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ROOT STRUCTURAL MODIFICATIONS IN THREE *SCHOENOPLECTUS* (REICHENB.) PALLA SPECIES FOR SALT TOLERANCE

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Abstract

Three species of *Schoenoplectus* (Reichenb.) Palla collected from three different sites of Punjab, Pakistan were evaluated for root morpho-anatomical modifications. All the three species were subjected to salt stress. The salt treatments, control (0 mM salt), 100, 200 and 300 mM NaCl were maintained in non-aerated solution culture. *Schoenoplectus triqueter* showed specific root anatomical adaptations for its better survival under harsh saline environments. Increased epidermis thickness, cortex thickness, cortical cell area, vascular bundle area, metaxylem area, phloem area and aerenchyma area in roots were critical for checking water loss and enhancing water storage capability. The dominant anatomical traits related to *S. triqueter* (the most tolerant among all species) were found to be increased aerenchyma area for better gas exchange and bulk salt movement. Increased cortex thickness (increasing water storage) and increased number and area of vascular tissue (increased water conduction) seemed to be crucial for its better survival under harsh saline environments.

Introduction

Salinity is an environmental stress that limits growth and productivity of plants worldwide (Maheswari *et al*., 2012). Halophytic plants adopt several structural and functional strategies to cope high concentrations of salts in a growth medium. Increasing salinity causes specific anatomical changes on cell and tissue levels (Çavuşoğlu *et al.*, 2007). Such morphological and anatomical modifications in plant body are capable of minimizing detrimental effects of salt stress (Poljakoff-Mayber, 1988).

The prominent anatomical adaptive features among a wide range of characteristics are succulence in root, stem and leaves, many layered epidermis, well developed water storing tissues in parenchyma, widening of casparian band and enhanced development of root endodermis (Hameed *et al*., 2010). Salinity affects cell division and expansion processes, and reduces the size of apical meristems, cortex and vascular cylinder (Córdoba *et al.*, 2001). Additionally, it stimulates exodermis and endodermis suberization (Sanderson *et al*., 1997).

Presence of sclerenchyma in the cortical region gives strength to the root tissues and may play a critical role in preventing tissue collapse, especially in the presence of large aerenchyma in plants of aquatic or terrestrial ecosystem. In addition, thick sclerenchymatous hypodermis and endodermis, and large metaxylem vessels can prevent water loss through root surface and regulate water and/or solute movement in roots, control radial flow of water (Cholewa and Griffith, 2004). All these structural modifications are incredible under extremes of environmental hazards (Steudle, 2000).

Genus *Schoenoplectus* contains a number of halophytic species, which dominate hyper-saline habitats in the Punjab region (Kukkonen, 2001; Zahoor *et al*., 2012). Although these can tolerate in highly saline and waterlogged areas (e.g., salt marshes and saline wetlands), these can also tolerate dry-land saline/arid conditions (Bernhardt and Kropf, 2006).

Keeping in view the high degree of tolerance of these species to salinity, it was hypothesized that *Schoenoplectus* (Reichenb.) Palla spp. may have some specific adaptive components relating to root structure and function to survive successfully in extreme salinities. Thus, the major objective of the study was to examine the morphological and anatomical markers for salt tolerance and the aquatic response of halophytic plant species to salt stress, which are extremely useful in improving salt tolerance in crop plants.

Material and Methods

Three halophytic species of *Schoenoplectus* (Reichenb.) Palla were collected from the salt-affected aquatic habitats in the Punjab region to investigate pattern of their growth, and anatomical characters of root. *Schoenoplectus lacustris* (L.) Palla was collected from the hyper-saline waters of Kallar Kahar Lake in the Salt Range, *S. triqueter* (L.) Palla from a saline waterlogged habitat near Sahianwala (Faisalabad), and *S. juncoides* (Roxb.) Palla from a saline drain near Jhang city.

Since each species inhabited a vast area in its specific habitats, 30 plants were randomly collected for each species from each site. All these plants were grown in the Botanic Garden, University of Agriculture, Faisalabad till their establishment in the local environment under non-saline waterlogged conditions. Twenty vegetative buds (ramets) of almost equal size were randomly detached from these mother plants for each replication and each treatment and grown in non-aerated flooded conditions. Fibre-glass containers (20 L capacity) were half-filled with sandy loam soil, the rest filled with water to create uniform conditions of the natural habitats of the *Schoenoplectus* spp. Since the natural habitat was predominantly affected with NaCl salinity, four salinity levels viz., control (no salt treatment), 100, 200, and 300 mM NaCl were maintained in a culture medium. The experiment was planned during May to July under full sun-light growth conditions, and the average day/night temperatures were 38-41°C and 24-26°C, respectively, and photoperiod from 13 to 16 h, relative humidity ranged from 46.8-59.3%. Under the wild conditions, the main growth season is equivalent to the experimental period, in which all species produce inflorescences.

Morphological characters, root length and root fresh weight were measured after the completion of the project after 12 weeks of salinity treatment. For root anatomical study, the material was fixed in FAA solution (v/v formalin 10%, acetic acid 5%, ethyl alcohol 50% and distilled water 35%) for 48 h and then transferred to acetic-alcohol solution (v/v 75% ethanol and 25% acetic acid). Double staining dehydration procedure (safranin and fast green) was used for the preparation of permanent slides (Ruzin, 1999) to study various cells and tissues of root. Measurements and micrographs were made with a digital camera (Nikon FDX-35) equipped on a Nikon stereo-microscope (Nikon 104, Japan). Anatomical characteristics recorded for root were root area, epidermis area, cortex thickness, cortical cell area, aerenchyma area, vascular tissue (xylem, phloem and vessel areas).

The experiment was planned in a completely randomized design (CRD) with two factors (plant species and salinity levels) and six replications. ANOVA of the data was computed using MStat Computer Programme (Anon., 1989). Standard error and LSD (least significant difference) at $p<0.05$ level of significance for each variable (species are in main factor, salinity levels in sub-factors) were calculated to test the differences among mean values (Steel *et al*., 1997).

Results

Root length showed a differential response under salt stress, it increased at 100 mM NaCl level in *S. lacustris,* and thereafter decreased significantly at higher levels. In *S. triqueter,* a consistent but significant increase in root length was recorded as the salinity level of the culture medium increased. An increase in root length was also recorded in *S. juncoides* with increase in salt level of the medium, but this increase was not significant, particularly at higher salt levels (200 and 300 mM NaCl).

Root fresh weight showed similar trend in response to salt stress, but with very few differences. Root fresh weight increased significantly in *S. lacustris* at 100 mM salt level, but further salt levels resulted in a significant decrease. In *S. triqueter,* root fresh weight increased at 100 mM salt level, but significantly decreased as there was a further increase in salt levels. In *S. juncoides,* root fresh weight significantly increase by the induction of salts in growth medium, but higher salt levels showed no impact on this parameter (Fig. 1).

The root cross sectional area was increased gradually and significantly with increasing salinity levels in *S. lacustris* (Fig. 2). In *S. triqueter* and *S. juncoides,* a significantly increased root area was observed at 100 mM salt level, and thereafter a gradual and significant decrease was observed at higher salt levels. In *S. lacustris*, a significant increase was observed in epidermal cell area with increase in salinity up to 200 mM level, but at the highest level, the difference was not significant (Fig. 2). The greater variation in epidermal area was observed in *S. triqueter* as compared to other two species, where a significant increase in this parameter was observed at up to 200 mM NaCl, and thereafter a significant decrease at the highest salt level. In *S. juncoides,* a significant increase was observed at 100 mM only, and thereafter a significant decrease was observed at higher salt levels (200 an 300 mM) (Fig. 2).

A significant and consistent increase in cortex region thickness was observed in *S. lacustris* with increasing salinity levels, but at the highest level, this increase in cortical region thickness was not significant (Fig. 2). Increased cortex region thickness was also observed in *S. triqueter,* but only at 200 mM NaCl level, and thereafter a decrease in this parameter was recorded. In contrast in *S. juncoides*, salinity imposed a negative impact, where a significant and gradual decrease was noted. Cortical cell area on the other hand, increased consistently and significantly in *S. lacustris* with increasing salt levels (Fig. 2). In *S. triqueter,* increasing salt levels in a culture medium resulted in a significant and huge increase in cortical cell area, at 200 mM NaCl level, and a significant decrease in cell area was recorded at 300 mM salt level. In *S. juncoides* a significant increase in cortical cell area was observed, but only at 100 mM NaCl level, and thereafter this parameter decreased significantly at higher salt levels (Fig. 2).

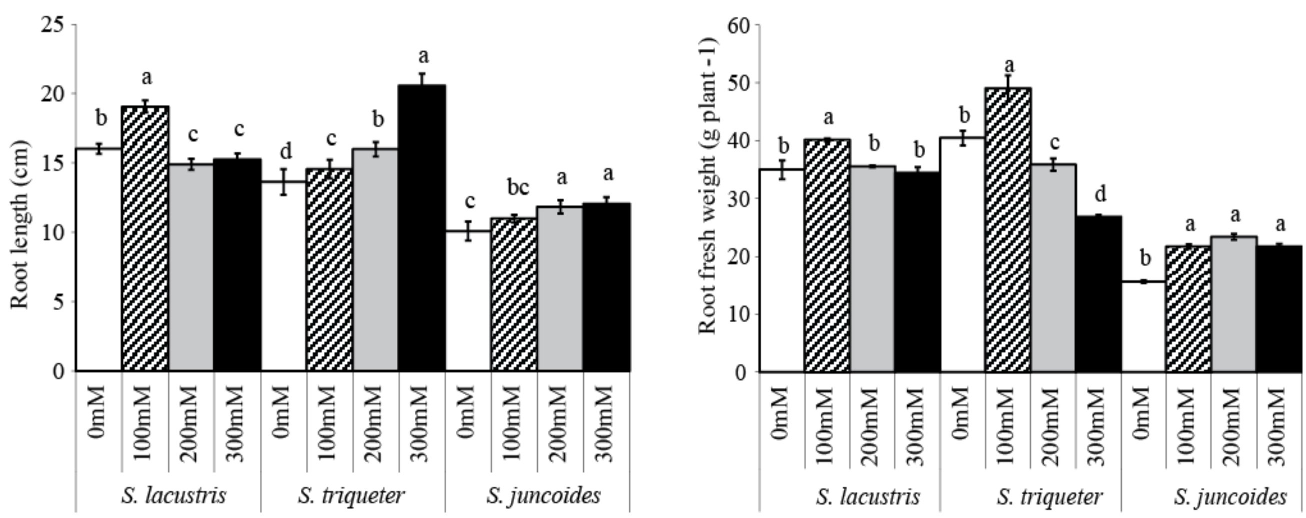

Fig. 1. Root length and fresh weight in three *Schoenoplectus* species collected from different salt-affected habitats in Punjab under salt stress ($n = 6$).

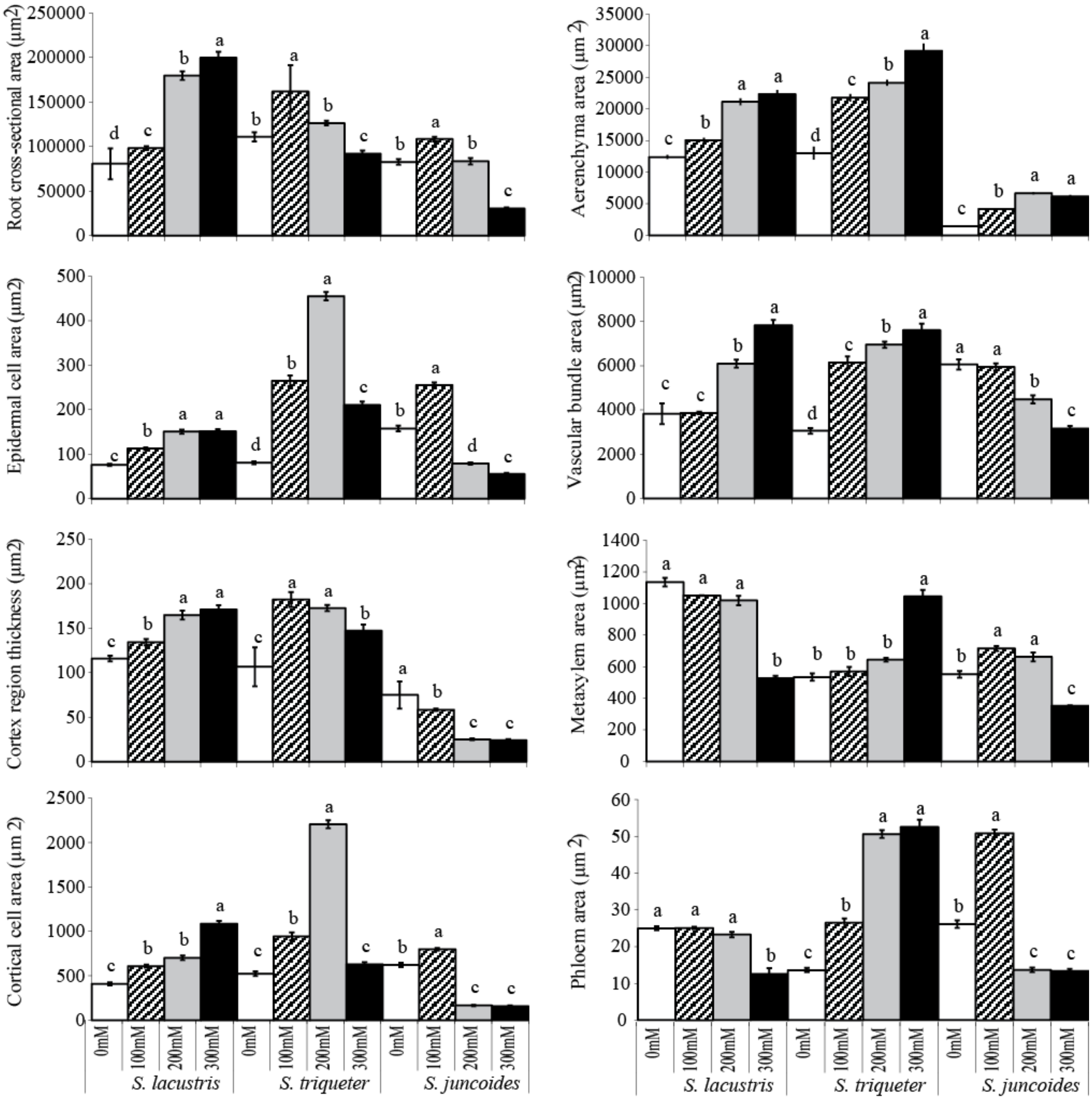

Fig. 2. Root anatomical characteristics in three *Schoenoplectus* species collected from different salt-affected habitats in Punjab under salt stress ($n = 6$).

Vascular bundle area increased significantly in *S. lacustris* and *S. triqueter* with increase in salinity levels. In *S. juncoides* vascular bundle area was not affected at 100 mM NaCl level, but thereafter significantly decreased with further increase in salinity level (Fig. 2).

Metaxylem vessel area, on the other hand, was not affected in *S. lacustris* by lower salt levels, i.e., 100 and 200 mM NaCl, but a significant decrease in vessel area was recorded at the highest salt level (300 mM NaCl) (Fig. 2). A gradual increase in vessel area was recorded in *S. triqueter,* but the differences were not significant up to 200 mM level and a significant increase was recorded at the highest level. Induction of salts resulted in an increase in metaxylem area in *S. juncoides,* but a gradual decrease was observed at higher salt levels (Fig. 2).

Phloem area showed no change in *S. lacustris* at 100 and 200 mM salt levels, while it decreased at 300 mM salt level. In *S. triqueter* phloem area significantly increased with increased salt levels, but the differences were not significant at the highest salt level. In *S. juncoides* a significant increase in phloem area was observed at 100 mM NaCl level, and thereafter it significantly decreased at higher salt levels. The differences between 200 and 300 mM NaCl levels were significant (Fig. 2).

Aerenchyma area increased significantly and consistently with increasing salinity levels of the medium in all three *Schoenoplectus* species. In *S. lacustris* and *S. triqueter,* size of aerenchyma was much greater than that recorded in *S. juncoides.* Size of aerenchyma was the maximum in *S. triqueter* at all salt levels than that recorded in other species (Figs. 2 and 3).

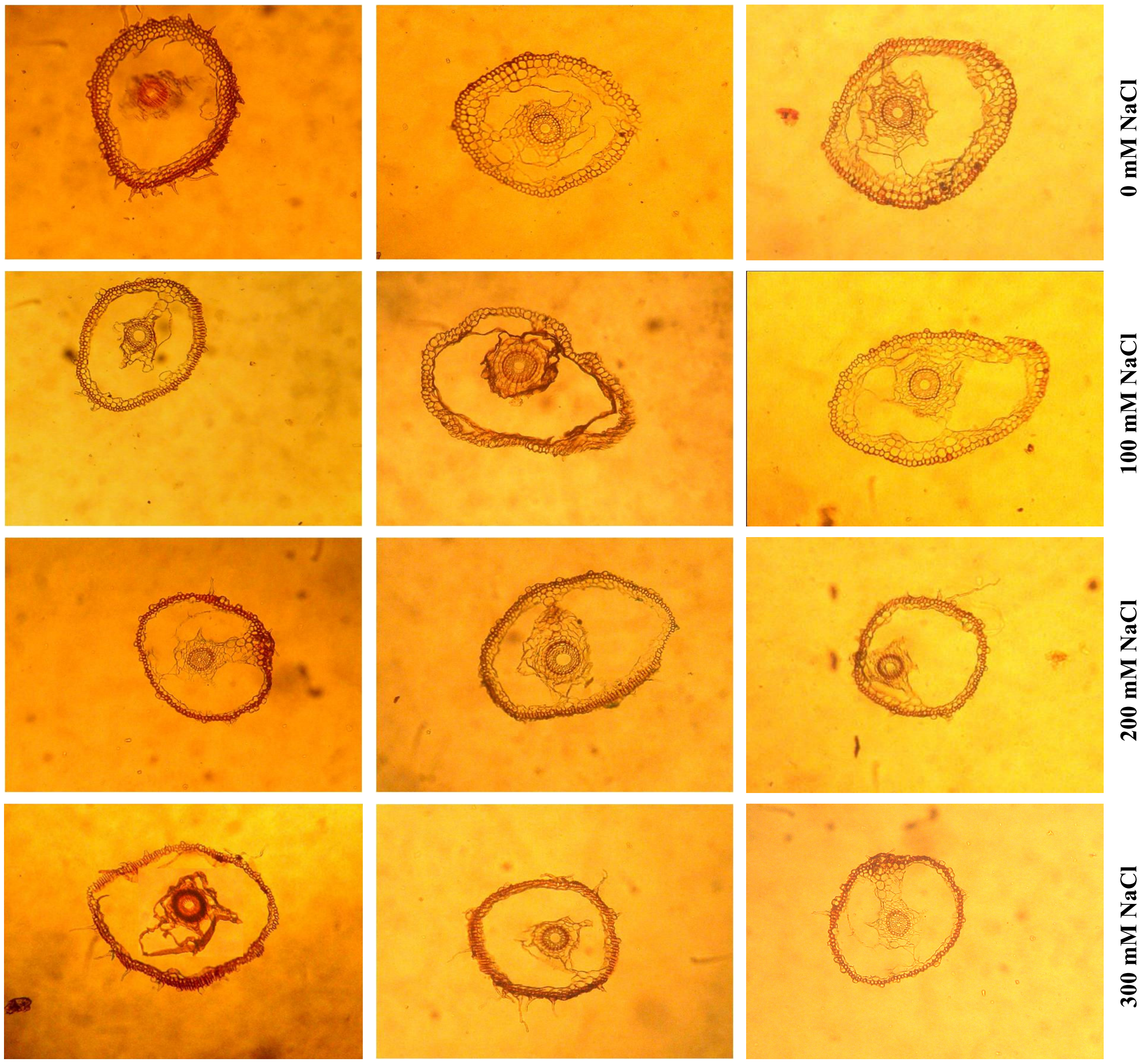

Fig. 3. Root transverse sections of three *Schoenoplectus* species collected from different salt-affected habitats in Punjab under salt stress.

Discussion

All *Schoenoplectus* species were seemed to be well adapted to moderately salt stress levels (200 mM or less), as were the halophytic or relatively more salt tolerant species (Aslam *et al*., 2011). The root parameters, root length and fresh weight generally increase under salinity stress in most halophytic species (Khan *et al*., 1999), whereas a reverse is true for glycophytic and less salt tolerant species (Horie *et al*., 2012). Longer and well proliferated roots under high salinities may provide the additional benefit to this species of extracting moisture from deeper layers under physiological drought, a common phenomenon in plants subjected to limited moisture availability (Liu *et al*., 2004).

Proliferated root system can provide the advantage to support accelerated growth of plants during the early plant developmental growth and extract water from the soil layers (Martinez *et al*., 2003; Padilla & Pugnaire 2007). However, the development of the root system increases water uptake and maintains the right osmotic pressure (Noctor *et al*., 2002; Pan *et al*., 2003). Roots are directly exposed to saline environments, and enhanced compactness of the epidermal layer along a salinity gradient may play a vital role in solute translocation inside the plant body (Rashid & Ahmed, 2011).

The anatomical structures are of significant importance and also varies greatly in many plants (Lersten & Curtis, 2001; Makbul *et al*., 2006; Makbul *et al*., 2008; Hameed *et al*., 2012). Increased root cross-section area, which mainly resulted from increased cortical thickness in this study, may provide the root with additional capacity to store water which is vital under limited moisture environments (Abdel & Al-Rawi, 2011). Reduced metaxylem cross-section area, particularly under high salinities, is another critical adaptation, as narrower vessels are less prone to damage caused by embolism (Kondoh *et al*., 2006). At the root level, increased sclerification near the root periphery (exodermis) and just above the endodermis is critical in preventing water loss.

Root area generally increased in relatively less tolerant species under salt stress. Bahaji *et al*., (2002) reported that increased root area is the characteristic feature of moderately salt tolerant species. Increased root cross-section area, mainly resulted from increased cortical thickness, may provide the root with additional capacity to store water which is vital under limited moisture environments (Abdel & Al-Rawi, 2011). In the present study, the most tolerant *S. triqueter* showed a substantial decrease in root area, especially at higher salt levels, but the reverse is true in the second best *S. lacustris.* Peng *et al*., 2007 also reported similar findings in some desert halophytes. However, root area generally related to increased parenchymatous region, and hence, can play a critical role in water conservation (Nawaz *et al*., 2013).

Epidermal area increased in almost all cases at moderate salt stress level. Naturally this layer is protective and have important role in controlling water and nutrient movement across the roots (Bagniewska-Zadworna & Zenkteler, 2006), and ultimately can limits water loss from roots (Taleisnik, 1999). Thick epidermis may help to reduce water loss through root surface (Hameed *et al*., 2010). Increased epidermal area under high salinities can play an important role to withstand osmotic stress for the survival of these species, as reported by Boughalleb *et al*., (2009) in *Nitraria retusa*, *Atriplex halimus* and *Medicago arborea*, and Dolatabadian *et al*., (2011) in *Zea mays*.

In most of the cases cortical thickness and cell area increased under salt stress, the best tolerant *S. triqueter* showed a significant increase at moderate salinities and the second best *S. lacustris* at high salinities. Some halophytic plant species have the ability to store additional water in cortical parenchyma, which can be a major factor for their survival. Grigore & Toma (2007) reported increased cortical parenchyma under salt stress in *Chenopodiaceae* halophytes. *Schoenoplectus juncoides,* however, showed a consistent decrease in this parameter, which indicates its less tolerance to salt stress as compared to other species.

In the present studies, vascular bundle area, metaxylem area, and phloem area increased with salt stress, and this is more prominent in relatively more tolerant *S. triqueter* and *S. lacustris.* Increased vascular region, and in particular, vessel area can certainly be useful in more and efficient flow of water, as well as nutrient towards other aerial parts of a plant (Baloch *et al*., 1998), and hence, extremely important under limited moisture availability such as physiological droughts caused by salinity. Increased xylem vessel area has been related to root hydraulic conductivity by Cachorro *et al*., 1993 in *Phaseolus vulgaris*.

Root aerenchyma area is a characteristic feature of plants that inhabit saline waterlogged environments (Barrett-Lennard, 2003). Depending on the species and environmental conditions, aerenchyma are formed over the entire plant body, with the exception of meristems, vascular bundles, sclerenchyma and covering tissues (Raven, 1996). In roots, aerenchyma are formed behind the apical meristem (Marschner, 1995; Malik *et al*., 2003). Aerenchyma may serve as an additional barrier to water and solute movement, because it can create cavitation in the cortical region, and hence, an interruption in the connection between different tissue systems (Ranathunge *et al*., 2003).

All *Schoenoplectus* species showed increased development of aerenchyma in roots, and this phenomenon was more prominent in more tolerant species like *S. triqueter* and *S. lacustris.* This may definitely contributes towards better tolerance and survival of these species under limited oxygen availability and high salt concentration. Aerenchyma is vital for oxygen supply, especially under anaerobic condition of the habitat (Barrett-Lennard, 2003).

In conclusion, the present study on the salt tolerance of natural *Schoenoplectus* species confirms the high degree of salt tolerance in these species, from the saline habitat, found to be because of morpho-anatomical adaptations of root. As estimating the extent of salinity tolerance of these species by exploring various roots anatomical attributes it was found that *S. triqueter* from the highly saline drainage near Sahianwala habitat was better adapted to salt stress than the other two species. While it showed better adaptive mechanisms for its survival under unfavorable condition (salt stress). However, from this study, it probably to conclude that these sedge species have appropriate genetic variation that was helpful to fix the high selection pressure of the high salted environment.

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