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Photosynthetic and growth responses of a perennial halophytic grass *Panicum turgidum* to increasing NaCl concentrations

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ABSTRACT

Several halophytes – plants which complete their life cycle in saline environment – have considerable economic potential as oil source, fodder, wood, ornamental, and medicinal plants. They may also serve as model plants to get insight in the mechanisms of salt resistance and with the future aim to develop halophytic crops. *Panicum turgidum* is, a C_4 perennial halophytic grass, widely distributed in saline and arid areas of Pakistan with a considerable potential as a fodder crop because of its high palatability and nutritional values. The aim of this work was to determine growth, physiological and biochemical responses of *P. turgidum* by subjecting plants to varying concentrations of NaCl (0, 125, 250, 375 and 500 mM) and to relate these data to photosynthetic parameters. When grown at low salinity (125 mM NaCl) fresh and dry biomass (shoot and root) were similar to non-saline control. Photosynthetic parameters such as net photosynthesis rate, transpiration rate, water use efficiency, Fv/Fm, and electron transport rate correlated with growth response. High salinity led to a significant decrease of water use efficiency mainly because of an over proportional reduction of carboxylation rate arising from non-stomatal factors such as decreasing Rubisco and chlorophyll contents. Reduction of carboxylation rate at higher salinity caused oxidative stress, electrolyte leakage, high malondialdehyde (MDA) and H_2O_2 levels in addition to photoinhibition and xanthine cycle dependent heat release.The data reported herein suggest that *Panicum* is a promising cash crop at low quality soils at moderate salinity. Its sustainable use can also help in desalinizing and reclaiming degraded land as well as sequestering CO_2.

1. Introduction

Global environment is rapidly changing due to increase in CO_2 concentration leading to higher ambient temperatures. Expected reduction of agricultural production will cause serious problems. These threats are aggravated by limited freshwater resources (Lieth et al., 1999) and impending soil salinization. Irrigated agricultural production already has decreased 20–35% due to increasing levels of salinity (FAO 2008; http://www.fao.org/ag/agl/agll/spush/; Hu and Schmidhalter, 2005). Fast growing population is suffering from severe shortage of water and food which will aggravate with time (Türkan and Demiral, 2009).

These problems could be partially alleviated by utilization of low quality irrigation water such as saline groundwater or seawater on appropriate wastelands for production of non-conventional crops especially in arid regions. Most of the conventional crops cannot tolerate salinity even al low concentrations. It is therefore necessary to develop sustainable biological production systems for brackish or high salinity water irrigation. The development of suitable halophytic crops has been considered for the production of food, forage, oil, wood, timber, ornamental, medicine and biofuel (Koyro and Eisa, 2008; Koyro et al., 2011). Halophytes are extremophiles and are equipped with physiological and biochemical mechanisms enabling them to cope with high soil salinity. A candidate for an economic and ecologically sustainable production system at arid conditions could be *Panicum turgidum* Forssk. (Khan et al., 2009). This xerohalophyte is a perennial tussock-grass, commonly found in the salt deserts of southern Pakistan (Khan and Qaiser, 2006) but also in other arid areas.

An integrated response of *P. turgidum* to withstand hyperosmotic salinity (the salt resistance) was studied on ecophysiological, biochemical, cellular and molecular levels. Parameters were selected with close relationship of salinity to biomass production and survival (Jenkins et al., 2010; Leake et al., 2002), photosynthesis and growth by inducing alterations in photosynthetic tissues, disturbing water balance and developing ionic toxicity (Galmés

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et al., 2011; Munns and Tester, 2008). Biomass production at saline conditions depends mainly on the ability to maintain high net photosynthesis at minimal water loss (WUE) and energy consumption (Álvarez et al., 2012; Naidoo et al., 2012). A critical point for the plant is reached if CO_2-fixation falls below the level of CO_2-release (CO_2 compensation point) therefore, it is necessary to study the relationship between growth reduction and net photosynthesis (Campbell et al., 2005; Schulte et al., 2003; Häusler et al., 1999).

Suppression of photosynthesis in saline environment is generally due to limitation of stomatal conductance, uptake of carbon dioxide, photosynthetic capacity, carboxylase activity of Rubisco, regeneration of RubP and chlorophyll content (Lambers et al., 2008; Lawlor and Cornic, 2002) leading to a reduction in plant growth (Naumann et al., 2007) and to the higher ROS production (Foyer and Shigeoka, 2011). Reduced availability of the electron and proton acceptor (CO_2) can lead the over-reduction of the reaction centers of photosystem II (PSII), and to photoinhibition or photodamage by production of reactive oxygen species (ROS) (Foyer and Noctor, 2005).

The aim of the present study was to evaluate the effects of elevated NaCl levels on *P. turgidum* growth and photosynthesis. The specific objectives were to: (1) determine the growth response to low and high salinity and the limit of salt resistance; (2) determine simple non-destructive parameters; (3) determine and relate the changes in chlorophyll fluorescence parameters, chlorophyll content, and gas exchange; (4) effect of salinity on Rubisco; (5) correlate gas exchange and morphometric parameters and (6) photo-damages on membrane level.

2. Materials and methods

2.1. Growth conditions and salinity treatment

Seeds were germinated in soil type LD 80 (Archut.Vechta, Germany) in an environmentally controlled green house. After 2 weeks young seedlings were transplanted to a soil less (gravel/hydroponics) quick check system (Koyro, 2006). Plants were irrigated with nutrient solution as modified by Epstein (1972) under 16 h light/8 h dark photoperiod. Temperatures were $27 \pm 2\,^{\circ}C$ during the day and $17 \pm 2\,^{\circ}C$ during the night. Relative humidity ranged from 45 to 65%. Irradiation intensity was in the range of 190 $\mu E\,m^{-2}\,s^{-1}$ at the plant level. NaCl concentrations were increased stepwise daily at the start of experiment by 50 mM (25 mM each at the beginning and at the end of the daily light period) until the final concentration was achieved: 0 (control), 125, 250, 375 and 500 mM NaCl. Plants were irrigated every 4 h for 30 min starting at midnight, 4 h, 8 h, 12 h and 20 h daily using timer and allow the saline solutions to drain freely from the pots. Solutions were changed every 2 weeks to maintain nutrient levels. The experiment was conducted for a total period of 14 weeks.

2.2. Growth measurements

Shoot and root separated immediately after plants harvested and their fresh weight was recorded. Aliquots were dried in an oven at 70 °C until constant weight was obtained.

2.3. Determination of electrolyte leakage, MDA content and H_2O_2

Electrolyte leakage was measured using leaf discs (1 cm dia., 3 replicates) after being incubated in 3 ml of deionized water in a desiccator under a negative pressure of $\approx 10^{-1}$ bar for 60 min. Total conductivity measured after boiling the sample at 95 °C for 2 h. The electrolyte leakage was calculated as percentage of total conductivity (Dionisio-Sese and Tobita, 1998).

Malondialdehyde (MDA) content as an indicator for the degree of lipid peroxidation of membranes was measured using thiobarbituric acid (TBA) assay (Cakmak and Marschner, 1992). Fresh leaf (0.1 g) was ground with pre-chilled pestle in a solution of 0.5% TBA in 20% trichloroacetic acid (TCA) followed by heating at 95 °C for 30 min. Samples were cooled at room temperature before centrifuging it for 5 min at 3000 rpm. The absorbance of supernatant was recorded at 532 nm (original OD), OD of the non-specific absorbance was taken at 600 nm and subtracted from the original OD (Cakmak and Marschner, 1992).

Plant material (0.03 g) was homogenized with pre-chilled TCA (3.5%) and centrifuged at 18,000 × *g* for 20 min at 4 °C (Loreto and Velikova, 2001). The supernatant was mixed with 1 M potassium iodide in a ratio 2:1 (v/v). The OD was measured at 390 nm and the hydrogen peroxide content was calculated using a standard curve.

2.4. Chlorophyll estimation, gas exchange and chlorophyll fluorescence

CO_2/H_2O gas exchange measurements were carried out by Li-COR 6200 (LI-COR, Lincoln, NE, USA) at ambient CO_2 partial pressure, temperature of 28–32 °C and relative humidity of the air. The light response curve was constructed from 0 to 2000 $\mu mol\ photon\ m^{-2}\,s^{-1}$ of photosynthetically active radiation (PAR). Dark respiration rate (RD), compensation irradiance (Ic) and saturation irradiance (Is) were calculated according to Schulte et al. (2003). Net photosynthetic rate (*A*), stomatal resistance (rs), transpiration (*E*), internal CO_2 (Ci) and water use efficiency (*A*/*E*) were measured on the fully emerged leaf (third and fourth node) blades at saturated irradiation of each treatment under constant light source. At the same time chlorophyll content was estimated by using SPAD-502 (Konica Minolta, Japan).

Pulse modulated chlorophyll fluorescence meter (Junior PAM, Walz, Germany) was used to determine chlorophyll a fluorescence on the same leaf on which CO_2/H_2O gas exchange measurements were made. The minimal fluorescence (Fo) value was measured after applying modulated light (<0.1 $\mu mol\ photon\ m^{-2}\,s^{-1}$) on dark adapted (25 min) leaf, while the maximal fluorescence (Fm) value was obtained by imposing a saturating pulse of 10,000 photons ($\mu mol\,m^{-2}\,s^{-1}$ for 0.6 s. Fo and Fm values were used to calculate maximum photochemical quantum yield of PSII (Fv/Fm = Fm − Fo/Fm) in predawn and noon by the method of Kitajima and Butler (1975) and photo-inhibition was calculated as described by Dodd et al., 1998:

$$\text{Photoinhibition}\,(\%) = 100 - \left(\frac{\frac{Fv}{Fm}\text{noon}}{\frac{Fv}{Fm}\text{Predawn}} \times 100 \right)$$

Subsequently, the leaves were continuously illuminated with actinic light, which was equivalent to the actual growth light of plants in order to measure steady-state (Fs) and maximal fluorescence (Fm′) in light-adapted leaves. The minimal fluorescence level in light-adapted leaves (Fo′) was estimated following the method of Baker and Rosenqvist (2004). Effective photochemical quantum yield of PSII was calculated as Fm′ − Fs/Fm′ (Genty et al., 1989). Non-photochemical quenching of fluorescence (NPQ) which is proportional to the rate of constant heat dissipation (Bilger and Björkman, 1990), was calculated as NPQ = Fm/Fm′ − 1. The coefficient of photochemical quenching (q_P) was calculated as (Fm′ − Fs)/(Fm′ − Fo′) (Kooten and Snel, 1990; Schreiber et al., 1986). PSII is used for calculation of the linear electron transport rate (ETR; Krall and Edwards, 1992) as ETR = PSII × PPFD × 0.5 × 0.84, where Photosynthetic Photon Flux Density (PPFD) incident on the leaf; 0.5: factor that assumes equal distribution of energy between the two photosystems; 0.84: assumed leaf absorbance.

2.5. Extraction and measurement of Rubisco

Mature leaves were harvested and stored at −80 °C. Protein extraction was performed according to Granier (1988), leaves were grind to fine powder on liquid nitrogen and 0.05 g polyvinyl-polypyrrolidon (PVPP) were added. The powder was diluted in extraction buffer (100 mM Imidazol and 1.25 mM EDTA; pH 7.8). Proteins were denatured using sodium-dodecyl-sulfate (SDS). Protein content was calculated on fresh weight basis using 5 replicates (Bradford, 1976). Protein was separated by polyacrylamide gel electrophoresis (agarose 6% (g/g) for stacking, 12.5% (g/g) for separation) according to Laemmli (1970). For calibration an internal SDS-PAGE molecular weight standard (BIO-RAD Laboratories GmbH, Munich, Germany) was used. Protein was stained with Coomassie brilliant R250 blue while gels were de-stained in 10% acetic acid. Rubisco large subunit was identified by molecular weight in the range of 53 kDa (Ishida et al., 1997). Ratio of Rubisco to the total protein content was calculated using the integrals of the signal strength on the gel using the image processing and analysis software ImageJ (National Institute of Health, Maryland, USA). Rubisco total amount was calculated with the protein analysis mentioned above.

2.6. Stomatal morphometry

Measurement of number of stomata, opening, length and area or upper and lower surfaces of fully emerged leaves were performed by peel off method (Hilu and Randall (1984). The nail varnish was applied with the brush to the upper and lower side of leaf by avoiding midrib and varnish was peeled off after 5–10 min. Peeled off piece was placed on the slide and glycerol was applied. Number of the stomata were counted at a magnification 100× under microscope and length, opening and area of stomata was calculated by using Carl Zeiss Axio Vision software.

2.7. Statistics

Data were analyzed by one-way ANOVA test using SPSS 11.0 for Windows and means were compared using Bonfferoni's test at the 5% level of significance.

3. Results

The trend indictes that at low salinity (125 mM NaCl) more biomass is produced however results are not significant at $p < 0.05$ level, however a further increase in salinity caused significant growth reduction (Fig. 1). Ion leakage, H_2O_2 and MDA contents are well known indicators of drought and high salinity effects. All measured parameters show no difference at lower concentration, a significant increase at 250 mM NaCl, and no change at high salinity (Fig. 2).

Increase in NaCl concentrations caused significant changes in various CO_2/H_2O gas exchange parameters. There is a transient increase in net photosynthetic rate (A) at 125 mM NaCl (48% of control; $P < 0.001$) and a decline at higher salinity (54% of control; $P < 0.001$; Table 1). The net photosynthetic rate is strongly correlated with saturation irradiance (Is) but also with stomatal resistance (rs), transpiration rate (E) and water use efficiency (WUE). However, the internal carbon dioxide concentration (Ci) was not influenced by increase in salinity and remained far above the lower carboxylation limit of PEP carboxylase and Rubisco at all conditions. Rising NaCl concentrations led to an increase of dark respiration rate (RD) in consequence of compensation irradiance point (Ic).

Relative chlorophyll content (SPAD values) was highest at 125 mM NaCl and decreased significantly at 500 mM NaCl substrate

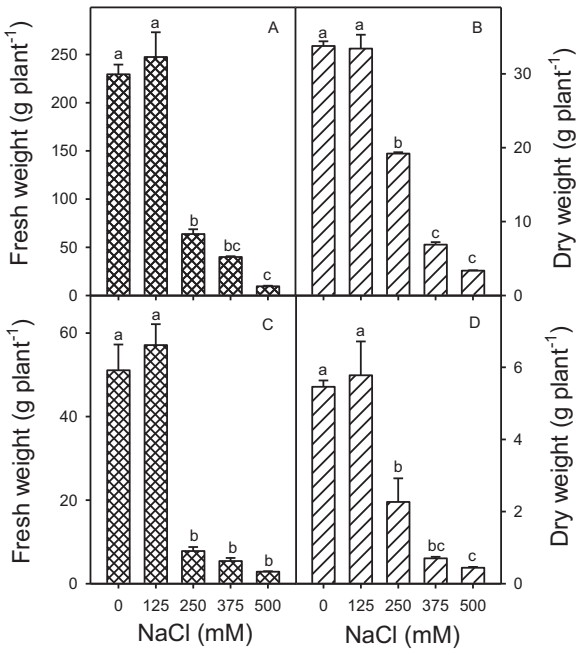

Fig. 1. Growth of *P. turgidum* in response to 0, 125, 250, 375 and 500 mM NaCl concentration. Fresh weight of shoot and root (A and C respectively) and dry weight of shoot and root (B and D respectively. Values represent mean ± SE. Different letters indicate significant difference between treatments at $P < 0.05$ using Bonferroni post hoc test.

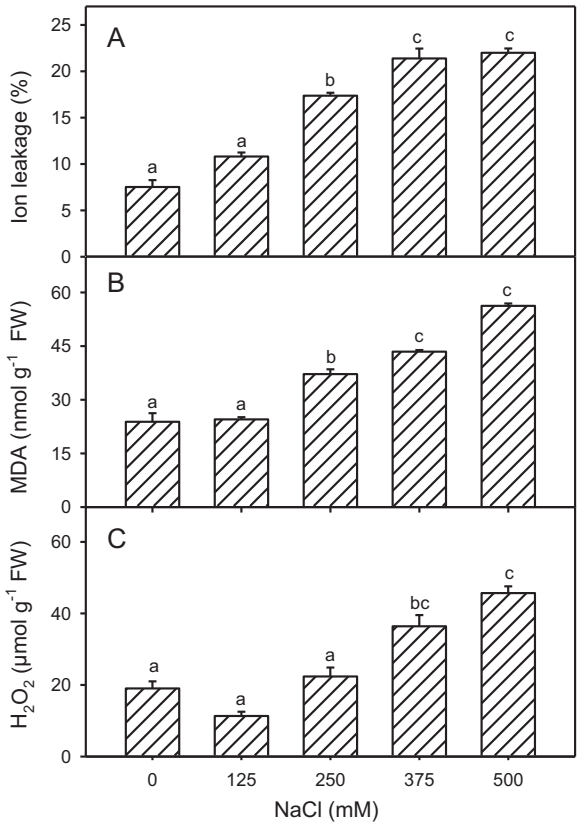

Fig. 2. Changes in the amount of electrolyte leakage (A), malondialdehyde (MDA) (B) and Hydrogen peroxide, H_2O_2 (C) induced by NaCl in leaves of *P. turgidum*. Each value represents the mean + SE and different letters indicate significant difference between treatments at $P < 0.05$ after Bonferroni Post hoc test.

Table 1
Measurement of gas exchange of 3rd and 4th fully emerged leaf of *P. turgidum* plants at saturated light.

NaCl (mM)	A (μmol m^{-2} s^{-1})	Is (μmol Photon)	rs (mol m^{-2} s^{-1})	E (mol m^{-2} s^{-1})	WUE (A/E)	Ci (μmol m^{-2} s^{-1})	RD (mol m^{-2} s^{-1})	Ic (μmol Photon)	ΔT (°C)
0	10.08a ± 0.15	629.23a ± 14.49	6.44a ± 0.19	1.55a ± 0.05	6.53a ± 0.32	245a ± 20.82	−0.26a ± 0.06	16.35a ± 2.05	1.50a ± 0.01
125	14.85b ± 0.17	794.90b ± 3.42	5.80a ± 0.16	1.95b ± 0.06	7.64b ± 0.24	230a ± 1.78	−0.32a ± 0.11	13.03a ± 1.06	1.93b ± 0.03
250	8.90c ± 0.05	508.47c ± 10.49	3.39b ± 0.06	1.38ac ± 0.05	6.50a ± 0.19	329b ± 1.12	−0.70b ± 0.10	18.56a ± 0.38	1.24a ± 0.21
375	6.25d ± 0.05	458.42c ± 13.42	7.96c ± 0.13	1.38ac ± 0.03	4.55c ± 0.11	259a ± 4.49	−0.76b ± 0.02	17.90a ± 0.33	1.58a ± 0.02
500	5.47e ± 0.03	275.86d ± 19.42	9.31d ± 0.27	1.20c ± 0.07	4.60c ± 0.27	315b ± 3.42	−0.90c ± 0.07	17.84a ± 0.21	2.39b ± 0.02

A: net photosynthetic rate, Is: saturation irradiance, rs: stomatal resistance, *E*: transpiration, WUE: ratio of net photosynthesis rate and transpiration, Ci: Intercellular CO_2, RD: dark respiration rate, Ic: compensation irradiance, and ΔT: change in temperature. Values represent mean ± S.E and different letters indicate significant difference between treatments at $P < 0.05$ after Bonferroni Post hoc test.

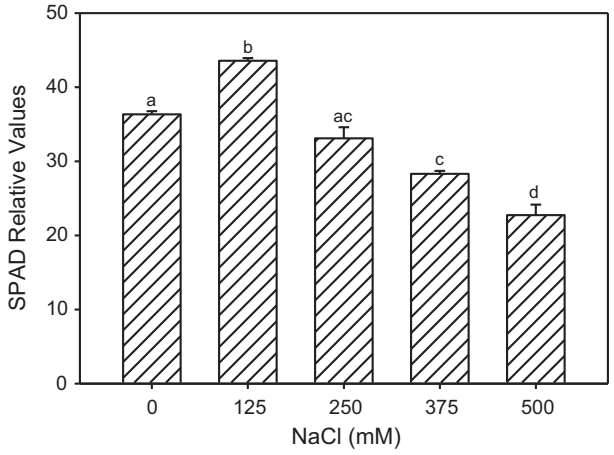

Fig. 3. Changes induced by NaCl solutions in the amount of Chlorophyll in leaves of *P. turgidum* expressed as SPAD values. Each value represents the mean + SE and different letters indicate significant difference between treatments at $P < 0.05$ after Bonfferoni post hoc test.

salinity (Fig. 3) showing a similar trend as the net photosynthesis and related parameters (Table 1). Net photosynthesis (Table 1), PSII maximum quantum efficiency (Fv/Fm) and actual yield (PS II) showed a similar curve shape although the increase of the latter two was not significant up to moderate salinity (125–250 mM NaCl; Fig. 4). However both chlorophyll fluorescence parameters decreased significantly with a further increase of salinity. A rise in salinity from 6.5% (control) up to 18% (500 mM NaCl) also led to a steady rise in photoinhibition. Photochemical quenching (q_P) was stable at all salinities. Non-photochemical quenching (NPQ) increased at high salinity treatments by a factor of 1.5–2 in comparison to the control. Expression of the large subunit of Rubisco decreased with increasing salinity (Fig. 5). Morphometric measurements of the stomata showed a maximum length (adaxial and abaxial surface), opening area (adaxial and abaxial surfaces) and number of stomata at 125 mM NaCl (Table 2).

4. Discussion

We intended to determine salt resistance range of *P. turgidum* as a first step of our study. Our data indicate that the resistance threshold is close to seawater salinity. Growth of halophytes is commonly stimulated by low salinity (Riadh et al., 2010; Khan et al., 2000). Like many other monocotyledenous plants (Naidoo et al., 2008; Glenn et al., 1999), *P. turgidum* shows similar growth pattern in control and in presence of moderate salinity, respectively. In our experiments we did not observe significant differences between control plants and those grown in presence of 125 mM NaCl (about 25% seawater salinity). Trend of the data indicates that the growth may be promoted at 100 mM NaCl like reported in the studies of Al-Khateeb (2006) who found a significant growth promotion in *P. turgidum*. Therefore *P. turgidum* meets the essential condition for utilization in a saline environment.

As optimal growth was found only in a narrow NaCl concentration range, it is essential for scaling up of experimental data to establish a reliable system for monitoring of plant performance under saline conditions. Several parameters may act as bottle necks for plant growth in high salinity (Koyro, 2006; Flowers et al., 1986). In most relevant papers limitations of photosynthesis could be aligned to observed reductions in plant growth and development (Chaves et al., 2009; Hamilton et al., 2001). Accordingly growth of *P. turgidum* was found to correspond to chlorophyll content, electron transport rate (ETR), net photosynthetic rate (A), transpiration (E), water use efficiency (WUE), the temperature gradient between

Table 2
Morphometeric measurement of stomata of fully emerged leaves (3rd and 4th leaf from top) of *P. turgidum*.

NaCl (mM)	Length of stomata		Opening area of stomata		Number of stomata	
	Upper (μm)	Lower (μm)	Area upper (μm²)	Area lower (μm²)	Upper	Lower
0	16.15 ± 2.01	17.64 ± 0.11	232.45 ± 14.94	315.12 ± 6.33	41.00	47.00
125	22.88 ± 1.07	21.68 ± 1.36	399.15 ± 19.29	352.82 ± 17.95	54.00	60.00
250	14.05 ± 0.17	10.57 ± 0.54	218.31 ± 15.97	226.40 ± 6.32	51.00	58.00
375	15.36 ± 0.16	15.67 ± 0.89	233.92 ± 5.91	288.09 ± 7.50	61.00	60.00
500	14.25 ± 1.95	8.24 ± 0.79	301.30 ± 7.06	249.34 ± 19.46	31.00	51.00

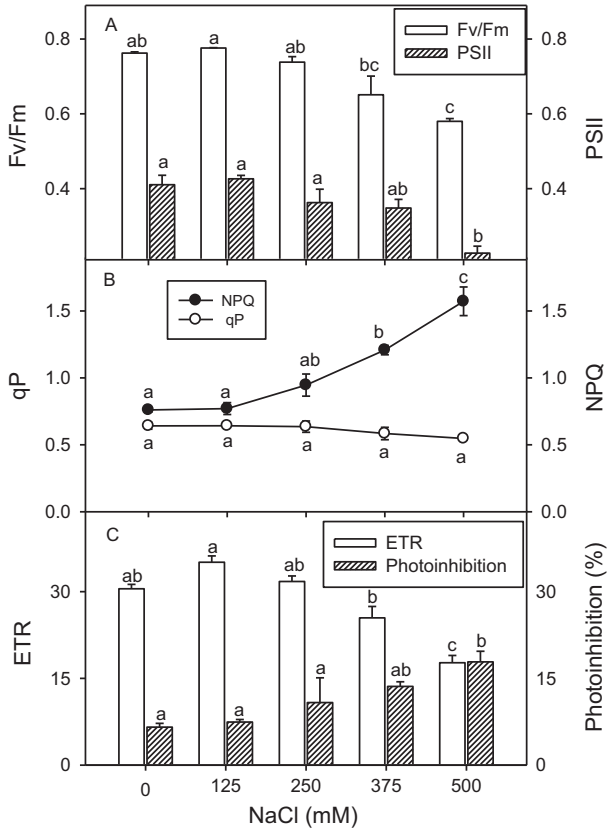

Fig. 4. Maximum quantum efficiency of PSII photochemistry, Fv/Fm and actual yield (PSII) (A), Photochemical (qP) and non-photochemical quenching (NPQ) (B) and electron transport rate (ETR) and photoinhibition(C) in randomly selected, fully expanded (3rd and 4th node) leaves *of P.turgidum* in response to various NaCl concentration. Values represent mean ± SE and different letters indicate significant difference between treatments at $P < 0.05$ after Bonferroni post hoc test.

leaf and atmosphere (ΔT) and the size of the stomates. These parameters provide a broad range of options for a non-destructive diagnosis at field site.

Gas exchange rate and growth vary with plant species and abiotic factors such as salinity, CO_2, drought and humidity (Geissler et al., 2009a,b; Ball and Munns, 1992; Drake, 1992). However, since growth declined in the same range as above-mentioned photosynthetic parameter, it is the decline in photosynthesis that explains growth inhibition at high salinity levels. Therefore it is pertinent to relate the results of chlorophyll fluorescence and CO_2/H_2O gas-exchange and leaf morphometric parameters to find the causal connection.

On anatomical level, inhibition of plant development at increasing salinity was related to several structural changes that most probably optimize gas-exchange. Increase of salinity led to a transient increase of stomata number, their size and maximum opening area; with highest values at 125 mM NaCl indicating an adjustment to a particular demand of CO_2 (Parida et al., 2004; Chartzoulakis et al., 1999; Orsini et al., 2011; Shabala et al., 2012). Stomatal resistance and WUE increased at higher salinities. Shabala et al. (2012) interpreted such reduction of stomata number under hyperosmotic stress conditions as an important adaptive feature aimed to reduce leaf cuticular transpiration. The increase in stomatal resistance is one of the main responses of plant under salinity to minimize water loss (Kim et al., 2010) at the expense of CO_2-fixation. Consequently, changes in stomatal resistance appeared to provide an explanation for the parallel decline in photosynthetic assimilation rates.

WUE is often discussed as an indicator for salt resistance (Gleick et al., 2011). Salinity led to an increase of the *WUE* in case of *Sarcocornia fruticosa*, *Beta vulgaris* ssp. *maritima* and similar results were reported for *Atriplex portulacoides* (Redondo-Gómez et al., 2007; Koyro, 2006) but it declined at higher salinities in *Odyssea paucinervis* (Naidoo et al., 2008). However the increase in stomatal resistance does not lead to a loss of leaf water content in *P. turgidum* and therefore is likely to be the result of a controlled regulation (signaling process) rather than an effect of water loss. However, the reduced gas-exchange observed did not lead to a decrease of the intercellular CO_2 concentration (Ci) or even to a significant increase at high salinity. It may reflect that photosynthetic decline at this condition might be caused by a reduction of the carboxylation activity of photosynthesis and lowering of RWC (data not shown) rather than any effect on diffusion limitation. The impaired assimilation rate correlates with the Rubisco content in *P. turgidum* suggesting a reduction of the Rubisco activity while CO_2 starvation under high salinity was not found. The internal CO_2 concentrations remained unchanged at all salinity values far above the lower limit of PEP-carboxylase. If biochemical limitation occurs, this is often related to the Rubisco activity (Galmés et al., 2011; Grassi and Magnani, 2005). However, as *P. turgidum* is a C_4 species, respective CO_2 affinity of PEP-carboxylase has to be taken into account.

Based on the discussion above it may be concluded that a low CO_2-assimilation rate often leads to the development of ROS due to

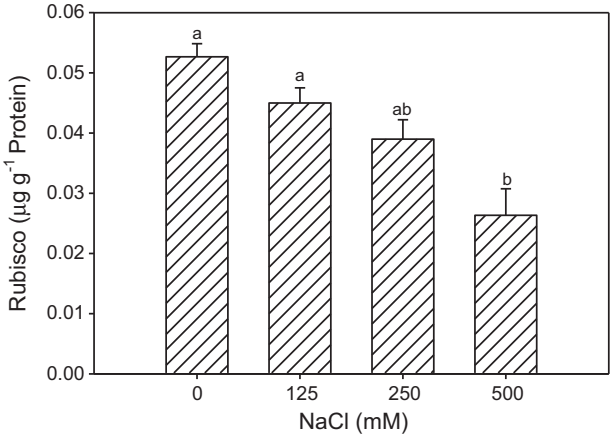

Fig. 5. Rubisco large sub unit was measured on fully expanded (3rd and 4th node) leaves of *P.turgidum* in response to treatment with various NaCl concentrations in the substrate. Values represent mean ± SE and different letters indicate significant difference between treatments at $P < 0.05$ after Bonferroni post hoc test.

over-reduction of reaction centers (Ben Amor et al., 2005; Arneth et al., 2002). The levels of H_2O_2 production, lipid-per-oxidation (MDA content), and ion leakage are well known as stress markers (Elkahoui et al., 2005) to assess the capacity of oxidative damage under stress condition. They all indicate a higher net ROS production by *P. turgidum* cells under saline conditions. A positive correlation between growth inhibition and enhanced lipid per-oxidation levels under salinity stress in *P. turgidum* also has been reported (Ben Hamed et al., 2007; Koca et al., 2007; Yazici et al., 2007). This may be due to membrane leakage after production of ROS and peroxidation of membrane lipids. However, it will be a gross oversimplification to assume that the observed electrolyte leakage is merely a result of lipid peroxidation. It was shown that even small concentrations of ROS may rapidly activate cation-permeable plasma membrane channels causing substantial leak of potassium (Demidchik et al., 2007, 2010) and tissue (Cuin and Shabala, 2007) levels, for both H_2O_2 and hydroxyl radical ROS species.

The Fv/Fm ration of *P. turgidum* is constant up to 375 mM NaCl. Excessive NaCl concentrations in substrate leading to the production of ROS could be inhibitory to photosynthesis (Debez et al., 2008; Mateos-Naranjo et al., 2008) causing a significant decline of the Fv/Fm ratio in *P. turgidum*. In most of halophytes reported, the maximal efficiency of PSII (Fv/Fm) is at low salinity and no effect at higher salinities (Yıldıztugay et al., 2011; Debez et al., 2006; Naidoo et al., 2008; Maricle et al., 2007; Redondo-Gómez et al., 2007; Wei et al., 2006; Qiu et al., 2003). In salt sensitive plants it is reduced even at moderate salinity levels (Zhao and Ren, 2007; Netondo et al., 2004).

High Fv/Fm ratios in combination with increasing values of thermal energy dissipation (NPQ) are protecting *P. turgidum* from over reduction of the photosynthetic reaction centers at moderate salinity. Photoinhibition led to the reduction of ETR during the day and protected the plants from over reduction of PSII centers. This is also evident from the decline of PSII efficiency and net CO_2 assimilation rate at hyperosmotic salinity. It can be concluded from our data that either light harvesting or consumption of redox energy were affected by soil salinity.

Decreasing Rubisco concentration and reduced CO_2 fixation rate (activity) might be the main reason for the latter observation. (Van den Berg and Perkins, 2007). We have shown with our data that the plants are under high risk of chlorophyll mediated ROS production at higher salinity. This may also cause the damage of D1 protein of photosystem, a main precursor of photodamage. In *P. turgidum* membrane leakage, MDA content and H_2O_2 content increased with increasing salinity indicating oxidative stress leading to photodamage as reported before (Moradi and Ismail, 2007; Redondo-Gómez et al., 2006; James et al., 2002; Naidoo et al., 2002).

The reduced chlorophyll content of the leaves can fulfill a similar protecting function as photoinhibition and decline of ETR at higher salinities. On the one hand, it reduces the assimilation rate of *A. tripolium* (Lorenzen et al., 1990), but on the other hand (and in case of *P. turgidum* more important), it decreases the light absorption of the leaves (Wang et al., 2003; Christian, 2005). However at high salinity neither the decrease of chlorophyll content nor the increase of heat emission (NPQ) reduce the flow of electrons sufficiently through the photosystems to prevent *P. turgidum* from over excitation of the photosynthetic reaction centers (see photoinhibition, Fig. 5).

This study has demonstrated physiological tolerance of *P. turgidum* to salinity under controlled conditions which correlated quite well with its distribution in dry habitats with saline and alkaline soils. Similar to other monocotyledenous halophytes, growth is not affected at low salinities and decreases at higher salinities. *P. turgidum* shows persistent growth under moderate salinities, however the range of salinity resistance is narrow. Photosynthesis and growth were remained unaffected at moderate salinity. Growth rate and photosynthesis reached its limits at seawater salinity (500 mM NaCl). This impact of high salinity on photosynthesis was mainly due to reduction in carboxylation capacity, not to stomatal parameters thus leading to a reduced water use efficiency with increasing salt concentrations. Our results on membrane leakage, photoinhibition, H_2O_2 production, and lipid per-oxidation clearly indicate the presence of oxidative stress at high salinity. However, more research is needed (i) on the exact regulation of the oxidative defense system (Halliwell-Asada Sytem, violaxanthin cycle, (Zhu et al., 2011; Foyer and Halliwell, 1976) of *P. turgidum*, and (ii) on the regulation of stoma size, number, and regulation of their opening, as well as (iii) on pigment and enzyme synthesis under moderate and severe saline conditions. The data reported here suggest that *P. turgidum* may be a potential candidate for cultivation as fodder on low quality soils irrigated with brackish water.

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