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STRUCTURAL ADAPTATION OF *SALSOLA SODA* L. (CHENOPODIACEAE) FROM INLAND AND MARITIME SALINE AREA

ABSTRACT: The microscopic analysis of leaf and stem in two populations of *Salsola soda* was carried out in order to examine mechanism of anatomical adaptations to environmental condition on saline habitats and to determine if there exists a morpho-anatomical differentiation between populations from maritime and inland saline area. Analysis included 26 quantitative characters of leaf and stem. The results showed that both populations exhibited halomorphic and xeromorphic adaptations, which refered to ecological plasticity and adaptations of plants to their habitats. Our research also showed that *S. soda* had quite a stable morpho-anatomical structure, since only quantitative changes were recorded.
KEYWORDS: anatomy, halophytes, leaf, *Salsola soda,* stem

INTRODUCTION

Soil salinization is an increasing problem world-wide. Global estimates indicate that at least 1.5 billion hectares of land are salt-affected (Choukr-Allah, 1996). In many oil production areas, contamination of soils with oilfield brines is a significant environmental problem (Merrill et al., 1990). Brine salts are predominantly chlorides, 90% or more NaCl (McMilion, 1965). Some ions contained in the brine solution, such as N^{a+}, Cl^-, Ca^{2+}, Mg^{2+}, K^+ and SO_4^{2-}, can be phytotoxic if concentrations are above levels that plants can tolerate, even though most of these elements are essential for plant growth (Munn and Stewart, 1989).

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The United Nations Environment Program (UNEP) estimates that 20% of the agricultural land and 50% of the cropland in the world is salt stressed (Flowers and Yeo, 1995). Because of this the latest investigations were focused on amelioration methods (Qadir et al., 2001, 2002, 2005; Li et al., 2004). On the other hand salt-accumulating halophytes could be used to revegetate and improve the quality of saline soils (Flowers et al., 1986; Zhao, 1991). Halophytes have adopted different strategies in order to survive periodic soil saturation. They are usually divided into euhalophytes, which have succulent structure and accumulate salt in their tissues, and crinochalophytes, which are capable of excreting salt, usually through salt glands and bladders (Zhao et al., 2002; Voronkova et al., 2008). Specific conditions of salt soils, primarily high concentration, different quality and quantity of salts and variability of water content in soils, affects specific morpho-anatomical adaptations of halophytes (Knežević et al., 1998; Polić et al., 2009). The leaf histological components are the most satisfactory parameters for the study of the relations between halomorphic structures of plants and their habitat, although anatomy of other plant organs could give additional information (Colombo & Trapani, 1992).

Of the Dicotyledoneae, the Chenopodiaceae has by far the highest proportion of halophytic genera (44%). With 312 halophytic species it is probably the family in which salt-tolerance is most widespread (Flowers et al., 1986). Many genera of Chenopodiaceae, especially *Atriplex, Suaeda* and *Salicornia*, are extremely salt tolerant and have been studied for their potential use as forage and oilseed crops (Watson, 1990; Glenn et al., 1991, Rozema et al., 1995).

Salsola L., a genus of 100 to nearly 200 species, is one of the largest genera within the Chenopodiaceae (Botschantzev, 1969, 1979; Cronquist, 1981).

S. soda is an annual, succulent shrub up to 70 cm tall. It has fleshy green leaves and either green or red stems. The tiny flowers develop from inflorescences that grow out of the base of the leaves near the stem (Slavnić, 1972; Akeroyd, 1993). *S. soda* is native in Eurasia and North Africa. It is also found on the Atlantic coasts of France and Portugal and on the Black Sea coast (Jalas and Suominen, 1989). It has become naturalized along the Pacific coast of North America, and there is concern about its invasiveness in California's salt marshes (Baye, 1998). In Serbia *S. soda* is an endangered species which distribution is limited to saline areas in the northern part of Serbia, while in Montenegro this plant can be found only on the Adriatic coast (Slavnić, 1972).

This study was performed in order to reveal structural features of *S. soda*, particularly anatomical characteristics of leaf and stem, allowing them to survive under specific environmental conditions. Another aim was to determine the structural differences and variability rate between populations from maritime and inland saline areas.

MATERIAL AND METHODS

Morpho-anatomical analyses were done of plant samples from two populations of *S. soda* growing in Ulcinj salina (maritime saline area, Montenegro) and Okanj (inland saline area, Serbia; Table 1). The soil at the collection site contained very small amount of salts in inland saline area – 0.03% compared with locality from maritime saline area (0.8%). The alkaline reaction was higher at Okanj locality (8.8), than in Ulcinj salina locality (7.5).

Table 1. Voucher data for *Salsola soda* specimens used in the study with climate and soil characteristics of their habitats in the year 2006

Collection site	Date	Voucher Number	Average annual temperature	Annual precipitation	% of salts in soil	Ph soil
Montenegro, Ulcinj salina UTM 34T CM4 54	09.09.2006.	2-1994	15.4° C	1272mm	0.8	7.5
Serbia, Okanj UTM 34T DR2 44	15.09.2006.	2-1995	11.1° C	571mm	0.03	8.8

Plants were determined at the Department of Biology and Ecology, University of Novi Sad. Voucher specimens were deposited in the Herbarium of the Department of Biology and Ecology, University of Novi Sad – BUNS (Table 1). For anatomical investigation ten plants of each population were used. For light microscopy observations leaf epidermal prints were made after Wolf (1954). The leaf surfaces were covered with liquid transparent lac, and epidermal prints removed using transparent adhesive tape. Stomata were counted on five randomly selected areas of the adaxial and abaxial surfaces and calculated per mm^2 of the leaf surface. The segments of leaves and stems from the middle part of the plants were separated and fixed in 50% ethanol. For light microscopy, cross sections were made using Leica CM 1850 cryostat, at a temperature of -18° C to -20° C, at cutting intervals of 25 mm. Sections, epidermal cells and stomata were observed and measurements made using Image Analyzing System Motic 2000. Relative proportions were calculated for leaf and stem tissues, and expressed as a ratio of the whole cross section area of each organ. Data were statistically processed by analysis of variance and means, and standard errors and coefficients of variation were calculated using STATISTICA for Windows version 10.0 (StatSoft, 2011). The significance of differences in measured parameters between the populations was determined using t-test ($p \leq 0.05$ and $p \leq 0.01$). The general structure of sample variability was established by Principal Component Analysis (PCA), based on correlation matrix.

RESULTS

The stem cross sections are rounded to elliptical in shape, with incisions. The stem has a single layer of epidermis (Figure 1).

Stem cortex was differentiated into one layer of collenchyma located subepidermally (Figure 2A), one layer of chlorenchyma beneath it and several layers of thin-walled parenchyma cells that do not contain chloroplasts. Parenchyma cells are generally large, except in incisions of peripheral part of cortex where they are much smaller. In central cylinder, numerous collateral vascular bundles are arranged in a circle, with well developed sclerenchyma tissue above them (Figure 2B). Pith parenchyma is compact, composed of relatively large parenchyma cells, with no cavity present.

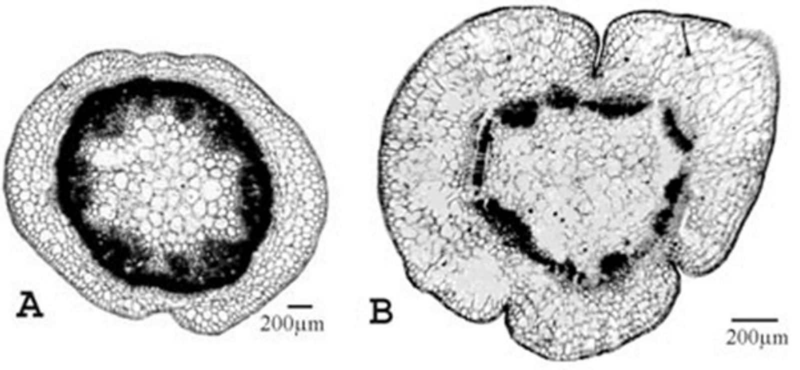

Figure 1. Cross section of the stem: A- Okanj, B- Ulcinj salina

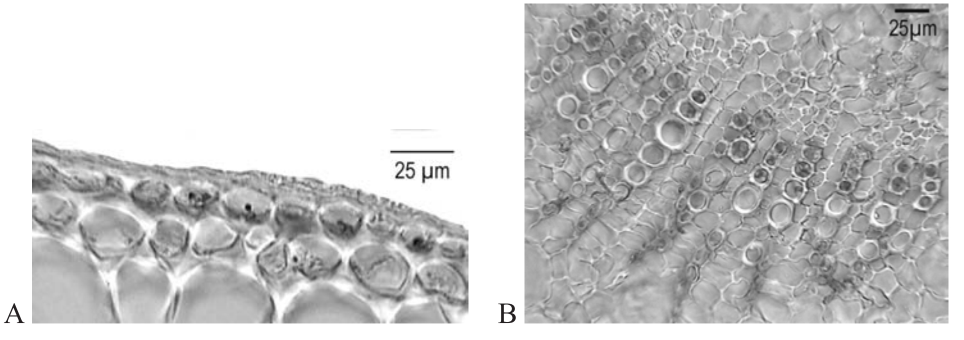

Figure 2. Cross section of the stem: A – collenchyma, B – vascular bundles

The plants of the population from Ulcinj salina had significantly higher stems (22.3 cm) than plants from Okanj (14.6 cm), with larger diameter and cross-section area (Table 2). They also had higher percentage of cortex and pith parenchyma. Significantly higher proportions of epidermis and vascular bundles with sclerenchyma were only recorded in plants from Okanj. The mean cortex thickness: stem radius ratio was 0.352 and 0.376, from population from Ulcinj and Okanj, respectively.

Table 2. Stem anatomical characteristics (mean values ± standard error and coefficient of variation %)

Characters	Ulcinj salina		Okanj		t-test
	$\bar{x}$±se	cv	$\bar{x}$±se	cv	
stem height (cm)	22.2±1.2	17.4	14.6±1.8	38.3	**
stem cross section area of (mm^2)	7.6±0.4	16.9	2.5±0.3	35.4	**
stem diametar (mm)	3.1±0.1	8.6	1.8±0.1	19.4	**
% epidermis	2.0±0.1	10.1	3.6±0.2	18.3	**
% cortex	60.2±1.6	8.6	52.9±2.9	17.5	*
cortex thickness (mm)	0.6±0.02	13.1	0.3±0.03	33.4	**
% cylinder	37.8±1.6	13.8	43.4±3.1	22.6	ns
% v.bundles+ sclerenchyma	15.8±0.8	16.7	25.9±1.9	23.7	**
% pith parenchyma	22.07±1.0	14.4	17.5±1.4	24.5	*

*, ** – differences between the localities significant for 0,05 and 0.01 level of significance respectively; ns – differences between the localities not significant

The leaves are of succulent structure (Figure 3). Their cross sections are round to triangular in shape.

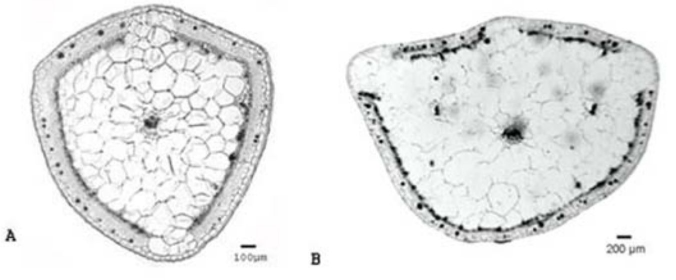

Figure 3. Cross section of the leaf from A-Okanj and B-Ulcinj salina

The leaves have a single layer of epidermis, formed of almost isodiametric, relatively large cells. The epidermis is provided with a thick cuticle. Stomata of paracytic type occur on both leaf surfaces of these species and are slightly under the level of epidermal cells. Underlying the epidermis is a layer of chloroplast containing hypodermal cells, which have calcium oxalate crystals. The mesophyll is differentiated into palisade tissue and atypical spongy tissue which expands to water storage tissue. Palisade tissue is uniseriate, composed of cylindrical cells, placed between hypodermis and chlorenchymatous bundle sheath (Figure 4). Together with bundle sheath layers it forms a discontinuous ring. Water storage cells are large and thin-walled. Those adjacent to bundle sheath often contain cubic crystals.

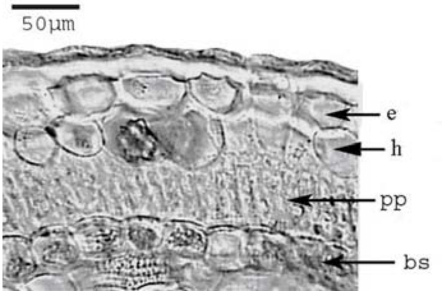

Figure 4. Cross section of the leaf: e – epidermis, h – hypodermis, pp – palisade tissue, bs – bundle sheath

The main vascular bundle is in the center of the leaf, surrounded by water storage parenchyma. Smaller, peripheral vascular bundles are in contact with bundle sheath cells (Figure 5).

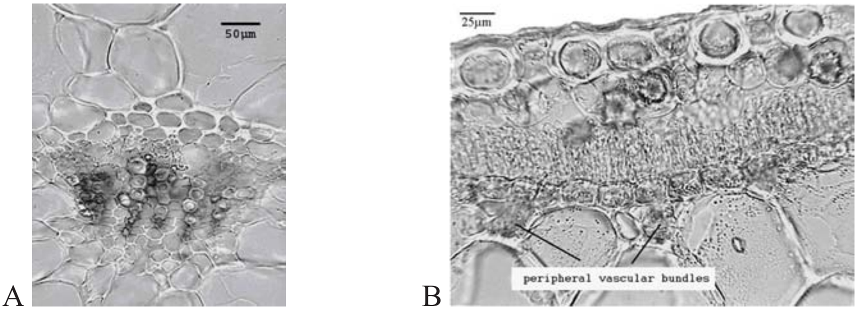

Figure 5. Cross section of the leaf. A – main vascular bundle, B – smaller, peripheral vascular bundles

The leaf cross section area was significantly higher in plants from Ulcinj salina locality, due to better developed water storage tissue (Table 3). Number of stomata /mm^2 on adaxial and abaxial leaf side, proportions of epidermis, hypodermis, vascular bundles and palisade tissue were significantly higher in plants from Okanj locality. No significant differences between plants of these two populations were recorded in stomata size on adaxial and abaxial leaf side, leaf and cuticle thickness, percentage of bundle sheath and the size of palisade cells.

Principal Components Analysis (PCA) showed that examined characters had generally low variability. It indicated three groups of characters, which explained 69.08% of the total variation (Table 4). The first principal component explained 43.51% of the variation. It was defined by the stem cross-section area, proportions of stem epidermis and vascular bundles with sclerenchyma, number of stomata per unit on adaxial leaf side, length of stomata on abaxial leaf side, leaf cross-section area and thickness, as well as proportions of all leaf tissues, except the bundle sheath. The second principal component explained 16.14% of variation due to the variability of proportions of stem cortex, cylinder, pith parenchyma and stomata width on adaxial leaf side. The third principal component explained 9.43% of variation due to the variability of cuticle thickness only. The most stable parameters, which did not contribute significantly to the total variation, were the most of the stomata parameters, percentages of bundle sheath tissue and the size of palisade cells.

Table 3. Leaf anatomical characteristics (mean values ± standard error and coefficient of variation %)

Characters	Ulcinj salina		Okanj		t-test
	$\bar{x}$±se	cv	$\bar{x}$±se	cv	
no. of stomata /mm^2(adaxially)	89.4±3.9	13.7	119.7±4.4	11.7	**
stomata length (adaxially)	30.8±0.8	8.1	28.5±1.0	11.6	ns
stomata width (adaxially)	19.9±0.4	6.6	20.4±0.6	10.1	ns
no. of stomata /mm^2(abaxially)	76.9±3.8	15.6	89.0±3.5	12.4	*
stomata length (abaxially)	31.4±1.0	10.6	29.4±0.7	7.3	ns
stomata width (abaxially)	20.1±0.3	5.2	20.1±1.3	20.8	ns
leaf cross section area (mm^2)	5.1±0.4	23.8	2.2±0.1	17.1	**
leaf thickness (µm)	2378±9	11.9	1682±6	11.6	ns
cuticle thickness (µm)	8.3±0.1	5.2	8.02±0.3	10.4	ns
% epidermis	4.9±0.2	12.9	6.9±0.2	10.3	**
% hypodermis	3.4±0.2	14.2	4.9±0.2	13.7	**
% vascular bundles	3.8±0.4	31.8	5.8±0.3	16.6	**
% bundle sheat	3.4±0.3	23.9	4.0±0.2	12.5	ns
% pallisade tissue	6.9±0.3	15.8	8.5±0.4	16.2	**
length of palisade cells (µm)	40.2±2.1	16.5	42.8±1.9	14.1	ns
width of palisade cells (µm)	8.3±0.4	15.1	8.7±0.3	11.7	ns
% water storage tissue	77.4±0.5	2.2	69.9±0.8	3.7	**

*, ** – differences between the localities significant for 0,05 and 0.01 level of significance respectively; ns – differences between the localities not significant

According to the type of variability, examined populations were grouped by PCA (Figure 6). The projection of the cases for the first two components showed that the two examined populations could be clearly separated according to the type of variation of the examined parameters along the first axis. Population from Montenegro showed higher level of homogeneity.

Table 4. Principal components analysis (PCA) of measured parameters. Factor coordinates of the variables, based on correlations and cumulative percentages of the vectors

Anatomical characters		Factor 1	Factor 2	Factor 3
stem	cross section area	-0.83891*	0.333944	0.055640
	% epidermis	0.75443*	-0.536530	-0.016999
	% cortex	-0.53440	-0.786692*	0.026596
	% cylinder	0.44617	0.849792*	-0.024612
	% v.bundles+ sclerenchyma	0.78259*	0.489109	-0.045702
	% pith parenchyma	-0.41126	0.825360*	0.026753
leaf	no. of stomata /mm^2 (adaxially)	0.82459*	0.077839	-0.111648
	stomata length (adaxially)	0.50039	-0.318316	-0.055230
	stomata width (adaxially)	-0.02652	-0.770675*	-0.285822
	no. of stomata /mm^2 (abaxially)	0.53883	-0.023148	-0.352040
	stomata length (abaxially)	0.76060*	0.239433	-0.366002
	stomata width (abaxially)	0.68880	0.149738	-0.523641
	cross section area	-0.88233*	0.252356	-0.022143
	thickness	-0.86765*	0.152934	-0.009624
	cuticle thickness	-0.15584	-0.119269	0.750124*
	% epidermis	0.88851*	-0.035401	0.186393
	% hypodermis	0.83737*	-0.112614	0.079522
	% vascular bundles	0.71987*	-0.020031	0.310511
	% bundle sheat	0.54703	-0.085024	0.606772
	% pallisade tissue	0.71701*	0.133486	0.448626
	length of palisade cells	0.28324	0.299464	-0.134504
	width of palisade cells	0.11422	-0.196672	-0.465631
	% water storage tissue	-0.85029*	-0.010936	-0.168549
cumulative percentages of the vectors		43.51	59.65	69.08

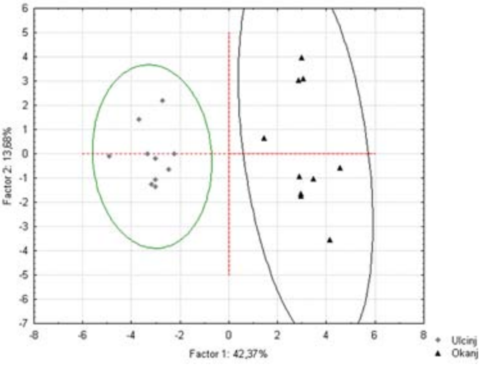

Figure 6. The projection of the cases of the first two components of the Principal Component Analysis

DISCUSION

On the basis of leaf and stem anatomical characteristics of the two examined *S. soda* populations, it could be seen that both of them show a combination of halomorphic and xeromorphic structures.

The ratio of the cortex thickness to stem diameter was 0.352 (Ulcinj salina) and 0.376 (Okanj), which is within the usual values found in xeromorphic stems (Fahn and Cutler, 1992).

The leaf is the organ that reacts the most to external environmental conditions, like those on examined localities (Fahn and Cutler, 1992). This was also proved in our examination. The results of PCA analysis showed that leaf parameters were dominantly present on the first axis and defined the most of the total variability. Therefore, two analyzed populations were clearly separated by PCA analysis along the first axis, mostly based on the variability of leaf anatomical parameters. Different environmental conditions on the two habitats and different types of leaf anatomical responses, induced this high variability.

Compared with the leaf thickness of *Salsola* species from South Africa, as well as *Salsola oreophila* and *Salsola australis*, the two examined populations of *S. soda* have thicker leaves (P'yankov et al., 1997; Klopper and Wyk, 2001).

The presence of a hypodermis is a common feature of many members of the Chenopodiaceae, as well as other *Salsola* species (Solereder, 1908, Carraro et al., 1993, Patrignati et al., 1993). The abundance of calcium oxalate crystals present in the hypodermis, might serve as a protective measure against insects and other small herbivores (Franceschi and Nakata, 2005). They also protected cells from excess calcium, regulate ion balance and help detoxication of the plant. Carolin et al. (1975) stated that presence or absence of a hypodermis appears to have no taxonomic significance in the Chenopodiace, but that statement was not supported by Klopper and Wyk (2001). These authors recorded that presence or absence of a hypodermis has been used to divide *Salsola* species into two main groups.

According to Solereder (1908), Metcalfe and Chalk (1983), Klopper and Wyk (2001), Voznesenkaya et al. (2001), the leaves of *Salsola* species have a thick mesophyll. Our results showed that palisade mesophyll is well developed in both studied populations. The spongy mesophyll is not typical, but is rather characterized by the absence of intercellular spaces. It consists of centrally placed aqueous tissue enclosing the main vascular bundle.

S. soda has so-called "Salsoloid" or Kranz type of photosynthetic cell arrangement (Voznesenkaya and Gamaley, 1986), which can occur in succulent cylindrical leaves. However, some *Salsola* species have different cross-section leaf anatomy. Carolin et al. (1975) described *S. webbii* as lacking Kranz type anatomy and they considered it an example of a reversion to non-Kranz anatomy in *Salsola*. Such features were also recorded in the genus *Sympegma* and were designated as "Sympegmoid" type. These authors defined Sympegmoid as having non-Kranz type anatomy when they observed multiple layers of mesophyll chlorenchyma. P'yankov et al. (1997) gave a hypotheses that reversion process of the Salsoloid Kranz type leaf anatomy from a C_4 to C_3 photosynthesis, in genus *Salsola* was in the first place connected with the reduction of biochemical systems for the C_4 dicarboxylic acid cycle and then with changes in anatomical features of the photosynthetic tissues. Our results showed that *S. soda* from Serbia and Montenegro has Kranz type of photosynthetic cell arrangement.

The inland saline locality in Serbia had significantly lower precipitation and lower percentage of salt in the soil, which induced the formation of certain xeromorphic anatomical adaptations in leaves of the plants from this habitat. These plants had significantly larger proportion of leaf epidermis, hypodermis, palisade and vascular tissue with sclerenchyma, as well as higher number of stomata on both leaf sides. These findings are in accordance with the descriptions of leaf xeromorphic characteristics of plants from dry habitats, given by Fahn and Cutler (1992).

Flowers et al. (1986) gave anatomical features of halophytes which respond to changes in salinity. These authors found that plants that grow on high concentration of salt had relatively small number of stomata per mm^2, thicker leaf and cuticle, larger water storage tissue and lower stelar diameter. Moreover, comparision of halomorphic characteristics of two populations indicated that plants from Montenegro (maritime saline area) had more halomorphic characteristics than plants from Pannonian plane, which could be explained by the higher salinity of the soil in Adriatic coast.

CONCLUSION

In Ulcinj salina (maritime saline area, Montenegro) and Okanj (inland saline area, Serbia) localities, studied populations grow in saline area with longer or shorter intervals of summer drought, which explains xeromorphic and halomorphic characteristics in their anatomical structure. These xeromorphic and halomorphic morpho-anatomical characteristics of two studied populations refer to ecological plasticity and adaptations of plants in their habitats. Beside this, our research has shown that *S. soda* has quite a stable morpho-anatomical structure, since only quantitative changes were recorded.

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СТРУКТУРНЕ АДАПТАЦИЈЕ ВРСТЕ *SALSOLA SODA* L. (CHENOPODIACEAE) СА КОНТИНЕНТАЛНИХ И МАРИТИМНИХ ХАЛОБИОМА

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РЕЗИМЕ: Детаљно упознавање еколошке варијабилности и диференцијације популација унутар врста неопходан услов је за сагледавање биолошког потенцијала врста. У том смислу, одабрана је врста *Salsola soda* фамилије Chenopodiaceae која је присутна и на континенталним (Окањ, Срем) и на маритимним халобиомима (Улцињска солана). Истраживања су обухватила анализу 26 квантитативних карактера листа и стабла. Резултати су показали да биљке и са континенталних и са маритимних халобиома поседују халоморфне и склероморфне карактеристике које им омогућавају да опстану на стаништима са повећаном концентрацијом соли у подлози. Јединке популације са континенталног халобиома имају већи број склероморфних карактеристика, док маритимна популација поседује већи број халоморфних карактеристика. Најважнији анатомски карактери који имају статистички значај у формирању разлика између популација са континенталног и маритимног халобиома су: број стома на адаксијалној страни листа, површина попречног пресека и дебљина листа, процентуални удео површине епидермиса, хиподермиса, ткива за магационирање воде и проводних снопића листа, као и површина попречног пресека и дебљине коре стабла, полупречник стабла, процентуални удео површине епидермиса и проводних снопића стабла. Истраживања су такође показала да врста *S. Soda* има стабилне морфо-анатомске карактере.

КЉУЧНЕ РЕЧИ: анатомија биљака, халофите, лист, Salsola soda, стабло