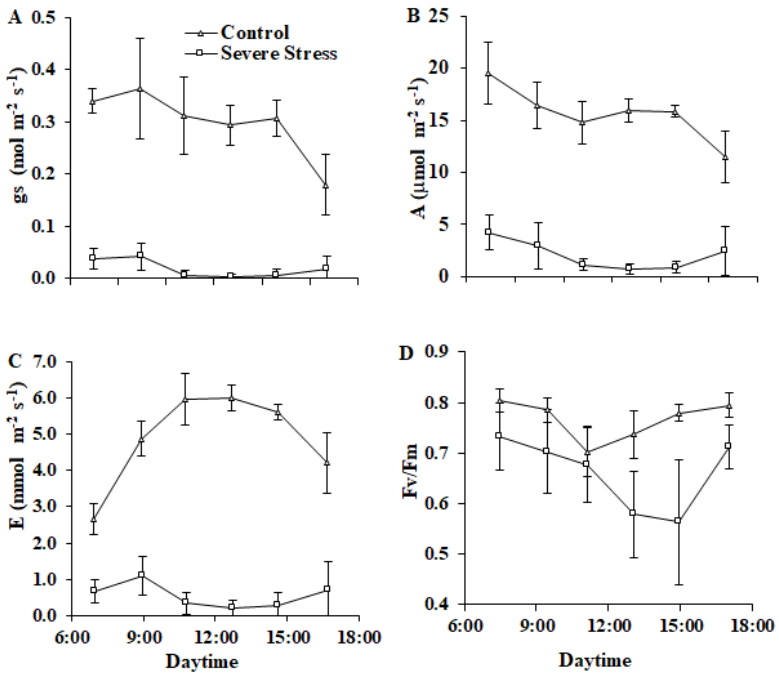

Fig 4. Stomatal conductance, gs (A), transpiration, E (B), photosynthesis, A (C), maximum quantum yield of photosystem II, Fv/Fm (D) of Jatropha curcas plants submitted to different concentrations of NaCl control (0 g NaCl Kg-1 of soil) and high salt stress (2 g NaCl Kg^{-1} of soil) throughout the day (last day of stress). The bars indicate the standard error of the mean.

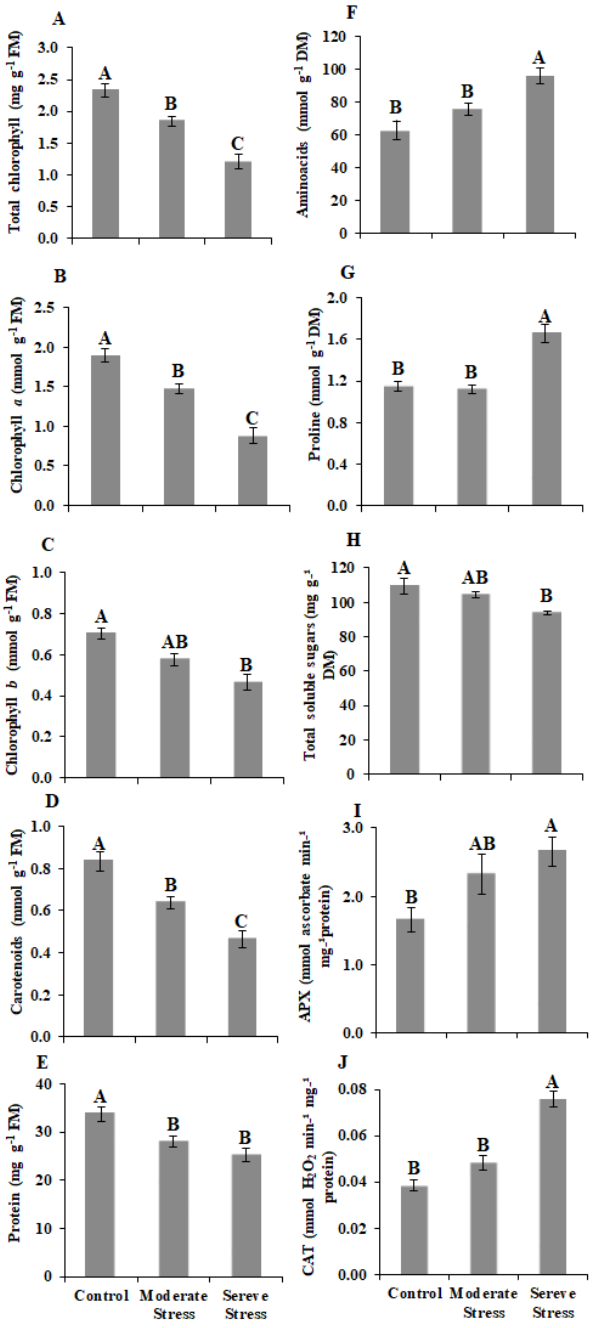

Fig 5. Total chlorophyll (A), Chlorophyll a (B), Chlorophyll b (C) and carotenoid concentrations (D), protein (E), amino acid (F), proline (G) carbohydrate (H) and antioxidant enzymes ascorbate peroxidase, APX (I) and catalase, CAT (J) of Jatropha curcas plants submitted to different concentrations of NaCl control (0 g NaCl Kg-1 of soil), moderate salt stress (1 g NaCl Kg-1 of soil) and high salt stress (2 g NaCl Kg^{-1} of soil). The bars indicate the standard error of the mean. Means followed by the same letter do not differ at 5% probability by Tukey test.

stress conditions; CAT eliminates excessive ROS accumulation, but organelle membranes are very permeable to H_2O_2, thus, the excessive ROS accumulation in the peroxisomes of *J. curcas* plants may migrate to cytosol and be eliminated by APX enzymes (Bienert et al., 2006; Davletova et al., 2005).

Materials and methods

Study area and experimental design

The experiments were conducted in greenhouse ($09^0$27'57.3"S, $35^0$49'57.4"W, 127 m) and arranged in completely randomized design, according to the following treatments: control (0 g NaCl Kg^{-1} of soil), moderate salt concentration (1 g NaCl Kg^{-1} of soil), high salt concentration (2 g NaCl Kg^{-1} of soil), and very high salt concentration (3 g NaCl Kg^{-1} of soil), with 12 repetitions per treatment. Each plot consisted of a pot containing 7 kg of soil.

Each pot received NaCl blended with soil, according to the dry soil weight. All pots were kept close to field capacity for seven months; fact that changed the physical and chemical properties of the soil, which were similar to the changes naturally recorded in salinized soils (Richard, 1954). Subsequently, the electrical conductivity (EC) of the saturated soil extract was measured through the EMBRAPA method (EMBRAPA, 1997)- EC values 0.29; 1.76; 2.61 and 3.79 dSm^{-1} for (1) the control, with no salt application; the (2) moderate salt concentration; the (3) high salt concentration; the (4) very high salt concentration, respectively. Next, *J. curcas* seeds were sown in individual pots (5 seeds per pot); each pot was irrigated with distilled water on a daily basis during the entire plant growth period to keep rates close to field capacity. Excess irrigation water was avoided in order to prevent salt leaching; however, there was excess of irrigation water when it was collected and reused in the same pot.

Seed germination was monitored up to 23 days after sowing (DAS); time when all seedlings (in soil without salt application) showed fully expanded cotyledons. From this time on, the seedlings were thinned in order to leave one plant per pot and assess plant growth and development. Plant height (cm), stem diameter (mm) and the total number of leaves were weekly measured with the aid of graduated ruler and digital caliper.

Environmental conditions were monitored during the experiment in an automatic weather station (model WS-GP1; DELTA-T Devices, Cambridge, England) located inside the greenhouse. Temperature and relative air humidity were recorded every 5 minutes; solar radiation was measured every 10 seconds. Vapor pressure deficit (VPD) was calculated based on temperature and relative humidity. Greenhouse environmental conditions during the experiment are shown in Figure 1.

Physiological and biochemical analysis

Photochemical efficiency was measured in the middle of the youngest fully-expanded leaves of each plant 102 days after planting. Photosystem II (Fv/Fm) maximum quantum yield was measured at 4:30 am, and at noon, with the aid of a portable chlorophyll fluorometer (model OS-1FL; ADC BioScientific, Ltd., Hoddesdon, England) at saturating light pulse 1 s duration, according to the method described by Maxwell and Johnson (2000). Plants were dark-adapted for 20 minutes by using leaf clips before the Fv/Fm measurement. The effective photosystem II quantum yield (Φ_{PSII}) was measured between 11:00 am and noon according to Schreiber et al. (1995), on the same leaves. Two readings were taken on individual plants.

Leaf gas exchange measurements were performed in the middle of the youngest fully-expanded leaves of each plant (one reading per plant), between 10:00 am and noon, with the aid of a portable photosynthesis system (IRGA) (model LCi; ADC BioScientific, Ltd., Hoddesdon, England). All measurements were taken at normal environmental CO_2 concentration and relative humidity. The CO_2 concentration inside the cuvette was kept close to 370 µL L^{-1}. Photosynthetic photon flux density in the IRGA cuvette was fixed at 900 µL mol m^{-2} s^{-1} by using an artificial light source. The following parameters were analyzed: photosynthesis (A), stomatal conductance (gs), transpiration (E), internal CO_2 concentration (Ci) and instantaneous carboxylation efficiency (A/Ci).

Plants exposed to the highest saline concentration, and the control treatment, were selected to have their leaf gas exchanges and Fv/Fm monitored throughout the day. Data were recorded every two hours, from 6:00 am to 5:00 pm, according to the previously described procedures. Pigment contents (chlorophylls and carotenoids) were determined at 102 DAP, after organic solvent extraction, according to Hendry and Grime (1993). Leaves were collected 128 DAS, immediately frozen in liquid nitrogen, and stored at -70ºC, until the time to perform the biochemical analyses described below.

The enzyme activity was determined through the spectrophotometric method; samples containing 20 mg of plant tissue were macerated in 2 mL of potassium phosphate buffer, and then centrifuged. The supernatant was collected and used to set ascorbate peroxidase (APX) (EC 1.11.1.11) and catalase (CAT) (EC 1.11.1.6) activity. The CAT activity was determined through the method described by Havir and Mchale (1987). The APX was determined according to Nakano and Asada (1981). Total protein concentrations were estimated through the Bradford assay method (Bradford 1976); bovine serum albumin was used as protein standard. The total protein concentration resulted from the same extract used for the enzyme activity.

Total amino acid concentrations were determined through the method by Yemm and Cocking (1955). Approximately 2 g of plant tissue were macerated in 2 mL of 0.01 M K-Na phosphate buffer (pH 7.6). Amino acid contents were determined by using absorbance at 570 nm. An amino acid pool was used as standard. The procedure described by Bates et al. (1973) was used in proline quantification. Proline PA was used as standard curve. Carbohydrate determinations were performed through the method proposed by Dubois et al. (1956). The D (+) anhydrous glucose was used as standard.

Six plants per treatment were selected to determine leaf area (cm^2), fresh weight and dry weight of plant parts (roots, stems and leaves) 129 DAS. Leaf area was quantified in a leaf area integrator (LI–3100, Licor). Leaves were dried in forced air circulation oven for 72 h at 65 ºC, and weighed. Root and stem dry weight were calculated through the same procedure adopted to measure the leaf dry weight. The following parameters were calculated:

- Biomass allocation to leaves = $\frac{Leaf\ DM}{Plant\ DM}\ x\ 100\ (\%)$ (1)
- Biomass allocation to stems = $\frac{Stem\ DM}{Plant\ DM}\ x\ 100\ (\%)$ (2)
- Biomass allocation to roots = $\frac{Root\ DM}{Plant\ DM}\ x\ 100\ (\%)$ (3)
- Root/A.P. = $\frac{Root\ DM}{Aerial\ part\ DM}$ (4)
- Leaf area ratio (LAR) = $\frac{LA}{Plant\ DM}$ (5)
- Specific leaf area (SLA) = $\frac{LA}{Leaf\ DM}$ (6)

Wherein:
DM = Dry mass
LA = Leaf area

Statistical analysis

Data were analyzed through analysis of variance and the means were compared by Tukey's test ($P \leq 0.05$). The daily mean of gas exchange curve was compared through *t*-test ($P < 0.05$; $P < 0.01$). Statistical analyses were performed in the ASSISTAT statistical software version 7.5 beta (2008).

Conclusion

J. curcas is very sensitive to salt stress. Salinity levels in the soil at EC 3.79 $dS.m^{-1}$ are deleterious to *J. curcas* seedlings; it leads to more than 85% seedling death few days after seed germination. Therefore, *J. curcas* plants should not be cultivated in saline soils presenting EC higher than 1.76 $dS.m^{-1}$. To some extent, salinity effects on the photochemical apparatus of *J. curcas* can be attenuated by the increased antioxidant activity of CAT and APX enzymes, by the higher accumulation of osmolytes, especially amino acids; and by the protective effect of proline on the enzymatic apparatus. However, this metabolic alteration is not sufficient to prevent growth reduction in response to salt stress in soil presenting EC as low as 1.76 $dS.m^{-1}$.

Acknowledgement

To CNPq, for financial support; CAPES and FAPEAL for financial scholarships.

References

Arruda FP, Macedo BN, Pereira AA, Pereira W, Soares SL (2004) Cultivo de pinhão-manso (*Jatropha curcas*) como alternativa para o semiárido nordestino. Rev Bras Ol Fibros. 8(1): 789-799.

Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. Photosynthetica. 51(2): 163-190.

Bates LS, Waldren RP, Teare ID (1973) Rapid determination of free proline for water-stress studies. Plant Soil. 39(1): 205-207.

Bienert GP, Schjoerring JK, Jahn TP (2006) Membrane transport of hydrogen peroxide. Biochim Biophys Acta (BBA)-Biomembranes. 1758(8): 994-1003.

Bor M, Özdemir F, Türkan I (2003) The effect of salt stress on lipid peroxidation and antioxidants in leaves of sugar beet *Beta vulgaris* L. and wild beet *Beta maritima* L. Plant Sci. 164(1): 77-84.

Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal Biochem. 72(1-2): 248-254.

Campos MLDO, Hsie BSD, Granja JADA, Correia RM, Almeida-Cortez JSD, Pompelli MF (2012) Photosynthesis and antioxidant activity in *Jatropha curcas* L. under salt stress. Braz J Plant Physiol. 24(1): 55-67.

Davletova S, Rizhsky L, Liang H, Shengqiang Z, Oliver DJ, Coutu J, Shulaevc V, Schlauchd K, Mittler R (2005) Cytosolic ascorbate peroxidase 1 is a central component of the reactive oxygen gene network of Arabidopsis. The Plant Cell. 17(1): 268-281.

De Azevedo Neto AD, Prisco JT, Enéas-Filho J, De Abreu CEB, Gomes-Filho E (2006) Effect of salt stress on antioxidative enzymes and lipid peroxidation in leaves and roots of salt-tolerant and salt-sensitive maize genotypes. Environ Exper Bot. 56(1): 87-94.

De Lima GS, Nobre RG, Gheyi HR, Dos Anjos Soares LA, Da Silva EM (2015) Irrigation water salinity and nitrogen doses affect the cultivation of castor bean (*Ricinus communis* L.) at different phenological stages. Aust J Crop Sci. 9(9): 870-878.

De Lucena CC, Siqueira DL, Martinez HEP, Cecon PR (2012) Efeito do estresse salino na absorção de nutrientes em mangueira. Rev Bras Frutic. 34(1): 297-308.

Deinlein U, Stephan AB, Horie T, Luo W, Xu G, Schroeder JI (2014) Plant salt-tolerance mechanisms. Trends Plant Sci. 19(6): 371-379.

Demiral T, Türkan I (2005) Comparative lipid peroxidation, antioxidant defense systems and proline content in roots of two rice cultivars differing in salt tolerance. Environ Exper Bot. *53*(3): 247-257.

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.

Divakara BN, Upadhyaya HD, Wani SP, Laxmipathi GCL (2010) Biology and genetic improvement of *Jatropha curcas* L.: a review. Appl Energy. 87(3): 732-742.

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956) Colorimetric method for the determination of sugars and related substances. Analytical Chemistry. 28(3): 350-356.

Embrapa (1997) Serviço Nacional de Levantamento e Conservação do Solo. Manual de métodos e análise de solo, 2ª edição, Rio de Janeiro. 221p.

FAO (2011) The State of the World's Land and Water Resources for Food and Agriculture. Managing systems at risk. Rome: FAO/Earthscan. 285p.

Flowers TJ (2004) Improving crop salt tolerance. J Exp Bot. 55(396): 307-319.

Foyer CH, Noctor G (2003) Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. Physiol Plant. 119(3): 355-364.

Gudeta TB (2016) Chemical composition, bio–diesel potential and uses of *Jatropha curcas* L. (Euphorbiaceae). American Journal of Agriculture and Forestry. 6(8): 35-48.

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genomics. 2014:1-18.

Havir EA, Mchale NA (1987) Biochemical and developmental characterization of multiple forms of catalase in tobacco leaves. Plant Physiol. 84(2): 450-455.

Hendry GAF, Price AH (1993) Stress indicators: chlorophylls and carotenoids. In: Hendry GAF, Grime JP. Methods in comparative plant ecology. London: Chapman & Hall. p.148.

Hishida M, Ascencio-Valle F, Fujiyama H, Orduño-Cruz A, Endo T, Larrinaga-Mayoral JÁ. (2014) Antioxidant enzyme responses to salinity stress of *Jatropha curcas* and *J. cinerea* at seedling stage. Russ J Plant Physiol. 61(1): 53-62.

Koca H, Bor M, Özdemir F, Türkan I (2007) The effect of salt stress on lipid peroxidation, antioxidative enzymes and proline content of sesame cultivars. Environ Exper Bot. 60(3): 344-351.

Kumar N, Pamidimarri S, Kaur M, Boricham G, Reddy M (2008) Effects of NaCl on growth, ion accumulation, protein, proline contents and antioxidant enzymes activity in callus cultures of *Jatropha curcas*. Biologia. 63(3): 378-382.

Lacerda CFD, Cambraia J, Cano MAO, Ruiz HÁ (2001) Plant growth and solute accumulation and distribution in two sorghum genotypes, under NaCl stress. Rev Bras Fisiol Veg. 13(3):270-284.

Levitt J (1980) Responses of plants to environmental stresses. Volume II. Water, radiation, salt, and other stresses. Physiological Ecology. Academic Press, New York. Li X,Wilson SD (1998) Facilitation among woody plants establishing in an old field. Ecology 79: 2694-2705.

Li G, Wan S, Zhou J, Yang Z, Qin P (2010) Leaf chlorophyll fluorescence, hyperspectral reflectance, pigments content, malondialdehyde and proline accumulation responses of castor bean (*Ricinus communis* L.) seedlings to salt stress levels. Ind Crop Prod. 31(1): 13-19.

Maxwell K, Johnson GN (2000) Chlorophyll fluorescence-*a* practical guide. J Exp Bot. 51(345): 659-668.

Meeta J, Mini M, Rekha G (2013) Effect of PEG-6000 imposed water deficit on chlorophyll metabolism in maize leaves. Journal of Stress Physiology & Biochemistry. 9(3): 262-271.

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci. 7(9): 405-410.

Moya JL, Primo-Millo E, Talon M (1999) Morphological factors determining salt tolerance in citrus seedlings: the shoot to root ratio modulates passive root uptake of chloride ions and their accumulation in leaves. Plant Cell Environ 22(11): 1425-1433.

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25(2): 239-250.

Munns R (2010) Approaches to identifying genes for salinity tolerance and the importance of timescale. Plant Stress Tolerance: Methods and Protocols. 25-38.

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59: 651-681.

Nakano Y, Asada K (1981) Hydrogen peroxide is scavenged by ascorbate-specific peroxidase in spinach chloroplasts. Plant Cell Physiol. 22(5): 867-880.

Niu, X, Bressan, RA, Hasegawa, PM, Pardo JM (1995) Ion homeostasis in NaCl stress environments. Plant Physiol. 109(3): 735-742.

Pinheiro HA, Silva JV, Endres L, Ferreira VM, De Albuquerque CC, Cabral FF, Oliveira JF, Carvalho LWT, Santos JM, Dos Santos Filho BG (2008) Leaf gas exchange, chloroplastic

pigments and dry matter accumulation in castor bean (*Ricinus communis* L) seedlings subjected to salt stress conditions. Ind Crops Prod. 27(3): 385-392.

Powles SB (1984) Photoinhibition of photosynthesis induced by visible light. Ann Rev of Plant Physiol. 35(1): 15-44.

Rahnama A, Poustini K, Tavakkol-Afshari R, Ahmadi A, Alizadeh H (2011) Growth properties and ion distribution in different tissues of bread wheat genotypes (*Triticum aestivum* L.) differing in salt tolerance. J Agron Crop Sci. 197(1): 21-30.

Richard LA (1954) Diagnosis and improvement of saline and alkali soils. USDA Hand Book. No. 60. US Govt. Press, Washington, 160.

Roy SJ, Negrão S, Tester M (2014) Salt resistant crop plants. Curr Opin Biotechnol. 26: 115-124.

Sairam RK, Rao KV, Srivastava GC (2002) Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. Plant Sci. 163(5): 1037-1046.

Schreiber U, Hormann H, Neubauer C, Klughammer C (1995) Assessment of photosystem II photochemical quantum yield by chlorophyll fluorescence quenching analysis. Funct Plant Biol. 22(2): 209-220.

Sharma PK, Hall DO (1991) Interaction of salt stress and photoinhibition on photosynthesis in barley and sorghum. J of plant physiol. 138(5): 614-619.

Silva EN, Vieira SA, Ribeiro RV, Ponte LF, Ferreira-Silva SL, Silveira JÁ (2013) Contrasting physiological responses of *Jatropha curcas* plants to single and combined stresses of salinity and heat. J Plant Growth Regul. 32(1): 159-169.

Silveira JAG, De Almeida VR, Da Rocha IMA, Moreira ACDOM, De AZevedo MR, Oliveira JTA (2003) Proline accumulation and glutamine synthetase activity are increased by salt-induced proteolysis in cashew leaves. J Plant Physiol. 160(2): 115-123.

Sreenivasulu N, Ramanjulu S, Ramachandra-Kini K, Prakash HS, Shekar-Shetty H, Savithri HS, Sudhakar C (1999) Total peroxidase activity and peroxidase isoforms as modified by salt stress in two cultivars of fox-tail millet with differential salt tolerance. Plant Sci 141(1): 1-9.

Vajpayee P, Tripathi RD, Rai UN, Ali MB, Singh SN (2000) Chromium (VI) accumulation reduces chlorophyll biosynthesis, nitrate reductase activity and protein content in *Nymphaea alba* L. Chemosphere. 41(7): 1075-1082.

Yemm EW, Cocking E C, Ricketts RE (1955) The determination of amino-acids with ninhydrin. Analyst. 80 (948): 209-214.

Zhang M, Smith JAC, Harberd NP, Jiang C (2016) The regulatory roles of ethylene and reactive oxygen species (ROS) in plant salt stress responses. Plant Mol Biol. 91(6): 651-659.