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RESEARCH ARTICLE

# Anatomical Adaptations to Salinity in *Spergularia marina* (Caryophyllaceae) from Turkey

**Tulay Aytas Akcin · Adnan Akcin · Erkan Yalcin**

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**Abstract** The present paper deals with the salt effect on root, stem and leaf anatomy of *Spergularia marina*. Salt tolerant populations of *Spergularia marina* from low (2.0–4.2 dS/m), medium (9.3–10.7 dS/m) and highly (18.4–26.2 dS/m) saline soils were evaluated for anatomical modifications. Root anatomical characteristics as cortex thickness and xylem vessel diameter were decreased in high saline environments. Increased aerenchyma and periderm thickness in the root were critical for checking water loss and enhancing water storage capability. In stem, higher salinity decreased the thickness of the epidermis and cortex. Increased aerenchyma and increased thickness of vascular tissue seemed to be crucial for its better survival under saline environments. The thickness of sclerenchyma was unchanged under low and moderate salinity but considerably increased under high salinity. Leaf anatomy shows that salt stress resulted in an increase of cuticle and parenchyma thickness as well as an increase of vascular bundle sheath thickness. The presence of the cells with calcium oxalate crystals in the stem and leaf increased at higher salinity. Additionally, under high salinity it was observed that both stomatal index and stomatal dimensions were considerably reduced. These results show that salinity stress shows significant anatomical modifications in *Spergularia marina*.

**Keywords** Anatomical adaptations · Salinity · *Spergularia marina* · Aerenchyma · Calcium oxalate crystals

## Introduction

Salinity is one of the most important abiotic stresses, limiting plant growth and productivity in arid and semi-arid regions [1]. High salt content, especially chloride and sodium sulphates, affect plant growth by modifying their morphological [2], anatomical [2, 3] and physiological traits [4, 5]. Therefore, plants display specific adaptations at structural and physiological level showing altered physiological and biochemical mechanisms, thus enabling to grow well in high salinity and maintaining their reproductive capacity [6, 7].

Morphological and anatomical modifications in the plant body are capable of minimizing detrimental effects of salt stress [8]. Salt tolerant species show a range of anatomical adaptive features like increased succulence (both in root and stem), thick cuticle and deposition of wax, salt-secretory trichomes and glands, thick and many layered epidermis and well developed water storing tissues in the cortex, widening of casparian band and enhanced development of root endodermis [9, 10]. Many studies have shown that anatomical alterations such as inhibited differentiation, change in diameter and number of xylem vessels are the result of high salinity. Based on these results it has been assumed that water transport capacity can be affected by this change in the xylem structure [11, 12]. Additionally, several studies reported that anatomical structures of plant organs, especially of leaves, change, thus enabling the plant to adapt to its environment [13], because the leaf is the main photosyntetic organ of the plant [14]. Morpho-

T. A. Akcin (✉) · E. Yalcin
Faculty of Arts and Science, Biology Department, Ondokuz Mayıs University, Kurupelit, 55139 Samsun, Turkey
e-mail: aytasakcin@hotmail.com; taytas@omu.edu.tr

A. Akcin
Faculty of Arts and Science, Biology Department, Amasya University, İpekköy, 05100 Amasya, Turkey

anatomical alterations of halophytes include an increase of cell volume, especially of spongy and water parenchyma, an increase in leaf thickness and a decrease in the number of stomata [15–17]. Also, under saline conditions, mesophyll resistance to the gaseous exchange increases as a consequence of structural changes in the mesophyll cells [18]. However, promoting effects of salt stress on leaf thickness [19, 20] and stomata number [19] have also been recorded.

*Spergularia marina* belonging to the family Caryophyllaceae, is a coastal annual halophytic herb, and is widely distributed among the sea shores of Turkey [21, 22]. It is commonly found in cultivated fields and waste lands of saline and sandy habitats [23]. In this species the salt resistance mechanism is often related with the relationship between $Na^+$ and $K^+$ accumulation and growth [24]. Keiffer and Ungar [25] showed that seeds of *S. marina* failed to germinate in 2 % NaCl. It has been reported that *S. marina* can grow in a wide range of salinity [22]. Therefore the aim of the present study was to investigate the effects of salinity on root, stem and leaf anatomy under increasing salinity levels. Further the main aim of the present study is to investigate the reaction of *S. marina* under different salinity levels and also to contribute to the understanding of the salt tolerance adaptation mechanism.

## Material and Methods

The plant species *S. marina* was collected from different localities of the Kızılırmak Delta, Samsun, Turkey in flowering period during the year 2010–2011(Fig. 1). Soil salinity was determined from 28 soil samples randomly collected in the study area. Soil samples were taken from the root zone of each population from different habitats. The electrical conductivity meter (EC meter) was used to determine the EC in the obtained soil extract. Therefore, three salinity levels were determined as 2.0–4.2 dS/m (low salinity), 9.3–10.7 dS/m (moderate salinity) and 18.4–26.2 dS/m (high salinity) in the study area. Subsequently the first *S. marina* population was collected from the low saline soils (coordinates 41° 40′ 09″ N, 36° 01′ 16″ E, ECe 2.0–4.2 $dSm^{-1}$); second population was collected from the moderate saline soils (coordinates 41° 40′ 05″ N, 36° 02′ 19″ E, ECe 9.3–10.7 $dSm^{-1}$) and the third population was collected from the high saline soils (coordinates 41° 40′ 11″ N, 36° 01′ 57″ E, ECe 18.4–26.2 $dSm^{-1}$).

For the anatomical studies, slides were made from transverse sections of middle parts of fully developed roots, stems and leaves and surface sections of leaf material preserved in 70 % ethanol. A light microscope (Nikon SE, Japan) was used for all microscopic observations and obtained images were photographed using a Nikon Coolpix

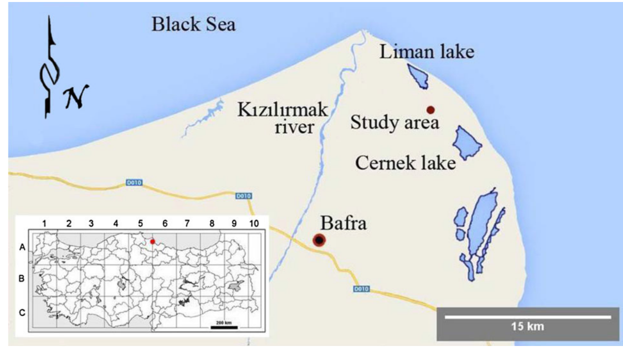


**Fig. 1** Map indicating the study area at Samsun, Turkey

P5100 digital camera. Image J program was used to measure of various cells and tissues on the figures. All anatomical measurements were determined on at least 30 specimens. The stomatal index (SI) was calculated using the following formula [26]:

$$\text{SI}\ \left(\text{per mm}^2\text{area}\right)\% = [\text{S}/(\text{E}+\text{S})] \times 100,$$

where SI is the stomatal index, S is the number of stomata per unit area and E is the number of ordinary epidermal cells per unit area.

The statistical package programme SPSS ($P < 0.05$) was used to compare mean values with one-way ANOVA. The Duncan post hoc tests was used to compare mean values in case of significant differences.

## Results

### Root Anatomy

Root anatomical characters significantly affected by increased salinity levels are shown in Table 1. Increasing salinity generally increased periderm thickness particularly at the highest salt level (Table 1; Fig. 2a–c). On the contrary, the cortex thickness was decreased reasonably with the increase in salinity levels (Table 1). The aeriferous cavities in *S. marina* root increased with increasing salt levels (Table 1; Fig. 2a–c). At the highest salinity level a remarkable decrease was determined in the xylem vessel diameter (Table 1; Fig. 3a–c).

### Stem Anatomy

The obtained results showed that stem epidermis and cortex thickness of *S. marina* was stimulated beginning from moderate to low salinity levels (Table 2). Stem anatomical parameters as thickness of phloem and xylem increased with the rise in salinity levels (Table 2). Pith width

**Table 1** Root anatomical characteristics in *S. marina* plants grown at low (2.0–4.2 $dSm^{-1}$), moderate (9.3–10.7 $dSm^{-1}$) and high salinity (18.4–26.2 $dSm^{-1}$)

| Characteristics | Low salinity | Moderate salinity | High salinity |
|---|---|---|---|
| PT (μm) | 98.83 ± 14.34 (a)* | 89.38 ± 14.53 (a) | 160.26 ± 14.57 (b) |
| CT (μm) | 782.94 ± 220.18 (b) | 867.12 ± 152.20 (b) | 663.56 ± 29.54 (a) |
| DAC (μm) | 113.01 ± 30.72 (a) | 137.64 ± 46.21 (a) | 157.40 ± 33.52 (b) |
| DXV (μm) | 28.00 ± 2.11 (b) | 21.10 ± 1.97 (a) | 20.87 ± 3.71 (a) |

*PT* periderma thickness, *CT* cortex thickness, *DAC* diameter of aeriferous cavities in cortex, *DXV* diameter of xylem vessels

* Data are mean values ± SE of 30 measurements. Means for each characteristic in each row sharing similar letters are statistically non-significant ($P = 0.05$)

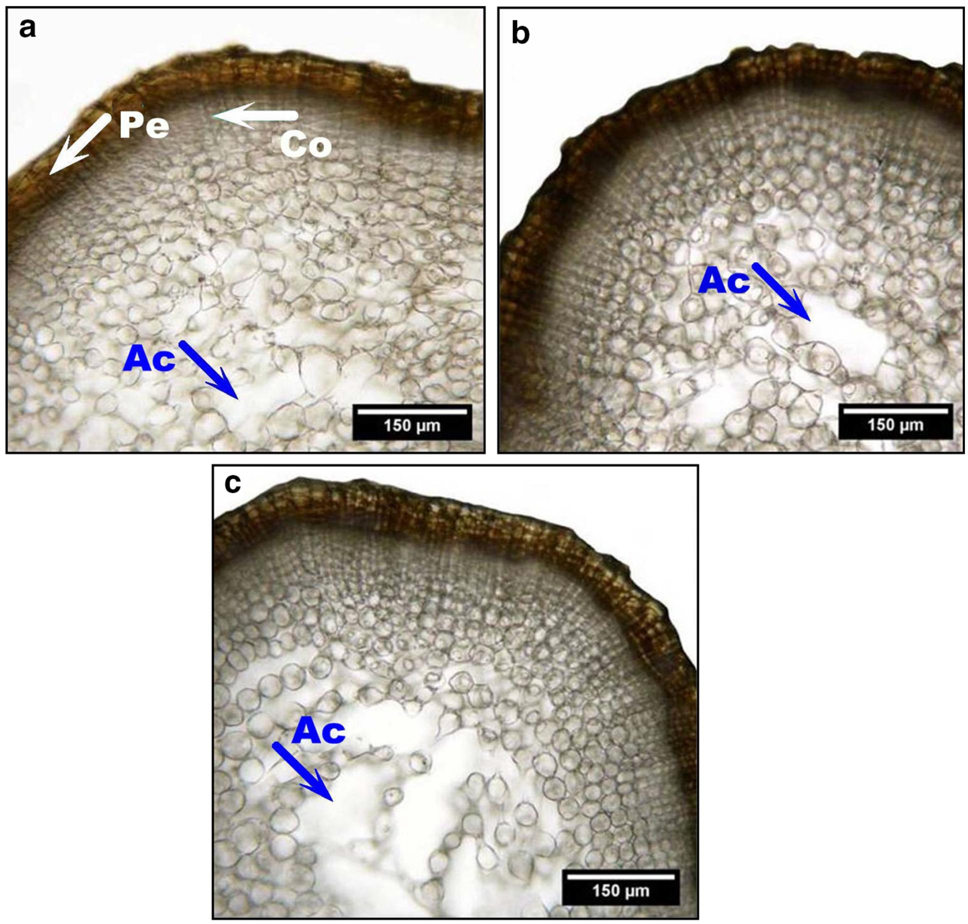


**Fig. 2** Root cross-sections showing changes in *S. marina* plants grown at low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *Ac* aeriferous cavities, *Co* cortex, *Pe* periderma. The aeriferous cavities in *S. marina* root were correlated with increasing salt levels (**a**–**c**)

increased significantly ranging from 205.56 to 450.92 μm with the increase in salt concentration (Table 2; Fig. 4a–c). There was an increase in pith length with increasing salt levels (Table 2). However, the sclerenchyma thickness was not much affected by increasing salt levels but the high salt concentration caused a significant increase in this character (Table 2; Fig. 4a–c). A significant increase in the aeriferous cavities of the cortex parenchyma of the stem was observed with increasing salt levels (Table 2; Fig. 4a–c). Calcium oxalate crystals in the cortical parenchyma of the stem increased with an increase in salt levels (Table 2).

## Leaf Anatomy

Leaf cuticle thickness increased with increase in salt intensity (Table 3; Fig. 5a–c). However, leaf epidermis thickness was not much affected by increasing salt level. Salt stress led to a significant increase in the thickness of the parenchyma in the leaves of *S. marina.* Their highest values were determined under highest salinity levels (18.4–26.2 dS/m) (Table 3; Fig. 6a–c). In addition, calcium oxalate crystals in the mesophyll of the leaf increased with the increase in salinity (Fig. 6).

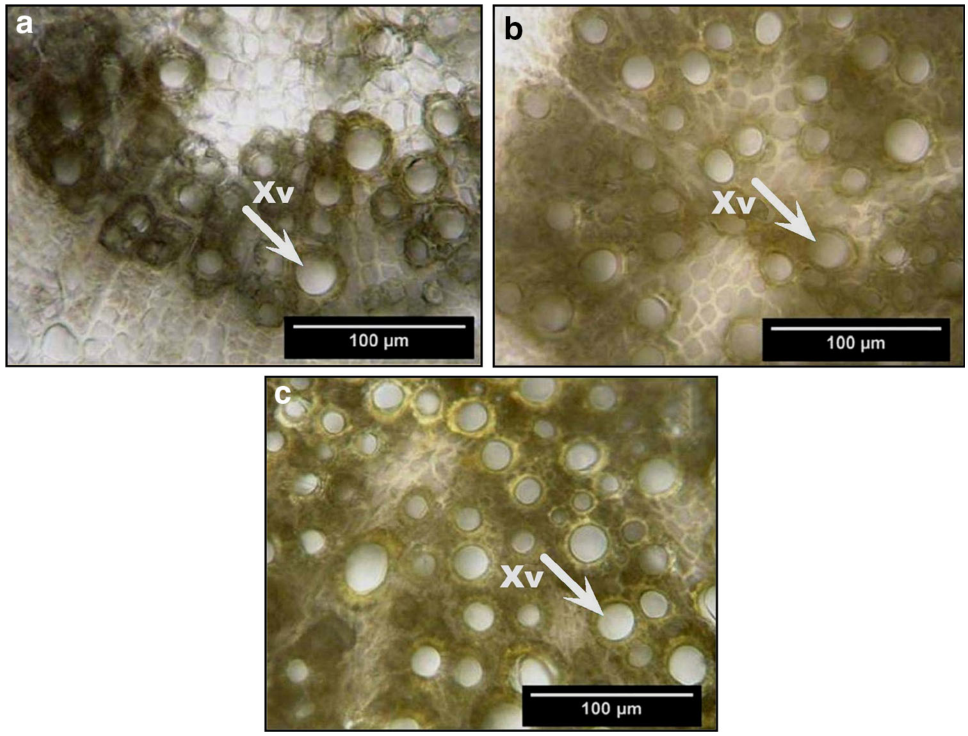


**Fig. 3** Root cross-sections showing the xylem tissue details in *S. marina* plants grown at low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *Xv* xylem vessels. High salinity levels led to remarkable decrease of xylem vessel diameter (**b**–**c**)

**Table 2** Stem anatomical characteristics in *S. marina* plants grown at low (2.0–4.2 $dSm^{-1}$), moderate (9.3–10.7 $dSm^{-1}$) and high salinity (18.4–26.2 $dSm^{-1}$)

| Characteristics (µm) | Low salinity | Moderate salinity | High salinity |
|---|---|---|---|
| CT | 7.66 ± 0.83* | 10.21 ± 1.38 | 13.45 ± 1.20 |
| ET | 28.03 ± 3.76 (a) | 24.65 ± 3.78 (b) | 12.90 ± 1.36 (b) |
| CXT | 279.63 ± 30.57 (a) | 260.70 ± 11.52 (a) | 200.47 ± 15.18 (b) |
| DAC | 48.50 ± 9.68 (a) | 71.35 ± 17.66 (b) | 78.01 ± 9.04 (b) |
| ST | 76.93 ± 18.96 (a) | 49.41 ± 13.37 (a) | 108.83 ± 13.74 (b) |
| PT | 54.24 ± 19.32 (a) | 90.78 ± 10.34 (b) | 104.70 ± 37.93 (b) |
| XT | 76.93 ± 18.96 (a) | 49.41 ± 13.37 (a) | 108.83 ± 13.74 (b) |
| DXV | 16.63 ± 3.34 | 15.81 ± 2.02 | 17.53 ± 3.43 |
| PW | 205.56 ± 46.01 (a) | 314.93 ± 62.56 (b) | 450.92 ± 38.78 (c) |
| PL | 716.03 ± 111.82 (a) | 594.88 ± 56.47 (a) | 935.58 ± 148.33 (b) |

*CT* cuticula thickness, *ET* epiderma thickness, *CXT* cortex thickness, *DAC* diameter of aeriferous cavities at the cortex, *ST* sclerenchyma thickness, *PT* phloem thickness, *XT* xylem thickness, *DXV* diameter of xylem vessels, *PW* pith width, *PL* pith length

* Data are mean values ± SE of 30 measurements. Means for each characteristic in each row sharing similar letters are statistically non-significant ($P = 0.05$)

Stomatal density on both adaxial and abaxial leaf surfaces showed almost a similar response to increasing salt levels (Fig. 7a–c). Stomata index both on the lower and upper surfaces was decreased with the increase in salinity (Table 4). Similarly, stomata length and width generally decreased with rise in salt levels (Table 3).

The length and width of the leaf main vein was unaffected by low and moderate salinity. However, this parameter significantly increased at high salinity (Table 3). Leaf sheath thickness increased gradually with increasing salinity (Table 3). On the other hand, salt stress imposed a distinct increase in sclerenchyma thickness (Fig. 8a–c).

## Discussion

As observed in the present study different salt levels affected the anatomical structure of the investigated species. These results showed that the root cortex area of *S. marina* was decreased with increasing salt level (Table 1).

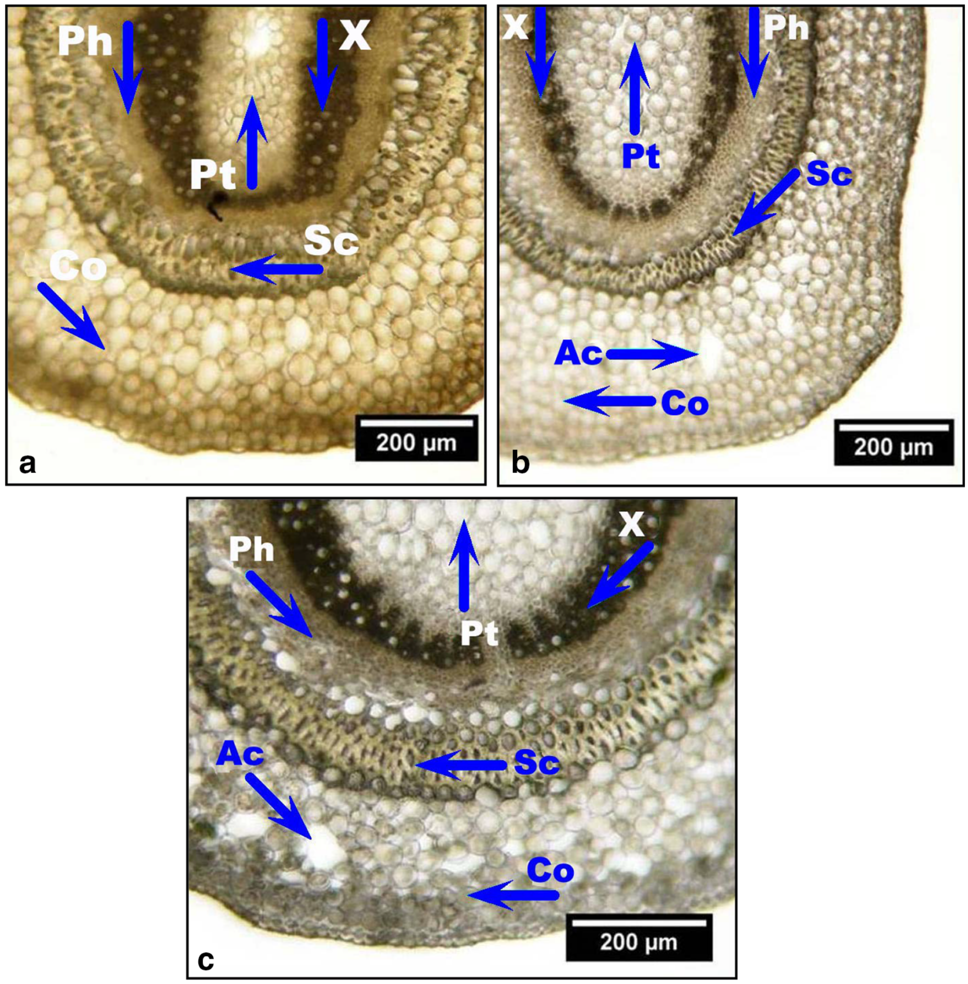


**Fig. 4** Stem cross-sections showing changes in *S. marina* plants grown at low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *Ac* aeriferous cavities, *Co* cortex, *Ph* phloem, *Pt* pith, *Sc* sclerenchyma, *X* xylem. Sclerenchyma thickness is seen to be highly thick as compared to the stem at low salinity in **a**. The aeriferous cavities at the cortex parenchyma were correlated with an increase in salt levels (**a**–**c**)

**Table 3** Leaf anatomical characteristics in *S. marina* plants grown at low (2.0–4.2 $dSm^{-1}$), moderate (9.3–10.7 $dSm^{-1}$) and high salinity (18.4–26.2 $dSm^{-1}$)

| Characteristics | Low salinity | Moderate salinity | High salinity |
|---|---|---|---|
| CT (µm) | 8.00 ± 1.55 (a)* | 8.62 ± 1.63 (a) | 10.33 ± 1.20 (b) |
| EW (µm) | 37.04 ± 7.66 (b) | 28.87 ± 7.01 (a) | 33.58 ± 4.07 (a) |
| EL (µm) | 41.50 ± 4.25 (a) | 35.13 ± 10.32 (a) | 47.02 ± 4.15 (b) |
| PT (µm) | 416.13 ± 34.41 (a) | 438.08 ± 29.79 (a) | 589.14 ± 35.24 (b) |
| ABSW (µm) | 21.08 ± 2.73 (b) | 15.89 ± 0.73 (a) | 14.86 ± 1.70 (a) |
| ABSL (µm) | 29.40 ± 1.77 (b) | 28.64 ± 2.64 (b) | 22.43 ± 1.21 (a) |
| ADSW (µm) | 19.14 ± 2.06 (b) | 18.25 ± 18.25 (b) | 16.39 ± 1.44 (a) |
| ADSL (µm) | 25.43 ± 2.40 (b) | 24.26 ± 2.41 (b) | 20.85 ± 1.34 (a) |
| MW (µm) | 100.06 ± 11.61 (a) | 103.70 ± 14.38 (a) | 149.11 ± 20.51 (b) |
| ML (µm) | 159.95 ± 21.90 (a) | 156.95 ± 10.54 (a) | 238.80 ± 15.41 (b) |
| BST (µm) | 26.92 ± 7.37 (a) | 32.17 ± 2.36 (a) | 46.22 ± 8.59 (b) |

* Data are mean values ± SE of 30 measurements. Means for each characteristic in each row sharing similar letters are statistically non-significant ($P = 0.05$)

*CT* cuticula thickness, *EL* length of epiderma cells, *EW* width of epiderma cells, *PT* parenchyma thickness, *ABSW* abaxial stomatal width, *ABSL* abaxial stomatal length, *ADSW* adaxial stomatal width, *ADSL* adaxial stomatal length, *MW* midrib width, *ML* midrib length, *BST* bundle sheat thickness

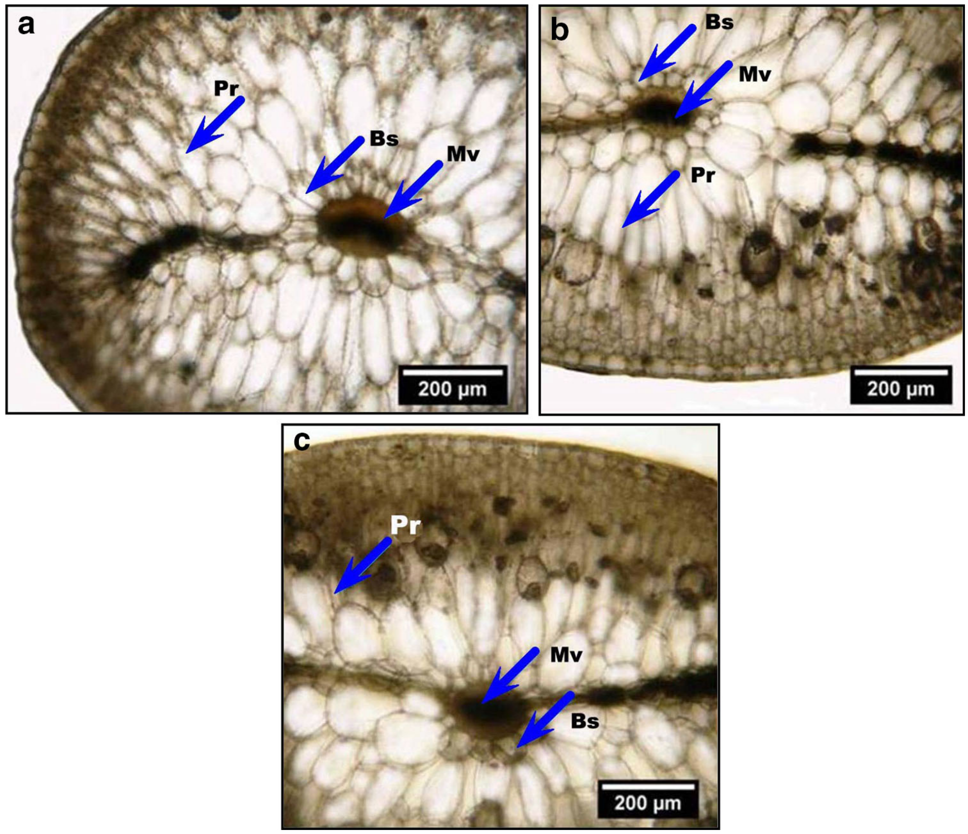


**Fig. 5** Leaf cross-sections showing changes in *S. marina* plants grown at low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *Bs* bundle sheath, *Mv* main vein, *Pr* parenchyma. High salinity led to a significant increase in the thickness of parenchyma (**c**). Leaf bundle sheath was correlated with increasing salt levels (**a**–**c**)

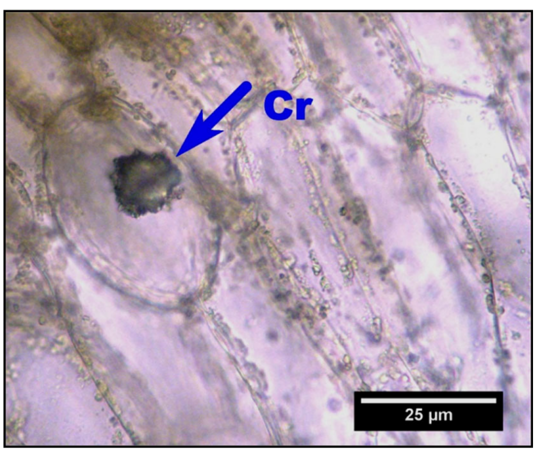


**Fig. 6** Calcium oxalate crystals in the mesophyll of the leaf in *S. marina* plants grown at high salinity. *Cr* calcium oxalate crystal

The results of the study of Hajibagheri et al. [27] confirms the present results. It shows that the cortical thickness and root stele diameter of *Suaeda maritima* was greater in the presence of 340 mM NaCl as compared to those grown in the absence of NaCl. The halophyte, *Kandelia candel* showed greater root growth in plants grown in low and moderate salinities. It might indicate an advantageous effect of NaCl on the growth [28]. In addition, Boughalleb et al. [17] reported that the cortical thickness of *Atriplex halimus* and *Nitraria retusa* decreased significantly at salinity exceeding 200 mM NaCl. A higher number of cortical layers accompanied by small vacuolated parenchyma cells have been reported in *N. retusa* and *A. halimus* roots grown in moderate salinity. These results are in agreement with the results of Shannon et al. [6], reporting that in numerous halophytes salinity induces vacuolisation. The aeriferous cavities in vegetative organs are common features for more halophyte species such as *Spergularia* [29]. It is known that the presence of aerenchyma in *Spergularia* root may be correlated with poor ventilation of saline soils [30]. Such root aerenchyma structures have also been reported in *Imperata cylindrica* [31]. In the present study a remarkable increase in aerenchyma formation in the root of *S. marina* with increased salinity level has been noticed (Table 1; Fig. 2a–c). This structural formation can lead to an increase in storage tissue area with increased vacuolar volume storing toxic ions. This is an important strategy in coping with high salinities [32]. In the present study, the xylem vessel diameter for *S. marina* root was reduced significantly with increasing salt levels (Table 1; Fig. 3a–c). In wild barley [2] and in cotton and tomato plants [33] also the similar diminution of the diameter of xylem vessel was observed under saline conditions [2, 33].

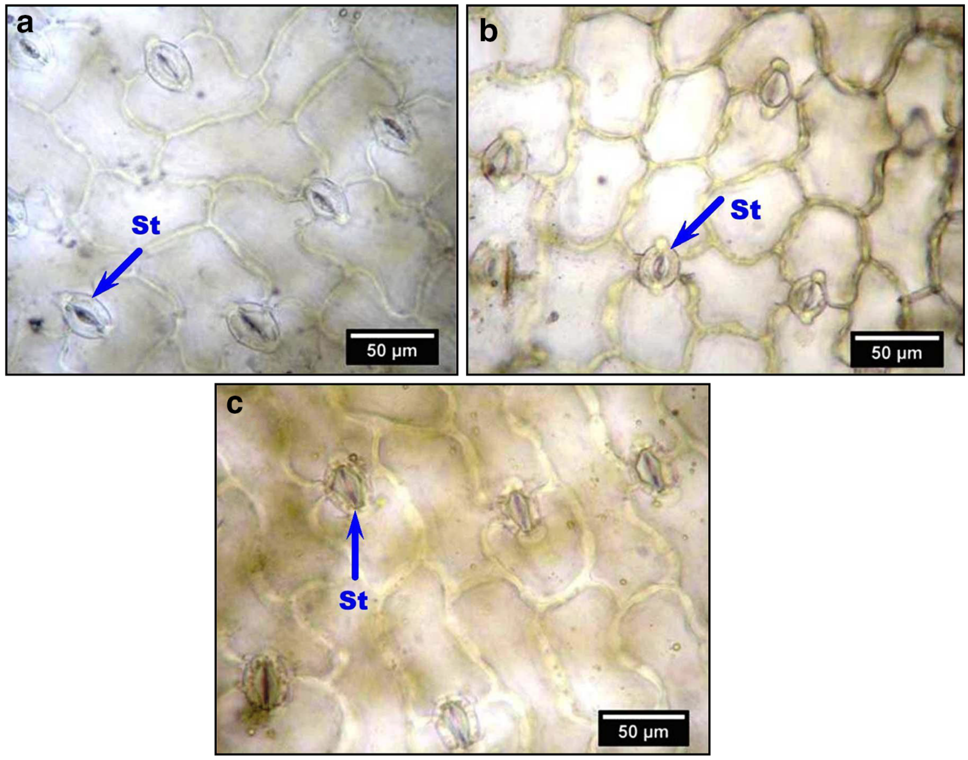


**Fig. 7** Surface sections of the lower surface of leaves in *S. marina* plants grown low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *St* stomata. High salinity levels led to a significant decrease in the stomata length and width (**a–c**)

**Table 4** Leaf stomata index in *S. marina* plants grown at low (2.0–4.2 $dSm^{-1}$), moderate (9.3–10.7 $dSm^{-1}$) and high salinity (18.4–26.2 $dSm^{-1}$)

| SI (number $mm^2$) | Low salinity | Moderate salinity | High salinity |
|---|---|---|---|
| LUC | 27,91 ± 1,610 (a) | 22,23 ± 2,059 (b) | 20,23 ± 1,592 (c) |
| LLC | 32,20 ± 1,817 (a) | 26,21 ± 2,253 (b) | 26,21 ± 2,253 (b) |

*SI* stomatal index, *LUC* leaf lower surface, *LLC* leaf upper surface

* Data are mean values ± SE of 30 measurements. Means for each characteristic in each row sharing similar letters are statistically non-significant ($P = 0.01$)

As compared to non-saline conditions the number of xylem vessels are more and they are narrower than those found under saline conditions [34]. The selection for narrow vessels leads to improved water use capacity of leaves. The risk of xylem embolism will be reduced in saline habitats [17].

The obtained results in the present study revealed that with low to moderate salinity the stem cortex area of the species *S. marina* was increased, but declined severely at higher salinity levels (Table 2). In addition, increased sclerenchyma thickness was observed with increasing salt levels (Table 2; Fig. 4). It is known that the sclerenchymatic and lignified ring of *Spergularia media* stem can be related to an excessive salinity in soil [30, 35]. It was also suggested that the lignin may be a cellular resistance element against the high osmotic pressure inside the plant body [36]. Hameed et al. [37] described that at high salt level the sclerenchyma thickness of *Cynodon dactylon* was greater confirming the present results. This characteristic may offer some resistance to water loss through the stem and may play a crucial role in adaptation to unfavourable conditions [30, 37, 38]. The thickness of xylem and phloem increased clearly under high salinity conditions. (Table 2). It was suggested that increased xylem and phloem area plays an important role in the conduction of water and photosynthates, particularly under adverse saline conditions [37]. This has been supported by previous reports in different plant species such as rice [39], *Kandelia candel* [28], *Ziziphus* cultivars [40] and *Arabidopsis thaliana* [41].

Kozlowski [34] determined that the production of calcium oxalate increased under salinity. According to Grigore and Toma [30], calcium also plays an important role in maintaining the integrity of plant cell membrane. It is a physiological barrier to free diffusion of potentially toxic ions prevalent in a saline environment. In agreement with this idea, it was seen that calcium oxalate crystals in the cortical parenchyma of the stem of *S. marina* were significantly increased at higher salinity.

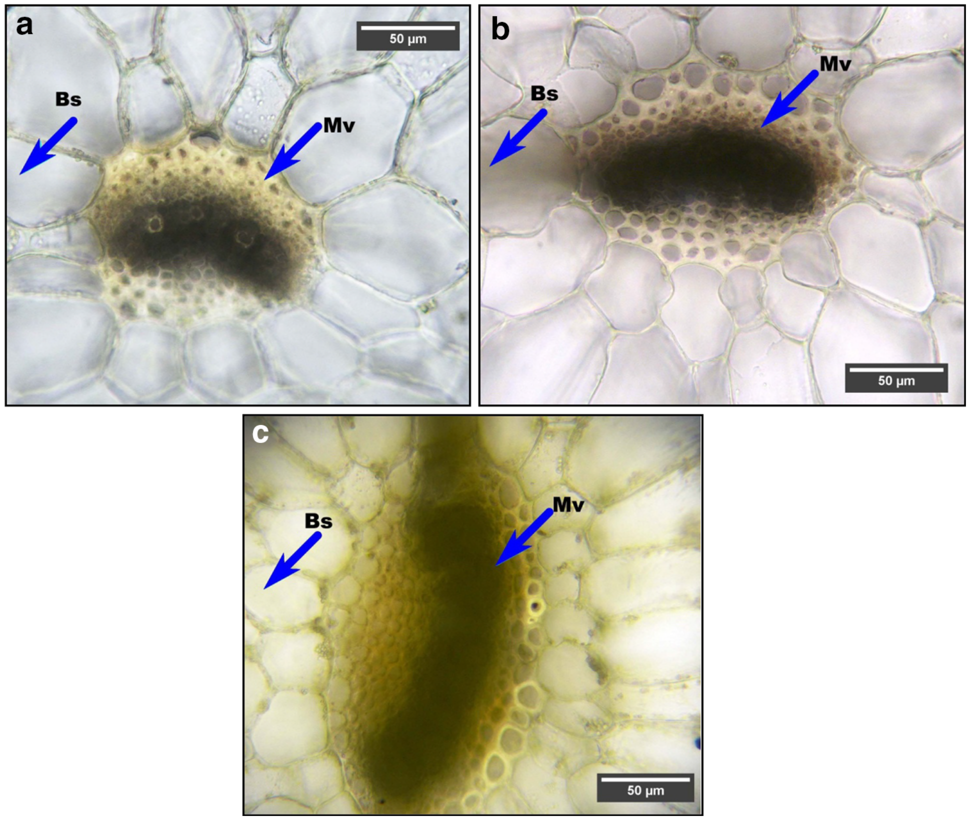


**Fig. 8** Leaf main vein and bundle sheath showing changes in *S. marina* plants grown at low salinity (**a**), moderate salinity (**b**) and high salinity (**c**), respectively. *Bs* bundle sheath, *Mv* main vein. The length and width of the leaf main vein was correlated with increasing salt levels (**a**–**c**). Increased thickness at the leaf sheath is seen in **c**

Salinity leads to significant changes in the leaf anatomy of *S. marina.* The thickness of leaf mesophyll parenchyma increases with high salinity and reduces the dimensions of leaf stomata. The greater leaf mesophyll parenchyma thickness was measured in *S. marina* at higher salinity (Table 3). Further published data that salinity increases succulence and leaf thickness in plants like *Cakile maritima* [42], *Nitraria retusa* and *Atriplex halimus* [17] are similar to the present results. Halophytes utilize different mechanism to deal with high internal ion concentrations. Debez et al. [42] showed that succulence is one of the adaptations to increased salinity. These results are consistent with the investigations on other halophytes as *Atriplex patula* [43] and *Suaeda maritima* [27] and glycophytes as *Gossypium hirsutum* [43] and *Hordeum vulgare* [19].

In the present study, the stomatal density and dimensions decreased particularly in the upper than in the lower surface under high salinity (Table 3). This could be explained with the changes in the leaf area under salt stress. This was further supported by Curtis and Lauchli [44] who reported a negative relationship between stomata density and leaf size under stress conditions. On the other hand, it has been known for a long time that high salinity has a decreasing effect on stomata number [45], stomata index [46] and this complies with the results of the present study. Robinson et al. [47] reported that the stomata get closed as a response to salt stress due to the increase in $Na^+$ and $Cl^-$ ions and the decrease in $K^+$ amount in the leaves of plants and so they can survive since transpiration and water loss decreases. The present data agrees with previous data which reports that the salt stress stimulates reduced stomatal density [16, 28].

Salt tolerant species generally possess thick epidermis and cuticle. This serves as an effective mechanism against water loss during limited moisture availability [48, 49]. In the present study, thickness of cuticle increases with the increasing salt level (Table 3).

Another remarkable leaf anatomical feature observed in *S. marina* under salt stress was a significant increase in the number of calcium oxalate crystals (Fig. 6). Therefore, it can be assumed that calcium ions are involved in increasing the salt tolerance in different ways. It ensures the preventing of water loss through the leaf. The same findings were obtained by Hajibagheri et al. [50, 51] in *Suaeda maritima* and by Bray and Reid [46] in *Phaseolus vulgaris.*

Leaves of *S. marina* showed modifications in the increase in the thickness of the midrib. (Table 3; Fig. 8a–c). Hameed et al. [38] stated that this anatomical feature may be helpful in the storage of ions inside the plant body. Examples of leaf succulence are common in *Kandelia candel, a* dicot species [28], grassland legumes [52] and halophytes [53].

Increased leaf bundle sheath thickness under the high salinity level may be of importance as it would provide rigidity to the leaf. These results show that the leaf bundle sheath thickness of *S. marina* increased with high salinity (Table 3; Fig. 8a–c). Similar results have been shown in *Nitraria retusa, Atriplex halimus* and *Medicago arborea* [17].

In the present study the changes in the root, stem and leaf anatomy of *S. marina* under increasing salinity levels were investigated. It can be stated that the root and stem anatomical mechanisms in the toleration of salinity are increasing aerenchyma, thickness of periderm, vascular tissues and sclerenchyma. This can be described as an adaptive strategy in the facilitation of water transport. In the studied species leaf anatomical parameters showed significant changes with high salt concentrations. The results obtained in the present study indicate that salt stress resulted in an increase of cuticle and parenchyma thickness (succulence) of the leaf. Furthermore, thickness of midribs and vascular bundle sheath increased under high salinity. The anatomical strategy like reducing the stomatal dimensions and density seems to be an efficient strategy regarding their tolerance against salinity and reducing water loss. It can be assumed that a significant increase in the number of calcium oxalate crystals in *S. marina* leaf under salt stress may be to ensure prevention of water loss through the leaf. From the present results, it can be concluded that the anatomical mechanisms used by *S. marina* to cope up with salinity might play a crucial role in adaptation to unfavourable conditions of plants.

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