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Relationship between leaf gas-exchange characteristics and the performance of *Ziziphus spina-christi* (L.) Willd. seedlings subjected to salt stress

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Abstract

Ziziphus spina-christi (L.) Willd., known as Christ's thorn jujube, is a multipurpose species of the Rhamnaceae family. Seedlings were subjected to various NaCl concentrations (0 to 200 mM) for 21 d. They grew well under control conditions, however, biomass production and relative growth rate decreased with increasing NaCl salinity. This decline in growth was closely associated with a reduction in photosynthetic characteristics and plant water relations. However, the intrinsic water-use efficiency significantly increased as salt stress intensified. The relative water content declined although it still maintained high values (≥ 57%). At high salinity, plants displayed more negative stem water potential (ψ_w) and osmotic potential values of –2.0 and –4.0 MPa, respectively. The net photosynthetic rate and stomatal conductance were positively correlated and the former variable also had a strong positive relationship with ψ_w. These findings suggest that this fruit tree is quite tolerant to NaCl-salinity during its seedling stage.

Additional key words: *Ziziphus spina-christi,* growth, salinity, gas exchange, water relations.

Introduction

Soil salinization has become a serious problem and an environmental issue of worldwide significance. This phenomenon represents about 7% of the Earth's continental area, 20% of agricultural lands, and 50% of cultivated land in the world (Cho *et al.* 2010), and its frequency is expected to increase as a consequence of climate changes. In arid and semiarid areas, excessive soil salinity is an important constraint limiting plant productivity and their distribution over time and space. The extent of agricultural land, which is affected by high salinity, is increasing worldwide, due to natural phenomena as well as irrigation practices (Munns and Tester 2008). It is estimated that 10% of the total land area of Tunisia is affected by salinity (Hachicha *et al.* 1994).

The ability of plants to survive and maintain growth under saline conditions is known as salt tolerance, which is associated with low osmotic potential of soil solution, nutritional imbalance, specific ion effect, hormonal imbalance, and induction of oxidative stress, or a combination of these factors (Parida and Das 2005, Gorai and Neffati 2011). Plants express various responses to salt stress through a multiplicity of ecophysiological features that allow them to cope with contrasting environment, which depend on several interacting variables, including the magnitude (salt concentration and time of exposure) of the stress, plant genotype, plant developmental stage, and cultural environment (Jaleel *et al.* 2007, Gorai *et al.* 2011).

Under salt stress conditions, plants manifest acclimation to success their establishment by lowering both leaf water potential (ψ_w), and osmotic potential (ψ_π) (Gorai and Neffati 2011, Gorai *et al.* 2011). Osmotic adjustment by net accumulation of solutes in cells in response to a fall in the ψ_w of their environment (Ashraf and Foolad 2007) can in part offset this deterioration of growth conditions. As a consequence of this net accumulation, the cell ψ_π is lowered, and turgor pressure tends to be maintained (Blum *et al.* 1996). Thus, cell homeostasis is maintained by an osmotic adjustment mechanism which consists of the sequestration of large amounts of salt ions in the vacuole and/or synthesis of organic osmolytes (Munns 2002) involved in protecting subcellular structures and reducing oxidative damage caused by free radicals, produced in response to high salinity (Zhu 2001).

Plant growth depends on the accumulation of carbon products through photosynthesis, but high salinity can adversely affect CO_2 and H_2O exchange (Gorai *et al.* 2011). Plants decrease the rate of CO_2 assimilation as a consequence of the reduced stomatal conductance and/or

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Abbreviations: C_i – intercellular CO_2 concentration; DM – dry mass; E – transpiration rate; FM – fresh mass; g_s – stomatal conductance; P_N – net photosynthetic rate; RGR – relative growth rate; RWC – relative water content; WUE – water-use efficiency; WUE_i – intrinsic water-use efficiency (= P_N/g_s); ψ_p – turgor potential; ψ_w – water potential; ψ_π – osmotic potential.

by direct damage to carbon metabolism (Ashraf 2004, Gorai *et al.* 2011).

The genus *Ziziphus* (Rhamnaceae) includes over 100 species of evergreen or deciduous trees or shrubs, usually armed with unequal stipular spines, three of them are found in Tunisia, *Z. spina-christi* (L.) Willd., *Z. vulgaris* Lam., and *Z. lotus* (L.) Lam. (Maraghni *et al.* 2010). *Ziziphus* species developed a series of adaptation mechanisms allowing them to tolerate severe conditions. Numerous reports have investigated their physiological and morphological adaptations to water deficit stress (*e.g.*, Clifford *et al.* 1998, Arndt *et al.* 2001, Kulkarni *et al.* 2010, Maraghni *et al.* 2014, 2019) and salt stress (*e.g.*, Gupta *et al.* 2002, Bhatt *et al.* 2008, Sohail *et al.* 2009, Agrawal *et al.* 2013, Shekafandeh and Takhti 2013).

Z. spina-christi, known as Christ's thorn jujube, is a multipurpose tree with edible fruits. It is cross-pollinated plant and highly outbred (Sudhersan and Hussain 2003). Establishment of *Ziziphus* species is constrained by poor germination and seedling emergence, mainly as a result of a stony endocarp, and dormancy types (Maraghni *et al.* 2010). Finch-Savage and Leubner-Metzger (2006) suggested that seeds of Rhamnaceae family presented non-dormancy, physiological (PD), physical (PY), and combinational (PY+PD). Under natural conditions, stone passage through the digestive tract of vertebrates is critical for endozoochorus seed dispersal because it enhanced germination for some *Ziziphus* species (Saied *et al.* 2008). The introduction of this species in agroforestry systems requires a good understanding of its ecophysiological behavior under restrictive environmental conditions. The plant is well adapted to dry and hot climates, but little is known about the physiological basis at the seedling stage under salt stress conditions. Analysis of the relationship between gas-exchange characteristics and plant-water relations provides a tool for understanding how plants cope with NaCl salinity, and how the mechanisms of adaptation to excessive soil salinity may affect its prospects for cultivation, restora-tion, and persistence in natural ecosystems in the face of climate change. Our primary hypothesis stated that seedlings subjected to NaCl salinity should display a trade-off between water loss and carbon gain allowing them to survive in contrasting environments. We aimed to identify the relationship between leaf gas-exchange characteristics, water relations, and the performance of Christ's thorn jujube seedlings.

Materials and methods

Plant material, growth conditions, and experimental design: Seeds of *Ziziphus spina-christi* (L.) Willd. were provided by the seed bank of the Laboratory of Pastoral Ecosystems and Valorization of Spontaneous Plants and Associated Microorganisms at the Arid Land Institute, Médenine, Tunisia. Fruits were obtained from six wild individual trees which were collected from a location in Tozeur (southwest Tunisia). This area is Saharan with a typical Mediterranean climate, characterized by irregular rainfall events and a harsh dry summer period. Annual rainfall is around 93.47 mm, mean annual temperature is 22.6°C with a minimum temperature 1.8°C in January and 47.6°C maximum in August.

When experiments were carried out, fruit pulps were removed and endocarps were cracked using a manual peeler. The stones contain two seeds embedded in the endocarp. Germinated seeds were transferred to 1-L plastic pots perforated at the bottom to facilitate drainage. A commercial peat (type *Floragard*) was used as a substrate with the following physicochemical characteristics: dry matter of 25–40%, organic material of 55–90%, water retention capacity of 50–78%, electrical conductivity (EC) of 0.62 mS cm^{-1}, and pH = 5.5–6. Watering was carried out every 2 d by rainwater with very low EC. Seedlings were grown in a growth chamber as follows: temperature of 25 ± 1°C, 50/70% day/night relative humidity, and 16-h light/8-h dark regime with PAR of 250 μmol(photon) $m^{-2} s^{-1}$. The experiment was arranged in a completely randomized design with four NaCl salinity treatments × five replicates. Seedlings were supplied with rain water (0 mM NaCl, EC = 0.78 mS cm^{-1}) lacking salt or the same solution supplemented with 50, 100 or 200 mM NaCl. To avoid osmotic shock, NaCl concentrations were increased stepwise in aliquots of 50 mM per day.

Growth measurements: Two harvests were carried out, at the beginning of the treatment (45-d-old plants) and 21 d later. At the harvests, leaves, stems, and roots were successively rinsed three times in cold water and blotted between two layers of filter paper. The fresh mass (FM) was measured immediately, and the dry mass (DM) after 48 h of desiccation in an oven at 60°C. Plant relative growth rate (RGR [d^{-1}]) was determined as: $RGR = \Delta M/\underline{M}\,\Delta t$, where Δ is the difference between values at the final and initial harvests, t is the time [d], and M is the whole plant DM [g]. $\underline{M}$ is the logarithmic mean of M calculated over the Δt period (Hunt 1990): $\underline{M} = \Delta M/\Delta \ln(M)$.

Plant water relations: The water status was evaluated by measuring relative water content (RWC [%]) on fully expanded leaves according to Morgan (1984): RWC = [(FM – DM)/(TM – DM) × 100], where FM, DM, and TM are the fresh, dry, and turgid masses, respectively. Stem ψ_w [MPa] was measured using a pressure chamber (*PMS Instruments Co.*, Corvallis, OR, USA) after 21 d of salt treatment, according to Scholander *et al.* (1965). After the measurement of ψ_w, the samples were frozen in liquid nitrogen and stored at –20°C. Leaf tissues were thawed and centrifuged at 1,200 × *g* for 25 min at 4°C to extract the cell sap. A vapor pressure osmometer (*Wescor 5520*, Logan, UT, USA) was used to determine osmolality of the sap expressed from leaves, which was converted to ψ_π [MPa], by the van't Hoff equation: $\psi_\pi = -ci\,R\,T$, where *ci* is the value read from the instrument, R is the ideal gas constant, and T is the absolute temperature (Nobel 1991). Turgor potential (ψ_p [MPa]) was determined using the relationship: $\psi_p = \psi_w - \psi_\pi$.

CO_2 and H_2O gas exchange: The net photosynthetic rate

(P_N [µmol(CO_2) m^{-2} s^{-1}]), stomatal conductance (g_s [mol(H_2O) m^{-2} s^{-1}]), transpiration rate (E [mmol(H_2O) m^{-2} s^{-1}]), and intercellular CO_2 concentration (C_i [µmol(CO_2) mol^{-1}]) of fully expanded leaves were measured between 10:00 and 12:00 h using an *LCpro+* portable photosynthesis system (*ADC*, *BioScientific Ltd*, UK). The CO_2 concentration in the leaf chamber was set at 360 µmol mol^{-1} and the leaf was irradiated with a light intensity of 1,500 µmol(photon) m^{-2} s^{-1}. The water-use efficiency [WUE, µmol(CO_2) mmol(H_2O)$^{-1}$] and intrinsic [WUE_i, µmol(CO_2) mol(H_2O)$^{-1}$] were calculated as P_N/E and P_N/g_s, respectively.

Statistical analysis: Data were analysed using *SPSS v. 17.0*. They were tested for normal distribution using the *Shapiro-Wilk*'s test, and heterogeneities of variance within treatments were tested using *Levene*'s test. *Tukey*'s test (honestly significant differences, HSD) was used to estimate the least significant range between means. Correlation coefficients between pairs of growth and physiological attributes were examined using *Pearson*'s correlation coefficient at 5 or 1% significance level.

Results

Growth attributes: The NaCl salinity affected development and growth of seedlings at the highest concentration (200 mM NaCl), which was associated with the appearance of foliar necrosis. A one-way *ANOVA* indicated that salinity significantly affected the average leaf number (Fig. 1*A*; $F = 5.69$; $P<0.01$). The average number just before the applied stress was *ca*. eight leaves per plant. At the final harvest, the leaf number on salt-free medium was four times higher relative to original plants, whereas in the presence of 200 mM, this parameter represented *ca*. 50% of the control value. As shown in Fig. 1*B*, plants grew optimally under control conditions (28.2 cm), and their height significantly decreased as salt stress intensified ($F = 25.01$; $P<0.01$). The average plant height was considerably reduced at 200 mM NaCl (*ca*. 69% of the control plants).

The presence of NaCl, even at low concentration (50 mM), caused a decrease in the dry matter of whole plants of *ca*. 27% as compared to control plants. This decline in dry mass was more pronounced at the highest NaCl concentration (*ca*. 55% of the control value, Fig. 1*C*). The RGR followed a similar trend for dry matter allocation and decreased significantly in all tissues at the highest NaCl concentration. At all levels of salinity, roots had the lowest growth activity. A one-way *ANOVA* on the biomass production indicated that salinity significantly affected DM (*ANOVA F* values 12.10, 10.22, 5.40 for leaves, stems, and roots, respectively, and all $P<0.01$) and RGR (*ANOVA F* values 12.78, 11.73, 4.76 for leaves, stems, and roots, respectively, and all $P<0.05$). The RGRs of different organs were reduced by *ca*. 27–71% as compared to control plants, depending on the NaCl concentration of the growth medium.

Water relations: The RWC was significantly reduced by 7–21% compared to control plants after 21 d of the salt stress treatment ($F = 10.67$, $P<0.001$; Fig. 2). A one-way *ANOVA* of the water status revealed that NaCl salinity significantly affected ψ_w, ψ_π, and ψ_p (*ANOVA F* values 24.96, 64.56, 11.21, respectively, and all $P<0.001$) of salinized plant relative to control ones. There were strong linear relationships between parameters of the plant water potential and the NaCl concentration of the watering solutions (Fig. 3*A*–*C*). Negative relationships were identified for ψ_w and ψ_π (R2 values of 0.82 and 0.90, respectively; Fig. 3*A*,*B*), whereas a positive relationship was found for ψ_p (R2 = 0.63; Fig. 3*C*). The average value of ψ_w dropped from –0.81 to –2.01 MPa at 0 and 200 mM NaCl, repectively. A similar pattern was observed in ψ_π but there was an additional decline from –1.89 to –4.0 MPa. There was a significant positive correlation between ψ_w and ψ_π ($R^2 = 0.82$, $P<0.01$). According to the relationship $\psi_w = \psi_\pi + \psi_p$, ψ_p corresponding to the difference between each point response and the line of equality at any value of ψ_w. Stem ψ_π decreased with decreases in ψ_w and the proximity of points to the zero line showed that variations in ψ_p were

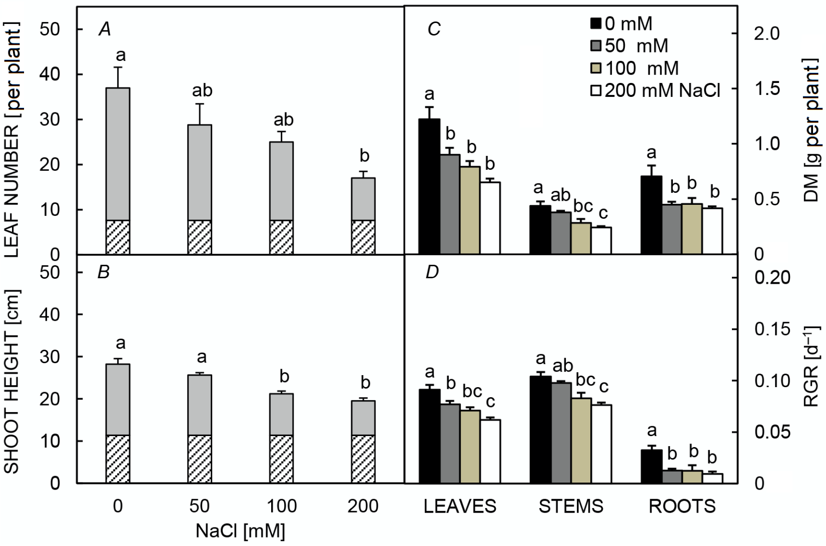

Fig. 1. Changes in leaf number (*A*), shoot height (*B*), dry mass (DM) (*C*), and relative growth rate (RGR) (*D*) of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). Values are means ± SE, $n = 5$. Hatched histograms correspond to the initial leaf number and shoot height before NaCl treatments. *The same letters* indicate no significant differences ($P<0.05$) according to the *Tukey*'s test.

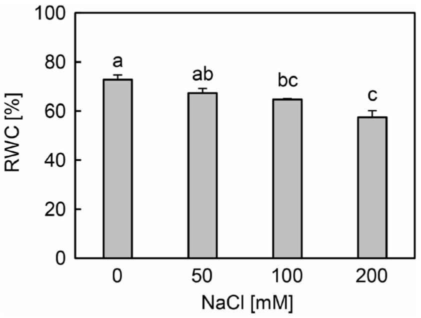

Fig. 2. Changes in leaf relative water content (RWC) of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). Values are means ± SE, $n = 5$. *The same letters* indicate no significant differences ($P<0.05$) according to the *Tukey*'s test.

smallest for control plants and largest for NaCl-stressed plants after 21 d, likely to be due to osmotic adjustment (Fig. 3*D*).

CO_2 exchange, transpiration, and stomatal conductance: A one-way *ANOVA* showed that NaCl salinity significantly affected P_N, C_i, E, and g_s (F-values 39.16, 9.39, 20.26, and 18.22, respectively; $P<0.01$). There was a significant negative relationship between NaCl concentration of watering solutions and P_N, C_i, E, and g_s with r values of 0.85, 0.63, 0.73, and 0.69, respectively (Fig. 4*A–D*). The P_N significantly decreased with the increase in osmolarity of solutions (*ca.* 19 and 67% of the control value at 50 mM and 200 mM NaCl, respectively). The C_i was reduced by 13–45% relative to control plants, when the medium NaCl concentration increased. The E was severely reduced as salt stress intensified. The highest average rate was recorded in control plants [1.73 mmol(H_2O) m^{-2} s^{-1}], and approximately fourfold lower rate in plants stressed at 200 mM NaCl (Fig. 4*C*). As compared to controls, g_s of salt-treated plants decreased by *ca.* 31 and 83% at 50 mM and 200 mM NaCl, respectively (Fig. 4*D*). This decline was more pronounced than those in P_N and E with increasing NaCl concentration. Stressed plants displayed higher P_N/E (WUE) and P_N/g_s (WUE_i) ratios than that in control plants, where the differences become significant with increasing NaCl concentration of watering solutions (F = 4.71, $P<0.05$; F = 8.70, $P<0.01$, respectively; Fig. 4*E*,*F*), with r values 0.41 and 0.57, respectively.

The correlation coefficients between growth and different physiological attributes are shown in Table 1. As expected, high correlation coefficients were found between growth (shoot DM and shoot RGR) and all photosynthetic parameters of plants except WUE, when exposed to NaCl salinity at varying concentration of watering solutions. Additionally, the plant water potential components (ψ_w, ψ_π, and ψ_p) and the RWC showed highly significant correlation coefficients with shoot DM, revealing strong relationships (shoot DM × ψ_w, $r = 0.79$; shoot DM × ψ_π, $r = 0.82$; shoot DM × ψ_p, $r = 0.67$; shoot DM × RWC, $r = 0.75$).

Discussion

The Christ's thorn jujube plants grew optimally under control conditions and at moderate salinity in comparison with high NaCl salinity (200 mM). The depressive effect of salinity on plant growth was more pronounced at the highest NaCl concentration. This was in agreement with previous reports on *Ziziphus* species including *Z. spina-christi* at 180

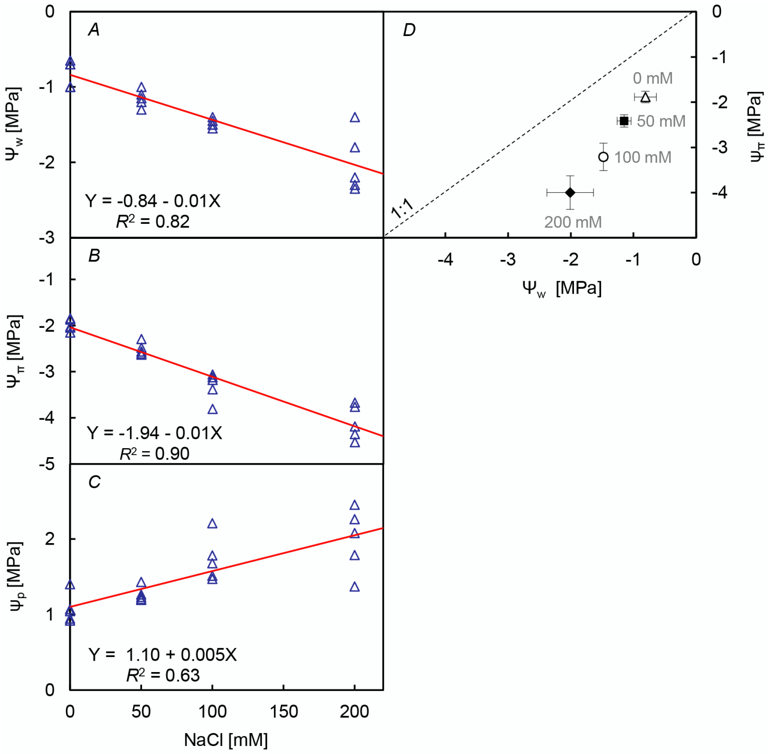

Fig. 3. Regression plots for water potential (ψ_w) (*A*), osmotic potential (ψ_π) (*B*), and turgor potential (ψ_p) (*C*), and relationship between ψ_w and ψ_π (*D*) in leaves of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). Lines describing the dependencies were obtained using a linear regression. *A–C*: Values are from four treatments with five replicates ($n = 20$). *D*: Values represent means ± SE ($n = 5$). *The 1:1 line* indicates $\psi_\pi = \psi_w$ and hence $\psi_p = 0$.

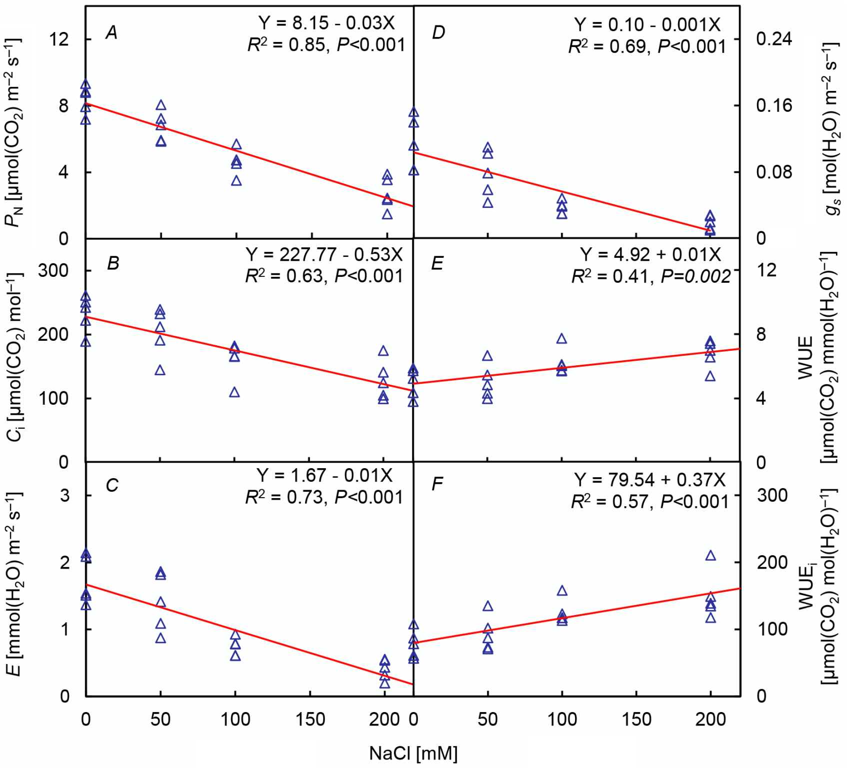

Fig. 4. Changes in net photosynthetic rate (P_N) (A), internal CO$_2$ concentration (C_i) (B), transpiration rate (E) (C), stomatal conductance (g_s) (D), water-use efficiency (WUE) (E), and intrinsic WUE (WUE$_i$) (F) of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). Lines describing the dependencies were obtained using a linear regression. Values are from four treatments with five replicates (n = 20).

Table 1. Correlation coefficients (R^2) between pairs of growth and physiological attributes of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). *, ** – significant at P<0.05 and P<0.01, respectively, ns – not significant; df (n = 20). C_i – intercellular CO$_2$ concentration; DM – dry mass; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; RGR – relative growth rate; WUE – water-use efficiency; WUE$_i$ – intrinsic water-use efficiency; ψ_p – turgor potential; ψ_w – water potential; ψ_π – osmotic potential.

Parameters	Shoot DM	Shoot RGR	C_i	E	g_s	P_N	WUE	WUE$_i$	ψ_w	ψ_π
Shoot RGR	0.99^{**}									
C_i	0.59^{**}	0.60^{**}								
E	0.70^{**}	0.72^{**}	0.91^{**}							
g_s	0.69^{**}	0.71^{**}	0.91^{**}	0.98^{**}						
P_N	0.83^{**}	0.84^{**}	0.82^{**}	0.94^{**}	0.92^{**}					
WUE	-0.40^{ns}	-0.42^{ns}	-0.94^{**}	-0.85^{**}	-0.81^{**}	-0.67^{**}				
WUE$_i$	-0.52^{*}	-0.53^{*}	-0.95^{**}	-0.87^{**}	-0.87^{**}	-0.78^{**}	0.92^{**}			
ψ_w	0.79^{**}	0.81^{**}	0.75^{**}	0.81^{**}	0.78^{**}	0.92^{**}	-0.58^{**}	-0.75^{**}		
ψ_π	0.82^{**}	0.84^{**}	0.82^{**}	0.85^{**}	0.83^{**}	0.90^{**}	-0.69^{**}	-0.80^{**}	0.91^{**}	
ψ_p	-0.67^{**}	-0.69^{**}	-0.71^{**}	-0.72^{**}	-0.70^{**}	-0.70^{**}	0.66^{**}	0.68^{**}	-0.61^{**}	-0.89^{**}

and 220 mM (Sohail *et al.* 2009, Shekafandeh and Takhti 2013, respectively), *Z. mauritiana* at 131 and 176 mM (Bhatt *et al.* 2008, Agrawal *et al.* 2013, respectively), *Z. mauritiana* grafted on *Z. spina-christi* at 220 mM (Bhat *et al.* 2009), and *Z. rotundifolia and Z. nummularia* at 220 mM (Gupta *et al.* 2002). Reduction in DM of *Ziziphus* species might be due to increased osmotic pressure in the root zone after progressive increase of NaCl salinity in the soil solution, ion accumulation (mainly Na$^+$ and Cl$^-$) in plant tissues to toxic concentrations, and excessive concentration of soluble ions that might have resulted in nutrient imbalance in the soil solution and plant tissues (Bhatt *et al*. 2008, Sohail *et al.* 2009, Agrawal *et al.* 2013).

Several research reports also show that plants grown under salt stress manifest acclimation by lowering both leaf ψ_w and ψ_π (Gorai and Neffati 2011, Gorai *et al.* 2011). Our data showed that increasing NaCl salinity was accompanied by a decrease in RWC, ψ_w, and ψ_π of Christ's thorn jujube plants. Maintaining leaf RWC under lowering ψ_w is an important adaptation exhibited by plants to cope with salt stress. Thus, ψ_p could be maintained, and obviously the osmotic adjustment was sufficient to compensate the stem ψ_w decline in these Christ's thorn plants. Numerous studies have reported an increase of the proline content (Gupta *et al.* 2002, Bhatt *et al.* 2008, Sankhla *et al.* 2008, Shekafandeh and Takhti 2013) and activity of antioxidant

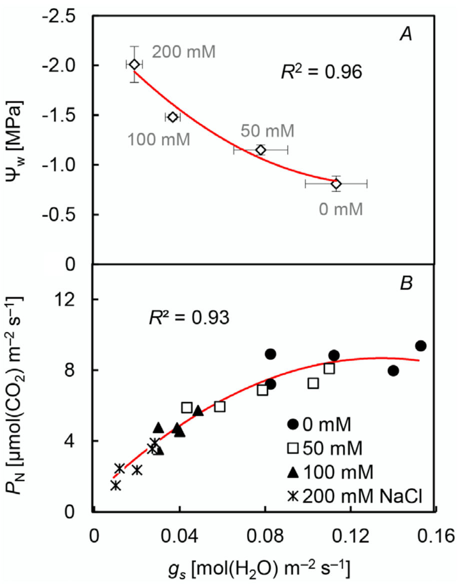

Fig. 5. Relationships between leaf water potential (ψ_w) and stomatal conductance (g_s) (*A*) and net photosynthetic rate (P_N) and stomatal conductance (g_s) (*B*) of *Ziziphus spina-christi* seedlings subjected for 21 d to various NaCl concentrations (0, 50, 100 or 200 mM). Lines describing the dependencies were obtained using a polynomial regression. Values are from four treatments with five replicates (n = 20).

enzymes (Sankhla *et al.* 2008, Agrawal *et al.* 2013) in leaves of *Ziziphus* species when exposed to NaCl-salinity. ψ_w and ψ_π were linearly related to RWC, which declined although it still maintained high values. This supports findings on drought-stressed plants of the same genus including *Z. mauritiana* (Clifford *et al.* 1998, Kulkarni *et al.* 2010), *Z. rotundifolia* (Arndt *et al.* 2001), and *Z. lotus* (Maraghni *et al.* 2014, 2019). In the present study, stem ψ_w of NaCl-stressed seedlings dropped to –2.0 MPa, which is in the range of ψ_w found by Zait and Schwartz (2018) on 12- to 15-year-old trees of the same species in the field at the end of hot and dry summer ($-1.8 > \psi_w > -2.2$ MPa).

Photosynthetic activity is one of the major factors controlling growth (Tezara *et al.* 2002, Ashraf 2004). The P_N presented here clearly shows a correlation with shoot growth of *Z. spina-christi* treated with increased osmolarity of solutions. The relationship between P_N and g_s reveals a trade-off between water loss and carbon gain experienced by plants in contrasting environments (Gorai *et al.* 2011, 2015; Maraghni *et al.* 2019). The present study depicts that P_N and g_s under salt stress were positively associated (r = 0.93, P<0.01; Fig. 5*A*) and the former variable also had a strong positive relationship with ψ_w (r = 0.93, P<0.01; Fig. 5*B*). Thus, g_s plays a strong control over photosynthetic assimilation and the diffusional limitations restricting the supply of CO$_2$ to metabolism of Christ's thorn plants. Our data are in accordance with the findings of Gupta *et al.* (2002) who showed that *Z. nummularia* and *Z. rotundifolia* are quite tolerant to salinity and the latter species showed a greater photosynthetic performance at high NaCl salinity. Our results also showed that stressed plants displayed higher WUE and WUE$_i$ values than that in control plants with increasing NaCl salinity. This corroborates findings of Zait *et al.* (2018) on the same species; they showed that improved WUE$_i$ of one-year-old saplings under intensified drought and salinity stresses was made possible by a greater decline in g_s.

In conclusion, Christ's thorn jujube grew and survived under severe saline conditions. It was able to overcome salt stress by reducing its photosynthetic performance and plant-water relations. This was achieved by lowering their stem ψ_w and g_s and by maintaining ψ_p as a tolerance mechanism to withstand salt stress.

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