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Photosynthetic and Antioxidant Responses of the Xero-Halophyte *Zygophyllum album* (L.) to Salt Stress

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Abstract: *Zygophyllum album* L., plants were exposed to NaCl salinity (0, 100, 200, 400 and 800 mM NaCl) for 60 days. Moderate salinity (100-200 mM NaCl) had a stimulating effect on Relative Growth Rate (RGR), net CO_2 assimilation (P_N) and stomatal conductance (g_s). At higher salinities levels (400-800 mM NaCl), these physiological parameters decreased significantly. *Z. album* PSII photochemistry was unaffected by salinity, only a slightly decrease in the efficiency of PSII (F'v/F'm) was occurred at 800 mM. The reduction in photosynthesis is most probably due to stomatal closure rather than damages in the photosynthetic apparatus. Increasing salinity from 400-800 mM NaCl caused a significant accumulation of H_2O_2 generation and lipid peroxidation and a concomitant decrease in membranes stability index. The antioxidative defence capacity of *Zygophyllum album* L., plants might be achieved by the increasing activities of Superoxide Dismutase (SOD), Peroxidase (POD) and Ascorbate Peroxidase (APX) and the accumulation of phenols which showed to participate efficiently in restriction of oxidative damages caused by the H_2O_2 generation while Catalase (CAT) was unaffected under salt stress.

Key words: Plant growth, photosynthetic status, phenols, antioxidative enzymes, salt stress

INTRODUCTION

Soil salinity is one of the major invasive environmental stresses that influences plants through osmotic effects, ion specific effects and oxidative stress (Munns and Tester, 2008). Salinity limits CO_2 assimilation, exposing chloroplasts to excessive excitation energy which in turn could increase the generation of Reactive Oxygen Species (ROS) and induce oxidative stress (Parvaiz and Satyawati, 2008). Salinity-induced limitation of photosynthesis under salinity is not only attributed to stomatal closure but also to non-stomatal factors (Kao *et al*., 2003). It has been indicated that NaCl salinity predispose plants to photoinhibition and photodamage of PSII and finally inhibit its activity (Netondo *et al*., 2004) whereas other studies have shown that salt stress had no significant effect on PSII (Morant-Manceau *et al*., 2004).

On the other hand, excess salt concentrations cause an overproduction of Reactive Oxygen Species (ROS) in plants which can damage cellular components including nucleic acids, proteins and membrane lipids (Silva *et al*., 2010). To minimize the effects of oxidative stress, plants have evolved a complex antioxidant system which includes both enzymatic and non-enzymatic components (Mittler, 2002) responsible for maintaining the levels of ROS under tight control. Non-enzymatic antioxidants such as phenolic compounds play an important role in adsorbing and neutralizing free radicals, quenching singlet oxygen or decomposing peroxide (Ksouri *et al*., 2007). In plants, polyphenol synthesis and accumulation is generally stimulated in response to salinity, suggesting that the presence of those metabolites is related to increased salt tolerance of plants (Kim *et al*., 2008). The antioxidative enzymes are the most important components in the scavenging system of reactive oxygen species. Superoxide Dismutase (SOD) catalyzes the first step of the enzymatic defence mechanism, the conversion of superoxide radicals to O_2 and H_2O_2. The hydrogen peroxide produced is then scavenged by Catalase (CAT) into water and molecular oxygen whereas Peroxidase (POD) decomposes H_2O_2 by oxidation of co-substrates (Meloni *et al*., 2003). The Ascorbate Peroxydase (APX) had a much higher affinity for H_2O_2 than CAT (Benavides *et al*., 2000). The capacity to scavenge ROS and to reduce their damaging effects on macromolecules appears to represent an important stress tolerance trait in higher plants (Ksouri *et al*., 2007; Abogadallah, 2010).

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Zygophyllum album L., is a wild salty desert herb common in Southern Tunisia belonging to the family Zygophyllaceae. It is largely used in traditional medicine as a drug active against rheumatism, gout, asthma and hypertension. It is also used as diuretic, local anaesthetic, antihistaminic, anti-diabetic agent, carminative, antiseptic and stimulant (Meng *et al*., 2002). Nevertheless, studies on the tolerance of *Z. album* to salt stress are still incomplete and preliminary. In the present study, researchers have examined the effects of salinity on plant growth, photosynthesis parameters, total phenols content, lipid peroxidation and antioxidant enzyme activity. In order to identify and understand the tolerance mechanism developed to confront salt stress in *Z. album* L.

MATERIALS AND METHODS

Plant growth conditions: Seeds of *Z. album* were sowed to germinate in plastic containers filled with a mixture of marketed peat and sterile sand (1:1, v/v) and irrigated with deionised water. When seedlings were around 5 cm in height, plants were placed in plastic pots (5 L) filled with mixture of peat and perlit (2:1, v/v) and maintained under greenhouse conditions. The pots were irrigated every day with Hoagland solution for acclimatization during 15 days. At the end of the acclimatization phase, salinity treatment was started by adding NaCl at graded levels (0, 100, 200, 400 and 800 mM) to the nutrient solution. Five replicates of each treatment were used to measure different parameters at 60 days after the salt treatments.

Growth activity: Relative Growth Rate (RGR) was calculated as follows:

$$RGR = [\ln (DW_2/DW_1)]/(t_2-t_1)$$

Where:

DW = Dry Weight
t = Time
1, 2 = Beginning and the end of a salinization period, respectively

Measurements of photosynthetic gas exchange and chlorophyll fluorescence: Net CO_2 assimilation rate (P_N) and stomatal conductance (g_s) of the seedlings were measured on leaves of five plants per treatment at 60 days after salt stress using a Portable Photosynthesis System (Li-6200, Lincoln). Measurements were made between 8-9 h to avoid photoinhibitory damage potentially resulting from high light stress at midday. Photosystem 2 (PSII) photochemistry was measured by portable fluorometer (PAM-2000, Walz). By using fluorescence parameters determined in both light and dark-adapted leaves, calculations were made of the maximal potential PSII efficiency, Fv/Fm = (Fm-F0)/Fm and the efficiency of excitation energy capture by open PSII reaction centers, F'v/F'm = (F'm-F'0)/F'm.

Hydrogen peroxide and lipid peroxidation estimation: The H_2O_2 content was determined as described by Velikova *et al*. (2000). Fresh leaf tissue (0.5 g) was homo-genized with 5 mL of 0.1% (w/v) Trichloroacetic Acid (TCA) inapre-chilled pestle and mortar. This homogenate was then centrifuged at 12,000 g for 15 min. To the 0.5 mL of the supernatant 0.5 mL of potassium phosphate buffer (pH 7.0) and 1 mL of potassium iodide were added. The mixture was vortexed and its absorbance was read at 390 nm. Lipid peroxidation was estimated by determining the Malonyldialdehyde (MDA) content in the leaves using the thiobarbituric acid method described by Cakmak and Horst (1991).

Analysis of phenolic compounds: Phenolic content was assayed using the Folin-Ciocalteu reagent following Singleton's method slightly modified (Dewanto *et al*., 2002). Total phenolic content of leaves (Three replicates per treatment) was expressed as mg Gallic Acid Equivalents (GAE) per gram of dry weight (mg GAE g^{-1} DW).

Determination of enzymatic activities: For the enzyme assays, 0.3 g leaves were ground with 2 mL ice-cold 25 mM HEPES buffer (pH 7.8) containing 0.2 mM EDTA, 2 mmol L^{-1} ascorbate and 2% Polyvinyl Polypyrrolidone (PVPP). The homogenates were centrifuged at 4°C for 20 min at 12,000×g and the resulting supernatants were used for the determination of enzymatic activity. Superoxide Dismutase (SOD) activity was estimated according to Rao and Sresty (2000). The absorbance was recorded at 560 nm and one unit enzyme activity (U) was defined as the quantity of SOD required to produce a 50% inhibition of reduction of Nitroblue Tetrazolium (NBT) and the specific enzyme activity was expressed as units mg^{-1} protein. Peroxidase (POD) activity was determined spectrophotometrically by measuring the oxidation of guaiacol at 470 nm. One unit of POD activity is defined by the increase in absorbance at 470 nm for 1 min due to guaiacol oxidation. Catalase (CAT) activity was estimated spectrophotometrically according to Chakraborty and Tongden. One unit of CAT activity is defined by the decrease at 240 nm for 1 min, due to H_2O_2 consumption. The activity of APX was assayed according to the method described by Nakano and Asada (1981), using ascorbic acid as a substrate. One unit of APX was defined as the amount of enzyme required to oxidize 1 mM of ascorbate.

Statistical analysis: The data were subjected to Analysis of Variance (ANOVA) and comparisons between the mean values of treatments were made by the Duncan post hoc tests ($p<0.05$). Statistical analyses were performed using the SPSS statistical package (SPSS 13).

RESULTS AND DISCUSSION

A one-way ANOVA (Table 1) showed a significant enhanced value of the Relative Growth Rate (RGR) at 100 and 200 mmol L^{-1} NaCl (Ca.120.4-122% of the control, respectively). Moderate salinity appeared thus to be optimal for the growth of *Z. album*. Whereas at higher salt levels (400-800 mM NaCl), RGR decreased significantly by 5.3 and 21% compared with the control, respectively. The photosynthetic ability of *Z. album* plants was optimal at moderate salt stress (>200 mM NaCl). Thus, the net assimilate rate of CO_2 (P_N) and the stomatal conductance (g_s) reached the maximum at 100-200 mM NaCl, they were 118.6-125.2% and 114.7-115.4% compared with control plants at the end of the experimental period. However, higher salinities (400-800) induced a significantly reduction in gas exchange parameters. As compared with the control, P_N and g_s decreased at 800 mM NaCl by 33.2 and 54.8%, respectively. This response to NaCl is similar to that of *Atriplex halimus* and *Nitraria retusa* (Boughalleb *et al*., 2009). The study of PSII photochemistry in the dark-adapted leaves showed that there was no significant difference in maximal efficiency of PSII photochemistry (Fv/Fm) between control and salt-treated *Z. album* plants (Table 1). For the PSII photochemistry in the light-adapted leaves, the values of the efficiency of PSII (F'v/F'm) were slightly below the control values in at the highest salinity level (800 mM), suggesting a little effect of salinity on the photochemistry of PSII and no damage to PSII (Table 1). The decrease in P_N at higher salinities (400-800 mM NaCl) and the consequent decrease in g_s may indicate that stomatal closure was imposing a limitation on photosynthesis under saline stress. In addition, a highly significant correlation between P_N and g_s ($r = 0.96^{***}$; Fig. 1) suggests stomatal conductance as one of the important causes limiting photosynthesis under salt stress. Regression analyses shows no significant relationship between P_N and Fv/Fm ($r = -0.27^{NS}$; Fig. 1) and a weedy correlation between P_N and F'v/F'm ($r = 0.50^{*}$; Fig. 1), indicates that variations of these fluorescence parameters were very slightly associated with variations of photosynthesis. The higher tolerance of PSII to photoinhibition suggests that the decreased CO_2 assimilation rate at higher salinities levels in *Z. album* leaves may be due mainly to the stomatal closure than non-stomatal factors (limitation of the photosynthetic electron transport). On the other hand, the highly positive relationship observed between DW and P_N showed that photosynthesis could be the growth-limiting factor. The fact that growth and net photosynthesis rate varied in the same manner with increasing salinity, suggest that the decrease in stomatal conductance and transpiration rate represent adaptive mechanisms to cope with excessive salt rather than only a negative consequence of it (Clark *et al*., 1999).

It is well known that excessive accumulation of Reactive Oxygen Species (ROS) in plants is one of the major damage induced by salinity. The product of lipid peroxidation (content of MDA) and the generation of hydrogen peroxide have been considered as indicators of oxidative damage (Meloni *et al*., 2003). In the study, H_2O_2 and MDA accumulation was increased significantly only at higher NaCl concentration (400-800 mM NaCl). In this range of salinities, the increase in H_2O_2 content reached 1.2-2- fold the control and 1.1-1.6-fold the control for the MDA content due to salt stress (Table 2). The high positive correlation between H_2O_2 generation and MDA amount ($r = 0.98^{***}$; Fig. 2) confirmed the hypothesis that H_2O_2 brings about lipid peroxidation leading to membrane damages (Hichem *et al*., 2009). Furthermore, a negative correlation was observed between shoot biomass production and leaf MDA contents ($r = -0.84^{***}$; Fig. 2), indicating that low lipid peroxidation resulted in increased biomass production which may be attributed to the highly tolerance of these species to moderate salinities and their effective detoxification mechanisms. However, the increase of MDA and H_2O_2 contents coupled with reduced plant growth at higher salinities, indicating that membrane stability had been destroyed and lipid

Table 1: Effects of NaCl concentrations on Relative Growth Rate (RGR), net CO_2 assimilation rate (P_N), stomatal conductance (g_s), maximum efficiency of PSII photochemistry (Fv/Fm) and the efficiency of excitation capture by open PSII reaction centres (F'v/F'm) in the shoots of *Z. album*

				Fluorescence parameters	
NaCl (mM)	RGR (g/g/day)	P_N (µmol/m²/sec)	g_s (mmol/m²/sec)	Fv/Fm	F'v/F'm
0	0.065±0.002^{b}	18.1±0.18^{b}	447±14.3^{b}	0.773±0.003^{bc}	0.414±0.002^{a}
100	0.078±0.003^{a}	21.6±0.41^{a}	516±21.5^{a}	0.776±0.004^{ab}	0.412±0.002^{a}
200	0.079±0.003^{a}	22.8±0.40^{a}	513±17.1^{a}	0.770±0.003^{c}	0.416±0.001^{a}
400	0.061±0.002^{c}	16.5±0.17^{c}	391±23.2^{c}	0.777±0.003^{a}	0.415±0.002^{a}
800	0.051±0.002^{d}	12.1±0.16^{d}	202±21.3^{d}	0.774±0.004^{ab}	0.407±0.001^{b}

Data are means values±SE of five measurements; values in each column with the same letter are not significantly different ($p = 0.05$) as described by to Duncan's test

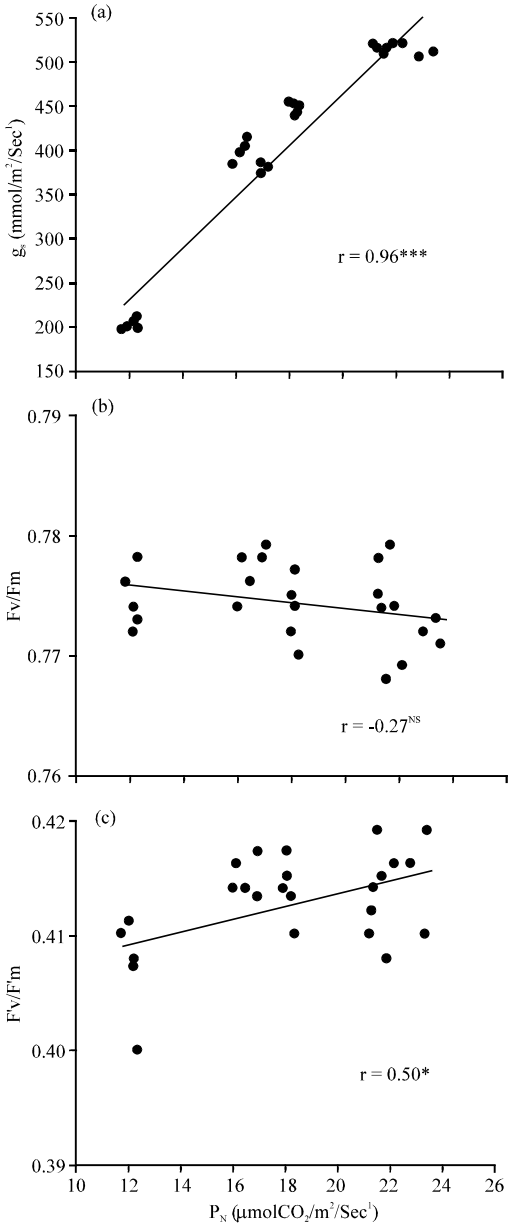

Fig. 1: Relationships between net CO_2 assimilation rate (P_N) and stomatal conductance (g_s) and between dark-adapted fluorescence (Fv/Fm), light-adapted fluorescence (F'v/F'm) and net CO_2 assimilation rate (P_N) at *Z. album* cultivated under salt stress; an average of 5 repetitions and confidence interval was calculated at the threshold of 95%

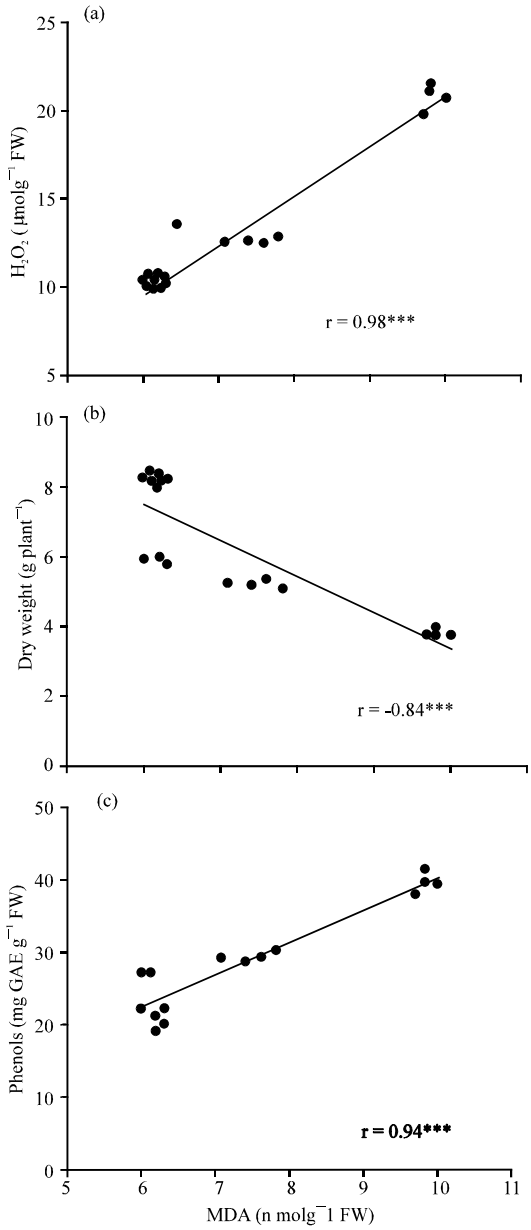

Fig. 2: Relationships between Hydrogen peroxide (H_2O_2) contents, shoots biomass accumulation and total phenols with Malondialdehyde (MDA) accumulation in *Z. album* plants cultivated under salt stress; an average of 5 repetitions and confidence interval was calculated at the threshold of 95%

peroxidation had occurred. The increase in lipid peroxidation may be due to the incapability of antioxidants to scavenger reactive oxygen species results from salt stress. Similar results were observed on other halophyte such as *Limonium bicolour*, *Atriplex halimus* and *Nitraria retusa* (Li, 2008; Boughalleb and Denden, 2011). To cope with oxidative damage induced by salt stress, plants have the ability to detoxify ROS by up-regulating antioxidant enzymes as well as some non-enzymatic antioxidant metabolites. The phenolic compounds has been considered pertinent in oxidative

Table 2: Effects of NaCl treatments (0, 100, 200, 400 and 800 mM) on Hydrogen peroxide (H_2O_2), Malondialdehyde (MDA) and total phenols content in *Z. album* plants

NaCl (mM)	MDA (nmol g^{-1} FW)	H_2O_2 (μmol g^{-1} FW)	Total phenols (mg GAE g^{-1} DW)
0	6.1±0.4^b	10.2±0.4^d	20.5±0.4^d
100	6.2±0.4^b	10.1±0.3^c	24.0±0.4^c
200	6.0±0.4^a	10.4±0.5^b	25.7±0.4^b
400	7.2±0.4^a	12.5±0.6^a	29.1±0.4^a
800	9.8±0.4^a	20.7±0.6^a	39.5±0.4^a

Data are means values±SE of four measurements; values in each column with the same letter are not significantly different (p = 0.05) as described by Duncan's test

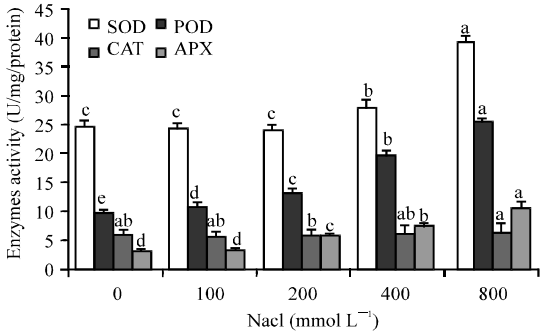

Fig. 3: Effect of NaCl treatments on the contents of Superoxide Dismutase (SOD), Peroxidase (POD), Catalase (CAT) and Ascorbate Peroxidase (APX) in the shoots of *Z. album*. Bars followed by the same letter are not statistically different at p<0.05 (Duncan's multiple range test); averages of four repetitions are presented with bars indicating SE

stress tolerance (Moyer *et al*., 2002). Their accumulation can be changed by salt stress but this is critically dependent on the salt sensitivity of plants (Kim *et al*., 2008). In the present study, the total phenols indicated a significant raise over salt stress, reaching 117% of control at 100 mmol L^{-1} NaCl and 193% of control at 800 mM NaCl. Furthermore, the significant positive correlation (r = 0.94***; Fig. 2) between leaf MDA and phenolic contents under salt stress, lest to conclude that phenolic compounds can play an important role in neutralizing ROS, alleviating ion-induced oxidative damage (Moyer *et al*., 2002; Ksouri *et al*., 2007) and protect cytoplasmic structures and chloroplasts from adverse effects of salinity.

The ability of plants to overcome oxidative stress partly relies on the induction of SOD activity and subsequently on the up regulation of other downstream antioxidant enzymes (Alscher *et al*., 2002). In the present study, the activity of SOD increased significantly at higher salinities reaching 113% of the control at 400 mM and 157% of the control at 800 mM NaCl. The significant increase observed in SOD activity in *Z. album* suggested that the enzyme may function as a ROS scavenger by converting O_2-H_2O_2. The increase in the SOD activity may be attributed to the increased production of active oxygen species as substrate that lead to increased expression of genes encoding SOD (Abedi and Pakniyat, 2010). POD is a key enzyme, involved in the detoxification of toxic compounds such as H_2O_2 which are produced in chloroplasts as a result of oxidative stress (Chaparzadeh *et al*., 2004). APX is an important antioxidant enzymes involved in ascorbate-glutathione cycle which plays a key role in destroying the H_2O_2 (Foyer and Noctor, 2005). The data showed enhanced activity of POD with increasing salinity reaching 113-266% of the control at 100 and 800 mM NaCl, respectively indicating that POD play an important role in eliminating ROS under salt stress. Similar results was occurred for APX activity which raised significantly with the increase of salinity, reaching 191-350% of the control at 200 and 800 mM NaCl, respectively. CAT decreased H_2O_2 level in cell by breaking it down directly to form H_2O and O_2 and increase the stability of membranes and CO_2 fixation (Yamazaki *et al*., 2003) (Fig. 3).

In the present study, CAT activity remained slightly changed with increasing salinity thus researchers observed a slight increase (102.2-109.4% of the control) only at higher salinities (400-800 mM NaCl). It suggested that *Z. album* may mainly employ POD and APX enzymes for the detoxification of H_2O_2 produced by SOD and their conversion to H_2O and O_2 under salt stress. In agreement with the findings of Abogadallah (2010) showing that salt tolerance in barnyard grass (*Echinochloa crusgalli*) mutants depended on higher activities of POD and APX. However, CAT has low affinity to H_2O_2 than POD (mmol and μmol range, respectively). Thus, CAT is suggested to be involved in mass scavenging of H_2O_2 whereas POD is suggested to be involved in fine regulation of H_2O_2 (Mittler, 2002). APX activity was likely to be more important than CAT in the detoxification (Benavides *et al*., 2000).

CONCLUSION

In this study, the results show that maximal growth of *Z. album* was occurred at moderate salinities and photosynthetic performance and biomass accumulation were reduced only at high NaCl concentrations beyond 400 mM and that PSII photochemistry was relatively unaffected by high salinity. This decrease in photosynthetic rate may be due at least in part to the stomatal closure. The results revealed that the ability to

survive at higher salinities of *Z. album* plants may due at least in part to the tolerance of PSII and to the improved resistance to oxidative stress via increased the accumulation of phenolic compounds and the activities of SOD, POD and APX.

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