

1 **Salt stress induced damages on the photosynthesis of physic nut young plants**

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25 **Salt stress induced damages on the photosynthesis of physic nut young plants**

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27 Abstract – The aim of this study was to evaluate the resistance of the photosynthetic
28 apparatus of *Jatropha curcas* plants under salt stress. The experiment was carried out in
29 a completely randomized design with treatments in a 2x3 factorial: two NaCl levels (0
30 and 100 mmol L⁻¹) and three harvest times: 7 and 14 days of exposure and 3 days of
31 recovery. The Na⁺ and Cl⁻ accumulation and the reduction in the K⁺/Na⁺ ratio after 7
32 days of salt exposure did not indicate ionic toxicity in leaves but the salt stress caused
33 significant reduction in leaf gas exchange parameters, such as CO₂ fixation, stomatal
34 conductance and transpiration and, in contrast, it did not change the photochemical
35 efficiency of the photosystem II. After 14 days of treatment, the saline ions achieved
36 very high concentrations, reaching toxic levels in leaves. In such conditions, both leaf
37 gas exchange and photochemistry suffered strong impairment caused by the ionic stress.
38 The recovery treatment did not relieve the ionic toxicity and none improvement was
39 observed in photosynthetic performance. In general, the photochemical activity is
40 tolerant to the osmotic stress but both leaf gas exchange and photochemistry are
41 strongly inhibited by NaCl-induced ionic stress in physic nut leaves.

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43 Key words: chlorophyll fluorescence, gas exchange, ionic toxicity, *Jatropha curcas*,
44 salinity.

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73 **INTRODUCTION**

74 Salinity adversely affects plant growth and development, with nearly 20% of the
75 World's cultivated area and nearly half of the World's irrigated lands being affected by
76 salt stress (Sairam & Tyagi, 2004). This problem is more relevant in semiarid regions
77 where rainfall and high evaporative demand contribute intensely to the aggravation of
78 soil salinization (Viégas et al., 2001). In these regions, the problem of soil secondary
79 salinization is exacerbated by the use of low quality water associated with inadequate
80 techniques of soil management (Ferreira-Silva et al., 2009).

81 The accumulation of salt ions in plants can cause osmotic stress, ionic toxicity
82 and induce nutritional deficiencies (Munns, 2002). When in high concentrations, Na⁺
83 and Cl⁻ ions cause impairments in both biochemical and photochemical processes of
84 photosynthesis (Munns & Tester, 2008). Sorghum plants exhibited reduction in stomatal
85 opening, which was the main limiting factor for photosynthesis under salt stress
86 conditions (Netondo et al., 2004). However, damage on the photosynthetic machinery
87 may also occur due to non-stomatal limitation, i.e., decrease in Rubisco activity
88 (Delfine et al., 1999).

89 Physic nut (*Jatropha curcas*) is a species adapted to semiarid environmental
90 conditions with high economic importance due to the seed oil quality, which can be
91 converted in biodiesel by industry (Silva et al., 2009a). Although this species had shown
92 satisfactory yield under constraining conditions of semiarid regions, the physiological
93 mechanisms controlling its salt stress tolerance are poorly understood.

94 Thus, this study was designed to evaluate the tolerance of photosynthetic
95 apparatus of physic nut plants to salt stress. Photochemistry activity and leaf gas

96 exchange were studied during salt stress and recovery, being the physiological response
97 analyzed together with changes in the Na⁺ and Cl⁻ leaf contents and K⁺/Na⁺ ratios.

98

99 MATERIAL AND METHODS

100 The experiment was carried out under greenhouse conditions (3°44'S; 38°33'W,
101 at sea level), where the environmental conditions were: minimum and maximum mean
102 air temperature of 24 and 36 °C, respectively; mean air relative humidity of 65%;
103 maximum photosynthetic photon flux density (PPFD) of approximately 700 μmol m⁻² s⁻¹
104 ¹. *Jatropha curcas* L. seeds supply by Fazenda Instituto Tamanduá (Santa Terezinha,
105 PB, Brazil), genotype FT-2, were previously selected taking into account the seed size
106 and weight. Eight days after germination in sand, seedlings were transferred to plastic
107 pots (2 L), containing Hoagland & Arnon (1950) nutrient solution (pH 6.0) with one-
108 four strength in the first week and full strength afterward.

109 After this period, nutrient solution was supplied with 100 mmol L⁻¹ NaCl and
110 then plants were subjected to stressful treatment during 14 days. The NaCl was added
111 gradually (50 mmol NaCl L⁻¹ d⁻¹) into solution in order to avoid osmotic shock. The
112 treatment with nutrient solution in absence of NaCl was taken as control. At the end of
113 two weeks of treatment, the salt-stressed plants were returned to control conditions for
114 three days. In previous experiment, a three-day period was sufficient for full recovery of
115 physic nut young plants subjected to 50 mmol L⁻¹ NaCl.

116 Leaf gas exchange was measured with an infrared gas analyzer (LCi, ADC,
117 Hoddesdonm, UK), operating in open system and with air flow of 200 mL min⁻¹.
118 Measurements of leaf CO₂ assimilation (A), transpiration (E), stomatal conductance (gs)

119 and intercellular CO₂ concentration (C_i) were taken. The instantaneous carboxylation
120 efficiency (A/C_i) was calculated (Zhang et al., 2001).

121 The chlorophyll fluorescence was evaluated with a modulated fluorometer
122 (FMS2, Hansatech, King's Lynn, UK). Basal (F_o) and maximal (F_m) fluorescence
123 yields were measured in dark-adapted (30 min) leaves, whereas steady-state (F_s) and
124 maximal (F_m') fluorescence yields were sampled in light-adapted tissues. Variable
125 fluorescence yields were determined in dark-adapted (F_v=F_m-F_o) and in light-adapted
126 (ΔF=F_m'-F) leaf tissues. The following photochemical variables were calculated:
127 potential (F_v/F_m) and effective (ΔF/F_m') quantum efficiency of PSII. Apparent electron
128 transport rate (ETR= ΔF/F_m' x PPFD x 0.5 x 0.84), photochemical [qP= (F_m'-F_s)/(F_s-
129 F_o')] and non-photochemical [qN=(F_m-F_m')/(F_m-F_o')] quenching (Roháček, 2002).
130 For ETR calculation, 0.5 was used as the fraction of excitation energy distributed to
131 PSII and 0.84 as the fraction of incoming light absorbed by leaves (Schreiber et al.,
132 1998). F_o' is the basal fluorescence yield measured after PSI excitation by far-red light.
133 The ratio ETR/A was calculated to estimate the use of electrons in other processes not
134 related to the photosynthetic CO₂ assimilation (Ribeiro et al., 2009). Therefore, an
135 increase in ETR/A indicates that more electrons are driven to other sinks (e.g.,
136 photorespiration, nitrogen metabolism or Mehler reaction), suggesting a stressful
137 condition.

138 Leaf gas exchange and chlorophyll fluorescence were measured simultaneously,
139 in fully expanded and mature leaves of plants exposure to 25 °C and PPFD of 590 μmol
140 m⁻² s⁻¹. Those measurements were taken after 7-d and 14-d of treatment (0 and 100
141 mmol L⁻¹ NaCl), and repeated again three days after returning plants to the nutritive
142 solution without the presence of NaCl.

143 At the end of experiment, leaves were sampled, frozen and stored at -80 °C.
144 After lyophilization, samples were placed into hermetically closed tubes containing
145 deionized water and heated under water-bath at 100 °C for 1 h. The extracts were then
146 filtered and used for determination of Na⁺ and K⁺ contents by flame photometry. The
147 Cl⁻ content was determinate through titration with AgNO₃ as described for Silveira et al.
148 (2009).

149 The experiment was arranged in a completely randomized design, with two
150 factors: NaCl (0 and 100 mmol L⁻¹); time (seven and 14 days of salt stress and three
151 days of recovery). Data were analyzed by ANOVA and mean values of four replications
152 were compared by the Tukey test at the 0.05 level of confidence.

153

154 **RESULTS AND DISCUSSION**

155 Leaves of physic nut young plants treated with NaCl (100 mmol L⁻¹) showed
156 significant changes in the Na⁺, Cl⁻ and K⁺ concentrations compared to control plants
157 (Table 1). After seven days of treatment, the Na⁺ and K⁺ concentrations reached values
158 around 603 and 581 mmol (kg DM)⁻¹ respectively, while the K⁺/Na⁺ ratio was reduced
159 from 5.4 to 0.96 in stressed plants. In spite of the Na⁺ accumulation associated with a
160 reduction in K⁺ concentration and consequent decrease in K⁺/Na⁺ ratio in treated plants,
161 the saline condition was not sufficient to induce an ionic stress and a great change in the
162 leaf ion homeostasis. In fact, the toxicity symptoms in physic nut plants appeared only
163 when the leaf K⁺/Na⁺ ratio was much lower than 1.0 (Silva et al., 2009b).

164 After seven days of treatment with 100 mmol L⁻¹ NaCl, the leaf Cl⁻ content was
165 just 236 mmol (kg DM)⁻¹ (Table 1). This result, together with the Na⁺ content reinforces
166 that the stress imposed by saline condition was predominantly osmotic. Nevertheless,

167 after 14-d of exposure to salt stress, the Na⁺ and Cl⁻ accumulations were intense and
168 reached toxic levels (Silva et al., 2009b). The Na⁺ and Cl⁻ concentrations were about
169 1,721 and 1,498 mmol (kg DM)⁻¹ respectively, in plant under salt stress. On the other
170 hand, leaf K⁺ content was decreased suddenly from 1,071 to 496 mmol (kg DM)⁻¹, when
171 considering control and stressed plants. As a consequence, the K⁺/Na⁺ ratio was reduced
172 from 5.0 (untreated plants) to 0.24 (treated plants).

173 The salinity toxic effects in physic nut leaves were also evidenced by the
174 appearance of leaf necrotic areas and even after the NaCl removal from the nutritive
175 medium (recovery), the toxicity symptoms persisted. After the recovery time, the Na⁺
176 and Cl⁻ contents decreased only by 15% and 17%, respectively while that the K⁺/Na⁺
177 ratio was not changed when compared to stressed plants after 14-d of exposure to NaCl
178 (Table 1). Thus, these results indicate that the salt stress was caused mainly by osmotic
179 component after seven days of treatment. However, a strong ionic stress was established
180 in physic nut leaves in the following seven days, i.e., after 14-d of exposure to NaCl.

181 Our results suggest that physic nut young plants have not efficient mechanisms
182 for salt ions redistribution and/or exclusion, which could contribute to impede excessive
183 accumulation of Na⁺ and Cl⁻ in plant shoot under salinity (Silva et al., 2009b).
184 Differently, cowpea plants (*Vigna unguiculata*) showed an efficient system for remove
185 Na⁺ from leaf tissues. The leaf Na⁺ content in cowpea plants submitted for six days to
186 NaCl (200 mmol L⁻¹) was 6-fold higher than control plants but after 3-d of recovery, the
187 ion concentration was reduced in similar magnitude (Cavalcanti et al., 2004).

188 Leaf CO₂ assimilation was strongly reduced in plants exposure to salt stress
189 compared to control ones, with plants submitted to NaCl showing reductions of 23%
190 and 85% after 7 and 14-d of treatment, respectively (Figure 1A). Salt stress also affected

191 transpiration, stomatal conductance and intercellular CO₂ concentration decreases. The
192 transpiration was reduced by 39% and 84% (Figure 1B), the stomatal conductance by
193 80% and 97% (Figure 1C) and the intercellular CO₂ concentration by 23% and 47%
194 (data not shown) at 7 and 14-d of treatment, respectively. In contrast, the instantaneous
195 carboxylation efficiency, estimated by the A/Ci ratio (Figure 1D), remained unchanged
196 after seven days of treatment but was strongly reduced (73%) after 14-d of exposure to
197 NaCl. After 3-d of recovery, the A/Ci ratio in stressed plants did not return to control
198 level (Figure 1D).

199 Our results indicate that the reduction of photosynthesis until the 7th day was
200 caused only by stomatal limitation, i.e. reduced CO₂ availability to carboxylation, while
201 both stomatal and non-stomatal limitations were observed in the 14th day of exposure to
202 salt stress. Leaf gas exchange variables showed a significant perturbation of plant
203 physiology even after a mild stress (seven days) and evidences of irreversible
204 photosynthetic damage as stressful condition was prolonged (14 days under salt stress).

205 The decrease of photosynthesis associated with low stomatal conductance in
206 plants subjected to saline conditions (Figure 1) is in accordance to Meloni et al. (2003),
207 who observed impairment in the photosynthetic efficiency of cotton cultivars exposed to
208 50 and 100 mmol L⁻¹ NaCl due to stomatal limitation. On the other hand, significant
209 decreases in intercellular CO₂ concentration and A/Ci ratio also indicate that salt stress
210 affected the photosynthesis by metabolic limitation. Reductions of A/Ci ratio are
211 probably associated with a decrease of the carboxylase Rubisco activity, which occurred
212 in parallel with a Na⁺ and Cl⁻ intense accumulation in leaf tissues (Table 1). Thus, the
213 reduction of photosynthesis may, at least in part, be a direct effect of Na⁺ and Cl⁻ ions
214 on the photosynthetic apparatus, as observed in sorghum (Netondo et al., 2004) and

215 orange (López-Climent et al., 2008) plants. In fact, stressed leaves of physic nut plants
216 showed visual symptoms of injury, evidencing intense and irreversible cell damages.

217 Regarding to photochemistry effects, the potential quantum efficiency of PSII
218 (Fv/Fm) was not affected by salinity, whereas the effective quantum efficiency
219 ($\Delta F/Fm'$) decreased significantly (39%) after 14-d of exposure to NaCl (Figure 2A,B).
220 The photochemical quenching (qP) was not affected by salt stress, while the non-
221 photochemical quenching (qN) increased significantly in plants subjected to 100 mmol
222 L⁻¹ NaCl (Figure 3C,D). The increase of qN was already significant on the 7th day of
223 treatment, showing increasing trend until the 14th day of salt stress (Figure 3D).

224 The reduction of $\Delta F/Fm'$ accompanied by decrease in apparent electron
225 transport rate (data not shown) in stressed plants differs from results reported by Lu et
226 al. (2002), who did not observe effects of salt stress in photochemical reactions of *S.*
227 *salsa*. Impairments in photochemistry of plants exposed to salinity may be related to
228 possible damages in primary electron acceptors, such as plastoquinone pool (Foyer &
229 Noctor, 2000). In addition, the continuous increase of qN during stress and recovery
230 treatments suggest the activation of a protective mechanism for dissipation of excessive
231 energy not used in photochemical reactions (Ribeiro et al., 2009; Roháček, 2002). In
232 fact, full inhibition of photochemistry occurs on the PSII apparatus just under severe
233 oxidative damage (Chagas et al., 2008).

234 After 14-d under salt stress, plants showed ETR/A ratio 4-fold higher than in
235 control ones. This difference was maintained even after recovery period (Figure 3). The
236 increase in ETR/A ratio represents an imbalance between the electron flow and the CO₂
237 fixation during photosynthesis, which is associated with increases in oxygenase activity
238 of Rubisco and represent electron flow to other physiological processes rather than CO₂

239 fixation (Baker et al., 2007; Ribeiro et al., 2009). Occurrence of increases in ETR/A and
240 decreases in A/Ci indicate loss of photosynthetic efficiency in physic nut plants under
241 salt stress.

242 The accumulation of toxic ions (Na^+ and Cl^-) accompanied by decreases in K^+
243 content and severe photosynthetic damage show that physic nut young plants are
244 sensitive to salinity caused by NaCl. The absence of any recovery even after three days
245 of salt removing also indicates that high Na^+ and Cl^- leaf contents cause permanent
246 damages on photochemical and carboxylation reactions of photosynthesis.

247

248 **CONCLUSION**

249 Physic nut plants are sensitive to saline conditions, showing high leaf Na^+ and
250 Cl^- contents and low K^+/Na^+ ratio and permanent photosynthetic damage due to
251 stomatal and non-stomatal limitations.

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253 **ACKNOWLEDGEMENTS**

254 We thank to Conselho Nacional de Desenvolvimento Científico e Tecnológico
255 (CNPq), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and
256 Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP)
257 for financial support. J.A.G.S. and R.V.R. are CNPq research scientist and E.N.S. and
258 S.L.F.S. hold Capes and CNPq fellowships, respectively. The authors gratefully
259 acknowledge the Tamanduá Farm Institute, Santa Terezinha-PB (Brazil), especially to
260 Dr. R.A.V. for supplying physic nut seeds.

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Table List

336 Table 1. Concentrations of Na⁺, Cl⁻ e K⁺ and K⁺/ Na⁺ ratio in leaves of physic nut young
 337 plants cultivated in absence and presence of NaCl (100 mmol.L⁻¹) during 7-d and 14-d
 338 and after 3-d of recovery. Values are the mean for four replicates. The values
 339 represented by the same upper case letters, between time of treatment and same lower
 340 case letters, into of each time of treatment are not significantly different to 0.05 by
 341 Tukey test.

Parameter	NaCl (mmol.L ⁻¹)	Days after treatment		
		7 days	14 days	Recovery
Na ⁺ (mmol kg ⁻¹ MS)	0	133 Bb	215 Ab	215 Ab
	100	603 Ca	1721 Aa	1458 Ba
Cl ⁻ (mmol kg ⁻¹ MS)	0	102 Bb	147 Ab	139 Ab
	100	326 Ca	1498 Aa	1240 Ba
K ⁺ (mmol kg ⁻¹ MS)	0	716 Ba	1071 Aa	1123 Aa
	100	581 Ab	423 Cb	496 Bb
K ⁺ /Na ⁺	0	5.4 Aa	5.0 Aa	5.2 Aa
	100	0.96 Ab	0.24 Bb	0.34 Bb

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Figure List

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354 Figure 1. Leaf CO₂ assimilation (A), transpiration (B) and stomatal conductance (C)

355 *Jatropha curcas* young plants cultivated in absence and presence of NaCl (100 mmol.L⁻¹)

356 ¹) during 7-d and 14-d and after 3-d of recovery. White bars represent control plants and

357 gray bars represent stressed plants. Values are the mean for four replicates. The values

358 represented by the same upper case letters, between time of treatment and same lower

359 case letters, into of each time of treatment are not significantly different to 0.05 by

360 Tukey test.

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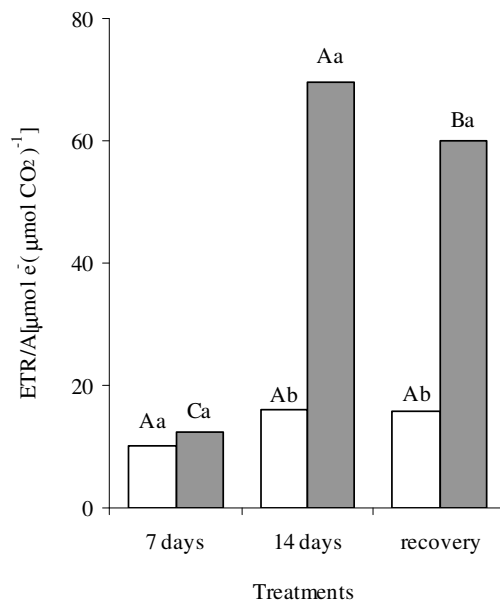
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Figure 2. Effective (A) and potential (B) quantum efficiency, photochemical (C) and non-photochemical (D) quenching in *Jatropha curcas* young plants cultivated in absence and presence of NaCl (100 mmol.L⁻¹) during 7-d and 14-d and after 3-d of recovery. White bars represent control plants and gray bars represent stressed plants. Values are the mean for four replicates. The values represented by the same upper case letters, between time of treatment and same lower case letters, into of each time of treatment are not significantly different to 0.05 by Tukey test.



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Figure 3. Ratio between apparent electron transport rate and CO₂ assimilation (ETR/A, in C) in *Jatropha curcas* young plants cultivated in absence or presence of NaCl (100

393 mmol L⁻¹) during 7-d and 14-d and after 3-d of recovery. White bars represent control
394 plants and gray bars represent stressed plants. Values are the mean for four replicates.
395 The values represented by the same upper case letters, between time of treatment and
396 same lower case letters, into of each time of treatment are not significantly different to
397 0.05 by Tukey test.