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Comparative effects of salinity and water stress on photosynthesis, water relations and growth of *Jatropha curcas* plants

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ABSTRACT

The aim of this study was to evaluate the physiological responses of physic nut (*Jatropha curcas* L.) plants exposed to water stress and salinity in order to elucidate some acclimatory mechanisms. Mild water and salt stresses were imposed by plant exposure to -0.22 MPa iso-osmotic solutions with PEG 6000 or NaCl 50 mM for 8 days. Stress recovery was evaluated under control conditions after three and eight days. PEG treatment caused higher reductions in Ψw and Ψs, but both relative water content and succulence were not affected by the two stress treatments, compared to the control. The PEG-stressed plants suffered higher restrictions in leaf growth compared to the salt-stressed ones. Moreover, only the PEG treatment caused a pronounced effect on leaf membrane integrity. Both treatments caused similar impairment of the CO_2 assimilation rate, but the PEG stressed plants showed higher restriction in stomatal conductance and transpiration. Although both stresses caused significant decreases on the leaf chlorophyll content, the photochemical activity was not affected. Since the plants subjected to mild water and salt stresses showed a rapid and almost complete recovery, these physiological alterations could represent a set of adaptive mechanisms employed by *J. curcas* to cope with these stressful conditions.

1. Introduction

Plants are often subjected to periods of soil and atmospheric water deficits during their life cycle. In many agricultural areas, plants also face soil salinity, another environmental constraint. It is estimated that 6% of the world's land and 30% of the world's irrigated areas already suffer from salinity problems (Munns and Tester, 2008). Expansion of agriculture in semi-arid and arid regions using intensive irrigation and fertilization will increase the secondary salinization due to progressive salt accumulation in the soils as a consequence of the salt dissolved in the water applied associated with high evapotranspiration rates (Chaves et al., 2008).

Photosynthesis and plant growth are among the primary processes affected by drought (Chaves, 1991) and salinity (Munns et al., 2006). Water stress and salinity can affect photosynthesis directly or indirectly by decreases in CO_2 availability caused by diffusion limitations (Flexas et al., 2007), alterations in photosynthetic metabolism (Lawlor and Cornic, 2002) or restrictions in the photochemical system apparatus under severe stress conditions (Souza et al., 2004). In parallel to impairment of photosynthesis, salinity and water stress induce strong alterations of leaf water relations and osmotic homeostasis. It is widely accept that after short term (days) exposure salinity induces osmotic effects, while under long term exposure it can cause ionic damages to the plant cells (Munns, 2002).

Under high salinity an irreversible impairment of the photosynthetic apparatus, associated with a reduction of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity, occurs when the stress is prolonged and salt continues to accumulate in the leaves (Delfine et al., 1999). Under drought conditions, there are controversies about the effects of this stress on Rubisco activity (Lal et al., 1996). Some authors did not observe water stress effects on that enzyme activity (Delfine et al., 2001), whereas others observed a significant reduction in the Rubisco activity in plants subjected to drought (Maroco et al., 2002). This apparent discrepancy is due to the fact that such studies were done under different environmental conditions, using different species subjected to different drought intensities (Bota et al., 2004).

Both the salt and drought stress might induce impairment of photosynthesis due to disturbances in the structure and function of

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the photochemical apparatus (Hura et al., 2007). As an indirect consequence of stomatal closure, restriction in intercellular CO_2 concentration should increase the susceptibility to photochemical damages as excessive light energy at PSII level increases due to low CO_2 assimilation rates. Several environmental stresses such as drought and high salinity might induce strong disturbances on the photochemical reactions (Tezara et al., 2005). In sorghum plants subjected to salt stress the photochemical activity was strongly affected (Netondo et al., 2004) whereas cowpea subjected to progressive drought displayed slight changes in the photossystem II activity (Souza et al., 2004).

Jatropha curcas is distributed over the arid and semiarid areas of South America and in all tropical regions. In the last years, it has received special attention because its high seed oil content and quality. Therefore, *J. curcas* is a crop with importance for biodiesel production, being considered potentially as a universally accepted source of energy (Kumar et al., 2008). *J. curcas* grows in environments with constraining conditions, such as reduced rainfall, high temperatures, poor soil conditions, where most of the agriculturally important plant species are not able to grow satisfactorily (Francis et al., 2005).

Although the seeds of *J. curcas* plants represent a promising bioenergy source, knowledge about the plant's physiological responses to drought and salt stresses is poorly known. An improved understanding is essential in order to adopt competitive strategies for improving crop production. The objective of this work is to evaluate the comparative effects of water stress and salinity on the leaf gas exchange, water relations, growth and chlorophyll fluorescence in *J. curcas* young plants.

2. Material and methods

2.1. Plant material and experimental conditions

The experiment was carried out under greenhouse conditions, where the environmental conditions were: minimum and maximum mean air temperatures of 24 and 36 °C, respectively; mean air relative humidity of 65%; maximum photosynthetic photon flux density (PPFD) of approximately 700 $\mu mol\, m^{-2}\, s^{-1}$; and 12 h photoperiod. *J. curcas* seeds cultivar T1 based on homogeneous size and weight were surface sterilized for 1 min. with sodium hypochlorite solution (5%, v/v). Afterwards, seeds were germinated in sand. Eight days after germination in sand, the seedlings were transferred to plastic pots (2 L) containing Hoagland and Arnon (1950) nutrient solution (pH 6.0) with one-fourth strength in the first week and full strength afterward. The seedlings were subjected to stressful treatments over eight days, in which nutritive solution was supplied with 50 mM NaCl or PEG 6,000 11.96% (m/v), both with $\Psi_{os} = -0.22$ MPa. NaCl and PEG were added gradually (25 mmol NaCl $L^{-1}\, d^{-1}$ and 59.8 g PEG $L^{-1}\, d^{-1}$) into the solution in order to avoid osmotic shock. The treatment with the nutrient solution in the absence of both NaCl and PEG was taken as the control.

2.2. Leaf gas exchange and chlorophyll fluorescence

Leaf gas exchange was monitored with an infrared gas analyzer (LCi, ADC, Hoddesdonm, UK), operating in the open system and with an air flow of 200 mL min^{-1}. Measurements of leaf CO_2 assimilation rate (P_N), transpiration (E), stomatal conductance (g_S) and intercellular CO_2 concentration (C_I) were taken. The instantaneous carboxylation efficiency (P_N/C_I) was also calculated (Ribeiro et al., 2009; Zhang et al., 2001). The chlorophyll fluorescence was evaluated with a modulated fluorometer (FMS 2, Hansatech, King's Lynn, UK). Minimum (Fo), maximum (Fm) and maximum variable ($Fv = Fm - Fo$) fluorescence intensities were sampled under steady-state conditions in dark-adapted (30 min) leaves. In addition, measurements were also taken under light-adapted conditions, being referred as Fo' (minimum) and Fm' (maximum). The Fo' signal was measured after PSI excitation by far-red light. The fluorescence signal under light-adapted conditions before the saturation pulse is referred as Fs' and the variable fluorescence signal under light conditions is $\Delta F' = Fm' - Fs'$. The following photochemical variables were measured: maximal (Fv/Fm) and actual ($\Delta F/Fm'$) quantum yield of primary photochemistry, apparent electron transport rate ($ETR = \Delta F/Fm' \times PPFD \times 0.5 \times 0.84$), and photochemical [$qP = (Fm' - Fs)/(Fm' - Fo')$] and non-photochemical [$NPQ = (Fm - Fm')/Fm'$] quenching (Rohácek, 2002). For ETR calculation, 0.5 was used as the fraction of excitation energy distributed to PSII and 0.84 as the fraction of incoming light absorbed by the leaves (Schreiber et al., 1998). Fo′ is the basal fluorescence signal measured after PSI excitation by far-red light.

The ratio ETR/P_N was calculated to estimate the use of electrons in other processes not related to the photosynthetic CO_2 assimilation rate (Ribeiro et al., 2009). Therefore, an increase in ETR/P_N indicates that more electrons are driven to other sinks and suggests a stressful condition. Leaf gas exchange and chlorophyll fluorescence were measured at the same time and environmental conditions (25 °C and PPFD of 260 $\mu mol\, m^{-2}\, s^{-1}$) with two equipments (an infrared gas analyzer and a fluorometer) and two persons utilizing the same leaf in two points (*J. curcas* has a large fully expanded mature leaf). These measurements were taken eight days after the onset of treatments and they were repeated again three and eight days after returning plants to the nutritive solution without NaCl and PEG.

2.3. Determination of inorganic solutes

Lyophilized leaf samples were transferred into hermetically closed tubes containing deionized water and placed in a 100 °C water bath for 1 h. The extracts were then filtered and stored at −20 °C for later determinations. Na^+ and K^+ contents were determined by flame photometry and Cl^- content through titration with $AgNO_3$, as previously described (Silveira et al., 2009).

2.4. Water relations parameters

The leaf water potential (Ψw) was evaluated immediately after sampling using the pressure chamber method (Scholander et al., 1965) at midday in leaves similar to those used for leaf gas exchange and chlorophyll fluorescence measurements. The leaf relative water content (RWC) was calculated from fresh, turgid and dry weight of leaf discs, as previously described (Silveira et al., 2009). The leaf succulence (LS) was calculated by the formula (FW)/A, where FW and A are the fresh weight and area of thirty leaf discs (diameter 1.0 cm), respectively.

For determination of the osmolality, small segments from fully expanded leaves and terminal 5 cm-segments of roots were macerated in a mortar. After extract filtration in a miracloth membrane, the sap was centrifuged at 10,000 × *g* for 10 min at 4 °C. After, the supernatant was collected and utilized to determine the osmolality (c) using a vapor pressure osmometer (Vapro 5520, Wescor, USA). The osmotic potential was determined using the formula: $\Psi s\ (MPa) = -c\ (mosmol\ kg^{-1}) \times 2.58 \times 10^{-3}$, according to the Van't Hoff equation.

2.5. Electrolyte leakage, leaf area and chlorophyll content

Electrolyte leakage was assessed as described by Lutts et al. (1996). Leaf discs were placed in closed tubes containing 10 mL of deionized water and incubated at 25 °C in a water bath for 6 h;