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Biochemical Conditionality of Differentiation of Halophytes by the Type of Regulation of Salt Metabolism in Prieltonye

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Abstract—The elemental composition and the content of pigments, proteins, lipids, free amino acids, and antioxidants of five wild halophyte species in Prieltonye were investigated. Plants differed in systematic location (Chenopodiaceae, Plumbaginaceae, Asteraceae), the type of regulation of salt metabolism (eu-, cryno-, and glycohalophytes), life form (annual grasses, shrubs), and the water regime (mesoxerophytes, xeromesophytes). A decrease in the ion content of K, Na, Ca among *Suaeda linifolia* > *Salicornia perennans* > *Halocnemum strobilaceum* > *Limonium gmelinii* > *Artemisia santonica* was noted. The reversed pattern was observed for the content of C. The increase in the total content of C in glyco-, cryno-, and euhalophytes was accompanied by an increased content of total and membrane lipids, proteins, and pigments. Halophytes varied considerably in terms of components of the antioxidant system—the content of endogenous proline, soluble protein, and lipid peroxidation and the level of total SOD activity. Cluster analysis revealed that the differentiation of the studied halophyte species by the type of regulation of salt metabolism was mostly determined by biochemical parameters.

Keywords: adaptation, amino acids, proteins, halophytes, saline soil, lipids, pigments

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INTRODUCTION

Plants that are able to carry out the life cycle in soils with high salt content are called halophytes (Genkel', 1982; Lokhande and Suprasanna, 2012). Despite the common name reflecting the attitude to one environmental factor, halophytes are a heterogeneous group of plants, which include representatives of different taxa, life forms, and ecological types of floras (Shamsutdinov et al., 2001). By the ability to accumulate salt in the aerial part, halophytes are divided into "salt-accumulating" (euhalophytes), "salt-excreting" (crynohalophytes), and "salt-resisting" (glycohalophytes) (Genkel', 1982). There are also obligate and facultative halophytes.

Different types of strategies with respect to the accumulation of salts impacted the structure of the vegetable organism of halophytes. For example, succulence is typical for euhalophytes, while glycohalophytes are characterized by xerophytic structure of leaves. Crynohalophytes have an excretory function with the help of specialized salt glands (Voronkova et al., 2008; Dajic, 2006). Euhalophytes are usually characterized by large size of photosynthetic cells, and cryno- and glycohalophytes have much smaller chlorenchyma cells (Jennings, 1968).

Adaptation of halophytes to salinity formed in the course of phylogeny and involves various levels of the organization: molecular, cellular, organismal, population, phytocenotic (Glenn and Brown, 1999; Flowers and Colmer, 2008; Munns, 2008). Currently, it is generally accepted that, in addition to a direct toxic effect, salinity causes osmotic stress in plants due to a sharp drop in water potential of the root-inhabited environment, as well as endogenous oxidative stress, resulting in a change in the conformation and the denaturation of structural and enzymatic proteins (Stroganov, 1962; Smirnoff, 1998). Resistance to osmotic stress is achieved by means of accumulation by plants of compatible inorganic and organic osmolytes, the most important feature of which is nontoxicity for the structure and function of proteins and nucleic acids (Franco and Melof, 2000; Hare et al., 1998). The mechanisms regulating transport of ions from the medium into the cells neutralize the toxic effect. Ions entering the cell at salinization are derived from cytosol using ion pumps (Cheeseman and Wickens, 1986). This type of adaptations is connected to the protective barrier functions of membranes. The barrier function of each membrane depends on its permeability determined by its structure. Lipids play a leading role in the regulation of membrane fluidity—one of the main

conditions for the functioning of proteins, including proteins of transport systems (Sui et al., 2010).

Antioxidant systems of halophytes include a wide range of low molecular weight compounds. A causal link was established between the high activity of antioxidant enzymes and the degree of protection against oxidation disorders caused by salinization of the substrate (Ksouri et al., 2010). Universal components making it possible to stabilize the osmotic potential of the plants and to resist water shortages and toxic effects of excess ions are some amino acids (AA) (Matysik et al., 2002).

Biochemical adaptation, unlike the specialized adaptations at physiological, morphological, and other levels, determines the qualitative and quantitative originality of metabolic functions necessary for functional activity of molecules and energy use (Khochachka and Somero, 1988).

The purpose of this study was to investigate the biochemical basis of differentiation halophytes with different type of regulation of salt metabolism.

MATERIALS AND METHODS

The region of Prieltonye is a part of the Caspian Depression. The climatic conditions of the territory are characterized by a sharp lack of moisture and severe drought, especially in spring and summer. Plants in these conditions in addition to salinization experience the impact of high insolation and temperature for much of the growing season.

As the objects of study, we chose *Salicornia perennans* Willd. (saltwort solonchak), *Suaeda linifolia* Pall. (seablite linear-leaved), *Halocnemum strobilaceum* Bieb. (sarsazan knobbly), *Limonium gmelinii* (Willd.) O. Kuntze (Gmelin statice), and *Artemisia santonica* L. (santonica wormwood).

For biochemical assays, we used the leaves of 15–20 plants collected on experimental plots 20 × 20 m in size within one phytocenosis. Three independent biological samples (2–4 g of fresh weight) were made up of the combined biomass of leaves. The features of selection of plants and soil analysis on the salt content are given in (Rozentsvet et al., 2013). Extraction and analysis of lipids and water-soluble and membrane-bound proteins (WP, MP) in the plant material were performed by the previously described methods (Rozentsvet et al., 2014). The total content of lipids (TL) was calculated as the sum of neutral lipids (NL), glycolipids (GL), and phospholipids (PL) analyzed separately. The intensity of lipid peroxidation (LPO) in plant tissues was determined by the content of thiobarbiture active compounds after reaction with thiobarbituric acid using a PromEkoLab PE-3000 UF spectrophotometer (Russia).

The hydration of tissues was calculated after determination of fresh and dry weight as the ratio of water to dry weight.

The ion content was determined in a dry, shredded material after mineralization of samples (*Metodicheskie ukazaniya...*, 2005) using the method of inductively coupled plasma optical emission spectrometry on a SPECTRO CIROS-CCD device.

The barrier properties of the membranes were evaluated by the degree of release (leakage) of electrolytes (Kholodova et al., 2005). Six to ten excisions were obtained from the leaves. To remove residual cells injured when cutting excisions and outer-membrane (apoplast) tissue content, a 15 min wash of samples in 10 mL of distilled water with shaking was conducted. Next, the samples dried from the surface were quickly transferred to clean bottles containing 10 mL of distilled water at 20°C and incubated for 30 min. The content of electrolytes in this solution characterized the size of the membrane leakage. Electrolytes remaining in the tissues were extracted with another portion of water upon boiling for 5 min, followed by extraction with shaking for at least 1 h. The conductivity of the solutions was measured using a PWT (HI 98 308) conductivity meter (HANNA Instruments, Germany). The measure of membrane leakage was assessed as a percentage of the amount of intracellular electrolyte emerging from the cells after removal of the extracellular content and extracted by boiling.

The pigment content was determined in an acetone extract (90%) on the PromEkoLab PE UF-3000 spectrophotometer (Russia) at λ 662, 645, and 470 nm. For extraction, 0.2–0.5 g of fresh weight of leaves was used. The calculation of the concentration of chlorophylls *a, b* and carotenoids and the fraction of chlorophylls in the light-harvesting complex was carried out by the method of Lichtenthaler (1987).

The activity of superoxide dismutase (SOD) was determined according to the recommendations described in (Beauchamp and Fridovich, 1971).

Free amino acids were determined in the lyophilically dried material after their removal by 70% ethanol on an 400-AAA analyzer (Czech Republic) in the system of lithium buffers.

The analysis of each component was performed three times in each biological sample. The data in the tables and figures are presented as the arithmetic mean with standard error.

RESULTS AND DISCUSSION

We investigated the biochemical properties of the five species of wild halophytes that characterize water and osmotic status, state of membranes, and antioxidant protection of cells. The plants differed in systematic position, life form, attitude to the water regime, and the type of regulation of salt metabolism. Thus, euhalophytes *S. perennans* and *S. linifolia* (family Chenopodiaceae) are annual herbaceous mesoxerophytes and *H. strobilaceum* is a xeromesophyte semishrub. Crynohalophyte *L. gmelinii* (family Plumbaginaceae) is a herbaceous perennial xeromesophyte and

Table 1. Physicochemical characteristics of the soil in the places of growth of plants

Species	Characteristics		
	humidity, %	pH	salinity, % (solid residual)
S. perennans	27.0	8.6	2.0
H. strobilaceum	7.0	8.6	4.2
S. linifolia	23.0	8.7	1.7
L. gmelinii	24.6	8.8	1.6
A. santonica	24.6	8.7	1.6

glycohalophyte *A. santonica* (family Asteraceae) is a xeromesophyte semishrub.

Growing conditions of the studied species of halophytes in the basin of Lake Elton differ mainly in the content and composition of salts and the moisture content in the soil. Analysis of edaphic factors showed that communities with participation of euhalophytes *S. perennans* and *H. strobilaceum* were formed in soils with a stronger salinity (2.0 and 4.2%) than crynohalophyte *L. gmelinii* and glycohalophyte *A. santonica* (1.6%) (see Table 1). However, *H. strobilaceum*, unlike the rest of the studied species, grew on drier soil—with humidity of only 7.0%. The acidity of the soil extract ranged from 8.6 to 8.8, which is characteristic of saline soils in which Na, Ca, K, and Mg displace ions of H.

The main conditions for the survival of any plant under the influence of salinity are resistance to water scarcity and toxic effects of excess ions. The hydration of leaves of the studied halophytes, despite the strong salinity of the soil, was in the range of 73–91%. In annual herbaceous euhalophytes, the moisture content in the aerial part was 89–91%, and in perennial eu-, cryno-, and glycohalophytes, it was 73–76% (see Fig. 1).

The data of elemental composition showed that the Na content in the leaves of euhalophytes was 3 times or more higher than that in cryno- and glycohalophytes (see Table 2). That is, the storage capacity of the plants with respect to the type of ions of Na corresponded to salt accumulation. The content of Ca and K was substantially lower than Na. In this case, the content of K was almost identical in the leaves of all species studied, and the amount of Ca varied from 2.4 to 12.0 mg/g of air-dry pulp. A particularly low content of Ca was observed in *H. strobilaceum*.

The total content of ions of K, Na, and Ca decreased in the series *S. linifolia* > *S. perennans* > *H. strobilaceum* > *L. gmelinii* > *A. santonica*. Ions of Na and K can be used by the cell as inorganic osmolytes to maintain intracellular osmotic homeostasis. In this respect, great osmolarity in salt-accumulating species of halophytes is evident. Ions of Ca, owing to its physical and chemical properties, are capable of forming functionally active complexes being part of structural formations of cells. In particular, ions of Ca form complexes with PL in the lipid layer of non-photosynthetic membranes (Stroganov, 1962).

In the content of C based on the dry weight, the opposite pattern was observed in comparison with metal ions—less content in annual euhalophytes (*S. perennans* and *S. linifolia*—223 and 224 mg) and more in perennials (*H. strobilaceum*, *L. gmelinii*, and *A. santonica*). A negative correlation between the accumulation of Na and content of C in the studied species of halophytes ($r = -0.88$) was revealed. The

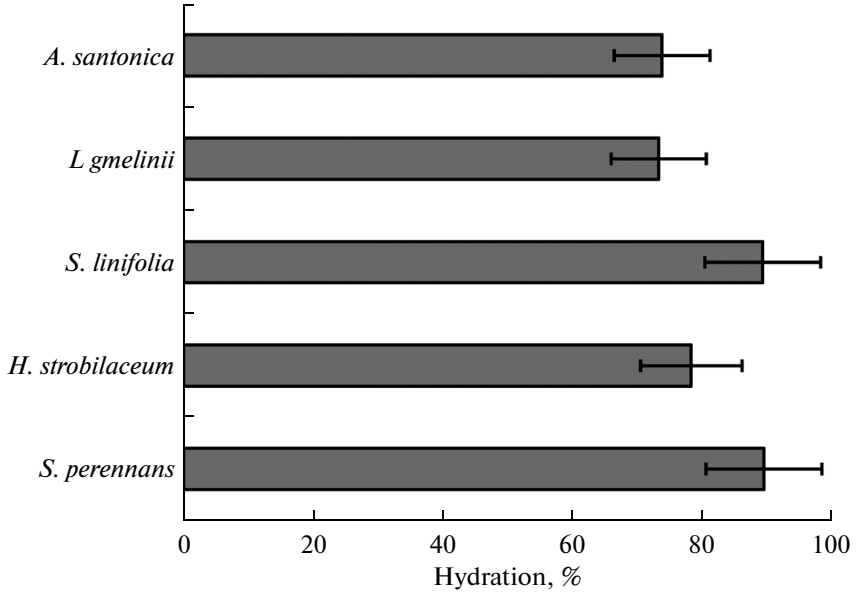

Fig. 1. Hydration of the leaves of halophytes in Prieltonye.

Table 2. Elemental composition of the leaves of halophytes, mg/g of dry weight

Species	Ca	K	Na	N	C	C/N
S. perennans	8.2 ± 2.5	11.0 ± 4.0	140.0 ± 60.0	22.0 ± 4,0	223.0 ± 7.0	10
H. strobilaceum	2.4 ± 0.70	16.0 ± 6.0	120.0 ± 50.0	31.0 ± 2.1	301.0 ± 10.0	10
S. linifolia	9.8 ± 2.9	19.0 ± 8.0	150.0 ± 60.0	14.5 ± 2.6	224.0 ± 7.0	15
L. gmelinii	12.0 ± 4.0	15.0 ± 6.0	37.0 ± 15.0	27.1 ± 1.8	345.0 ± 11.0	13
A. santonica	7.3 ± 2.2	11.0 ± 4.0	40.0 ± 16.0	28.4 ± 1.9	436.0 ± 14.0	15

Table 3. Content of lipids and proteins in the leaves of halophytes, mg/g of fresh weight

Index	*S. perennans*	*H. strobilaceum*	*S. linifolia*	*L. gmelinii*	*A. santonica*
GL	0.5 ± 0.1	1.3 ± 0.1	1.2	2.8 ± 0.1	5.1 ± 0.1
PL	0.5 ± 0.1	2.0 ± 0.4	0.9	2.2 ± 0.1	2.2 ± 0.1
NL	0.7 ± 0.1	1.5 ± 0	0.9	0.9 ± 0.1	7.1 ± 0.1
TL	1.7 ± 0.2	4.8 ± 1.0	3.0 ± 0.6	5.9 ± 1.0	14.4 ± 2.0
GL/PL	1.0	0.6	1.3	1.3	1.4
MP	2.5 ± 0.2	3.8 ± 0.3	2.0 ± 0.2	3.0 ± 0.2	12.0 ± 0.8
WP	4.4 ± 0.4	11.7 ± 0.6	10.0 ± 0.7	12.2 ± 0.8	23.5 ± 4.5
WP/MP	1.8	3.1	5.0	4.1	4.6
MP/NL	2.5	1.1	0.9	0.5	1.6

WP—water-soluble proteins, GL—glycolipids, MP—membrane-bound proteins, TL—total lipids, PL—phospholipids, NL—neutral lipids.

content of N in the leaves, as well as of C, depended on the life forms of plants with high content in perennials *H. strobilaceum*, *L. gmelinii*, and *A. santonica*. Increased content of N in plant leaves is sometimes associated with the content of photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase in plants compared with C_3 and C_4 type of photosynthesis, the content of which is about 75% of organic nitrogen of leaves (Evans, 1989). However, the test plants are plants with C_3 type of photosynthesis, which gives reason to believe that differences in the content of N were related to species characteristics. In the scientific literature, it was indicated that more informative is the ratio C/N (Ivanov, 2001). In our study, this figure ranged from 10 to 15 and was not associated with differences in the type of regulation of salt metabolism or in the form of plant life.

One of the first responses of the cell to the effects of stress abiotic factors is associated with the processes of lipid peroxidation (LPO). Analysis of the content of malondialdehyde (MDA)—the end product of LPO—showed that, in leaves of *L. gmelinii* and *A. santonica*, LPO processes occur two or more times more intensely than in leaves of *S. perennans*, *S. linifolia*, and *H. strobilaceum* (see Fig. 2a).

Let us note high ($r = -0.99$ at $p = 0.01$) negative correlation between the content of Na and LPO in the plants. The release of electrolytes from leaf cells of euhalophytes was 35–40% higher than that of cryno- and glycohalophytes (see Fig. 2b). In general, membrane systems of the studied halophytes are highly resistant to the damaging effect of salt—the degree of damage to membranes did not exceed 15% (see Fig. 2b). It was found that the content of C in the leaves of halophytes correlated ($r = -90$ at $p = 0.04$) with membrane permeability of cells. Thus, for the species *L. gmelinii* and *A. santonica*, we noted low membrane permeability and a higher amount of C against the background of low content of Na. We assumed that higher content of C in the leaves of *L. gmelinii* and *A. santonica* is associated with the intensity of synthesis and accumulation of organic matter, including the structural components of the membranes. This assumption was confirmed by analysis of the composition of lipids and proteins (see Table 3).

The content of TL in the leaves of halophytes can be described by a descending series: *A. santonica* > *L. gmelinii* > *H. strobilaceum* > *S. linifolia* > *S. perennans*, respectively, from 14.4 to 1.7 mg/g of fresh weight. In the same sequence, the total content of membrane GL and PL changed. Cryno- and glycohalophytes are characterized by predominance of GL constituting photosynthetic membranes, which is typical of the majority of higher plants of glycophytes. For true halophytes *S. perennans*, *S. linifolia*, and *H. strobilaceum*, there was established larger or equal content of PL—components of outer chloroplast membranes

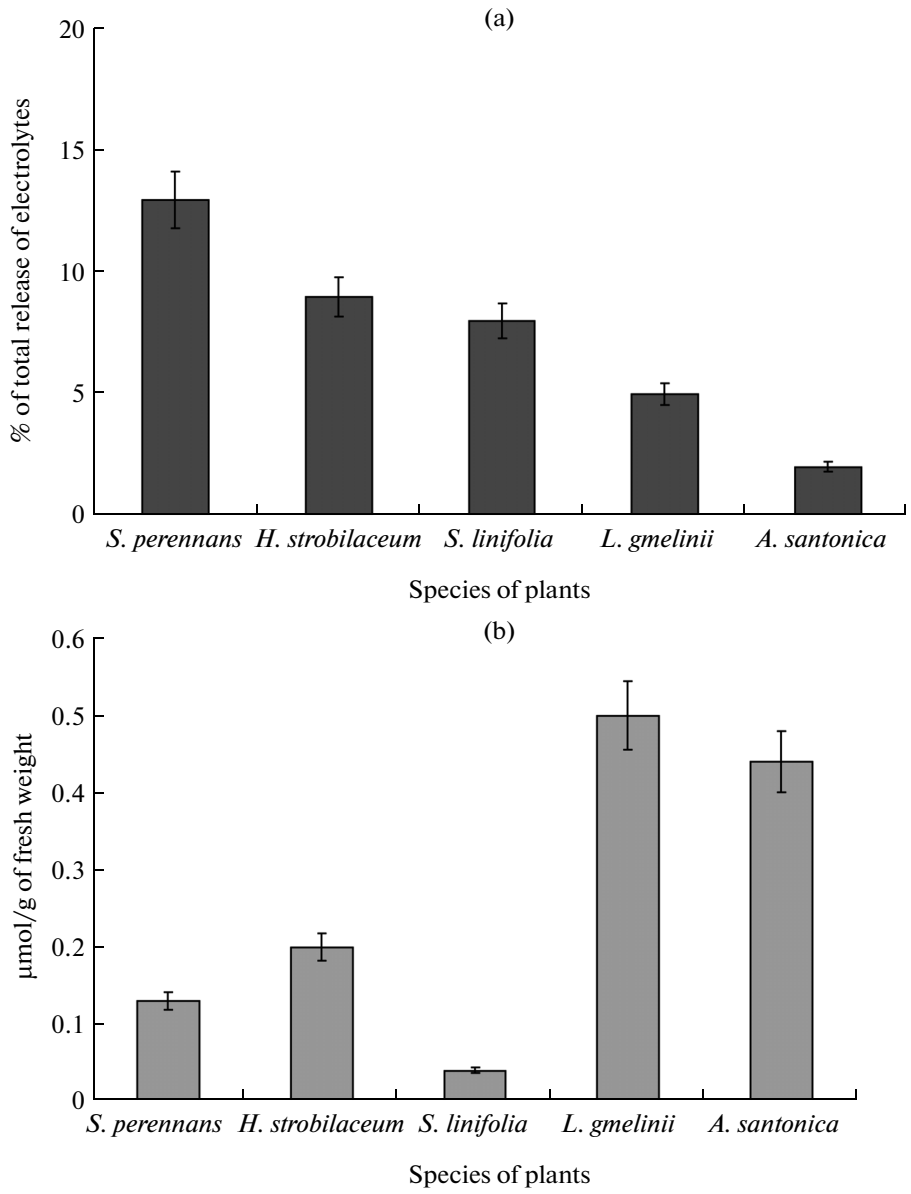

Fig. 2. Release of electrolytes from the cells (a) and MDA content (b) in the leaves of halophytes in Prieltonye.

and GL. In addition, in the leaves of *A. santonica* and *L. gmelinii*, a large amount of spare NL was found.

Analysis of the protein content showed that plants *A. santonica*, in comparison with the other species investigated, contain significantly more WP and MP. In a smaller quantity, proteins were found in plants *L. gmelinii* and *H. strobilaceum*. The minimum quantities of MP and WP are marked in the leaves of the species *S. perennans* and *S. linifolia*. Thus, euhalophytes, except for *H. strobilaceum*, contained fewer WP and MP in the leaves than crynohalophytes and glycohalophytes.

A more detailed study of the composition of individual MB showed that glycophyte *A. santonica* and crynohalophyte *L. gmelinii* have a relatively low content of phosphatidylethanolamines (PE) (not more than 6%) and high content of phosphatidylglycerol (PG) (20%) compared with euhalophytes (9–12 and 10–16% of the amount of PL, respectively) (see Fig. 3).

PG is the only phosphorus-containing lipid which is localized in the thylakoid membranes (Andrews et al., 1985). It is known that, under oxidative stress, the synthesis of PG can increase (Wallis and Browse, 2002). A higher content of PG can be seen as an adaptive response of the lipid components of cryno- and glycohalophytes aimed at stabilizing the photosynthetic apparatus. Thus, just in *L. gmelinii* and *A. santonica*, compared with euhalophytes, at high levels of PG content, high values LPO were also observed. Fur-

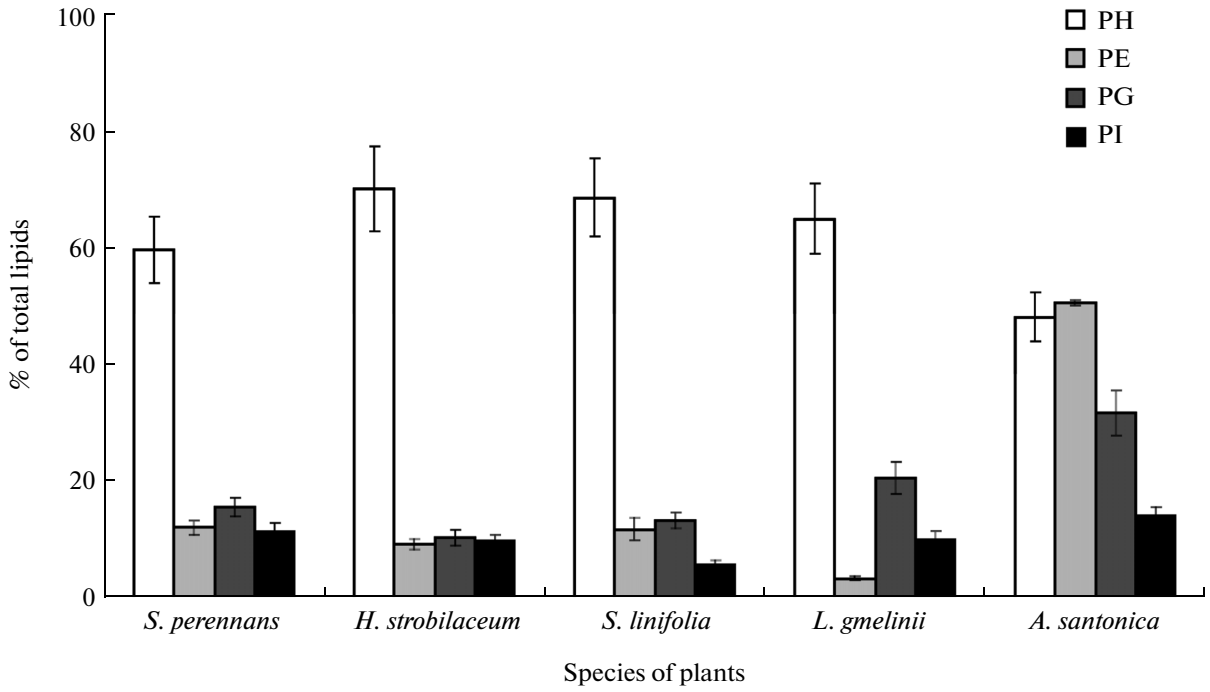

Fig. 3. Content of individual phospholipids in the leaves of halophytes in Prieltonye.

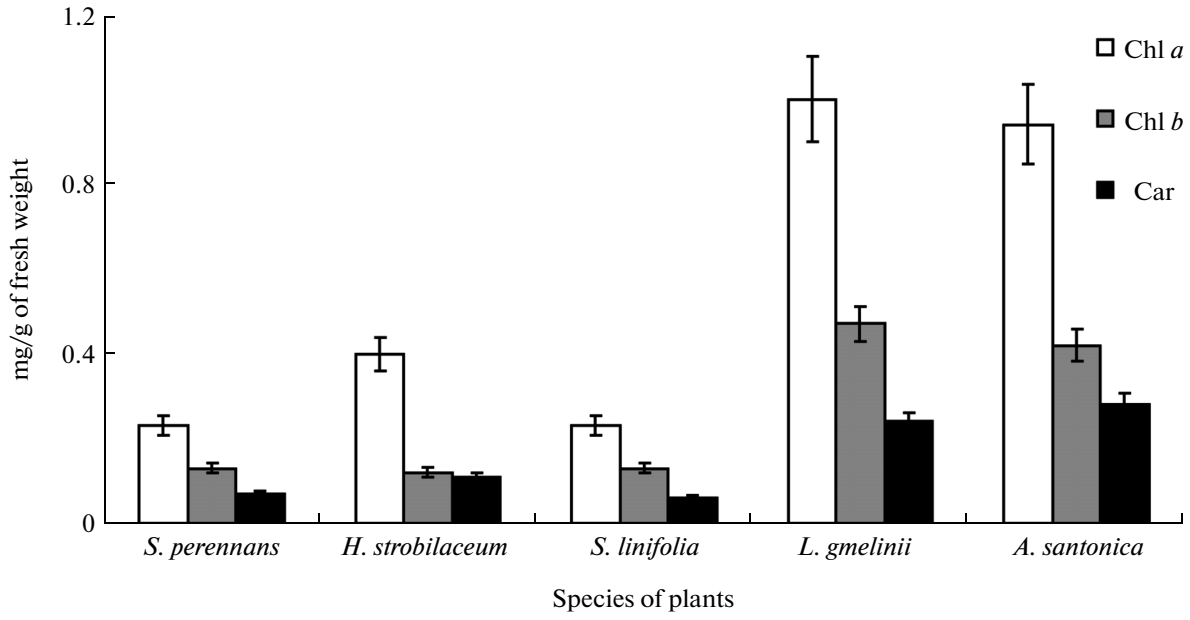

Fig. 4. Content of pigments in the cells in the leaves of halophytes in Prieltonye.

thermore, according to modern concepts, PG is an essential lipid for the structural organization of the reaction centers and antenna complexes of photosystems (Yu and Benning, 2003). Analysis of the pigment resources integral to the photosynthetic membranes showed that the content of green and yellow pigments was two times or more higher in leaves of cryno- and glycohalophytes compared to euhalophytes (see Fig. 4). Accordingly, a higher content of PG was observed in plants which have higher levels of pigment.

Hence, the increase in the total content of C in the series of glyco-, cryno- and euhalophytes is accompanied by the increased content of total and membrane lipids, total and membrane proteins, and pigments ($r = 0.87$ with $p < 0.05$). That is, the differentiation of

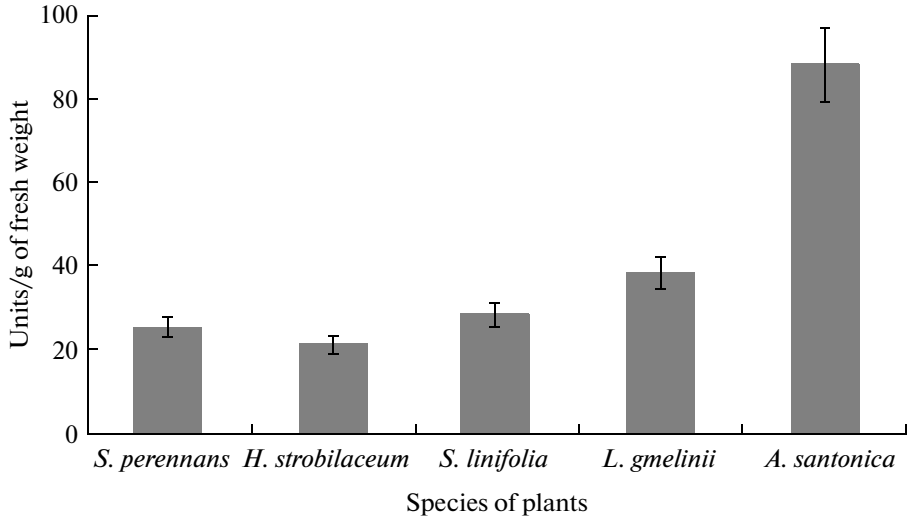

Fig. 5. SOD activity in the leaves of halophytes in Prieltonye.

halophytes with respect to the parameters characterizing the structure of the membrane and photosynthesis is obvious.

It should be noted that many of the adaptive features that lead to resistance of plants to salinity are inducible. For example, individual components of WP are responsible for the protection against oxidative stress (Orlova et al., 2007). Thus, a thylakoid-bound SOD is considered to be responsible for the neutralization of photogenerated superoxide radicals in the vicinity of photosystem II. The data on the SOD activity show that the greater activity is shown in glyco- and crynohalophytes compared to euhalophytes (see Fig. 5). The increase in SOD activity was correlated with the increase in MDA, which confirms the compensatory role of water-soluble proteins in response to activation of LPO processes characteristic of cryno- and glycohalophytes.

Similar results were obtained for *Crithmum maritimum*—increased activity of SOD in parallel with the increase in the intensity of LPO with the rise of exposure to NaCl (Ksouri et al., 2010).

Given that one of the resistance mechanisms of halophytes is a resistance to osmotic stress, the content of free AA was studied. The number of free AA depended on the type of plant: the leaves of euhalophytes *H. strobilaceum*, *S. salsa*, and *S. perennans* contained 0.9–1.5 mg/g of dry weight; the leaves of crynohalophyte *L. gmelinii* contained 1.2 mg/g of dry weight; and the leaves of glycohalophyte *A. santonica* contained 4.8 mg/g of dry weight (see Table 4).

Four non-proteinogenic acids were detected: cystathionine, β-alanine, ornithine, γ-aminobutyric acid. Participation of non-proteinogenic acids in the total pool of free AA in a glycohalophyte is 2.4%; in a crynohalophyte, 32%; and in euhalophytes, 15–27%. Stress AA, which include alanine, phenylalanine, γ-aminobutyric acid, and proline (Franco and Melof, 2000; Hare et al., 1998), were in the cells of euhalophytes 54–71%, in the cells of a crynohalophyte 71%, and in the cells of a glycohalophyte 88% of the sum of AA. In the composition of free AA of glycohalophyte *A. santonica*, proline dominates (82%), while in euhalophytes and a crynohalophyte a significant part of "stress" AA is represented by alanine and γ-aminobutyric acid. Furthermore, eu- and crynohalophytes stored more tyrosine and phenylalanine—AA of the shikimate pathway, which are precursors of many phenolic compounds having antioxidant properties and involved in processes lignification of cells.

In the literature, there is a large amount of indirect evidence that proline has antioxidant properties, which is associated with its ability to stabilize the structure of proteins and membranes owing to the formation of hydrophilic walls, which in turn prevents the inactivation of proteins by hydroxyl radicals and singlet oxygen (Matysik et al., 2002). Perhaps, vegetation of a glycohalophyte in conditions of salinity induces the accumulation of proline, since accumulation of sodium and proline is positively correlated.

It should be noted that halophytes varied considerably in the level of components of the antioxidant system. Thus, plants differ by an order of magnitude in the contents of endogenous proline, soluble protein, and LPO and the level of total SOD activity. This indicates that the contribution of the components in the antioxidant defense is not equal and depends on the plant species. There are expressed reciprocal relationships between some antioxidant reactions, which are most clearly visible between the level of proline and the release of electrolytes.

When analyzing the biochemical characteristics of the plant species studied, their differentiation was

Table 4. Content of free amino acids in the leaves of halophytes, mg/g of dry weight

Amino acids	*S. perennans*	*H. strobilaceum*	*S. linifolia*	*L. gmelinii*	*A. santonica*
Aspartic	45 (3.0)	14 (1.6)	6 (0.7)	0	82 (1.7)
*Proline	271 (18.1)	155 (17.3)	270 (32.2)	147 (12.1)	3941 (81.7)
Glycine	19 (1.3)	23 (2.6)	8 (1.0)	46 (3.8)	21 (0.4)
*Alanine	376 (25.2)	225 (25.1)	139 (16.6)	377 (30.9)	214 (4.4)
Valine	78 (5.2)	72 (8.0)	99 (11.8)	81 (6.6)	174 (3.6)
Cystathionine	151 (10.1)	76 (8.5)	6 (0.7)	35 (2.9)	56 (1.2)
Isoleucine	0	0	27 (3.2)	0	0
Leucine	53 (3.5)	63 (7.0)	17 (2.0)	32 (2.7)	19 (0.4)
Tyrosine	33 (2.2)	39 (4.3)	26 (3.1)	39 (3.2)	9 (0.2)
*Phenylalanine	56 (3.7)	51 (5.7)	21 (2.5)	35 (2.9)	27 (0.6)
B-alanine	39 (2.6)	0	0	39 (3.2)	0
* γ-aminobutyric	189 (12.6)	50 (5.5)	172 (20.5)	310 (25.4)	47 (1.0)
Ornithine	19 (1.3)	6 (0.7)	16 (1.9)	9 (0.7)	6 (0.2)
Lysine	25 (1.7)	47 (5.2)	12 (1.4)	20 (1.6)	21 (0.4)
Histidine	19 (1.3)	32 (3.6)	8 (1.0)	23 (1.9)	30 (0.6)
1-methylhistidine	17 (1.1)	0	0	0	0
3-methylhistidine	0	0	3 (0.4)	0	0
Arginine	106 (7.1)	45 (4.9)	8 (1.0)	26 (2.1)	175 (3.6)
ΣSAA	892 (59.6)	481 (53.6)	602 (71.8)	869 (71.3)	4229 (87.7)
ΣAA	1496 (100)	898 (100)	838 (100)	1219 (100)	4822 (100)

* Stress amino acids; ΣSAA—sum of stress amino acids; ΣAA—sum of amino acids; in parentheses, % of sum of amino acids.

found according to the type of regulation of salt metabolism (see Fig. 6).

According to the content of lipids, proteins, pigments, AA, etc., herbaceous annual euhalophytes *S. perennans* and *S. linifolia* were united into one cluster and differ from perennial euhalophyte *H. strobilaceum*. However, these types are closer to each other than to crynohalophyte *L. gmelinii*. In turn, the species *L. gmelinii* is separated from euhalophytes and from glycohalophyte *A. santonica*, which has the least resemblance to euhalophytes. Thus, biochemical differentiation of the studied species of galophytes coin-

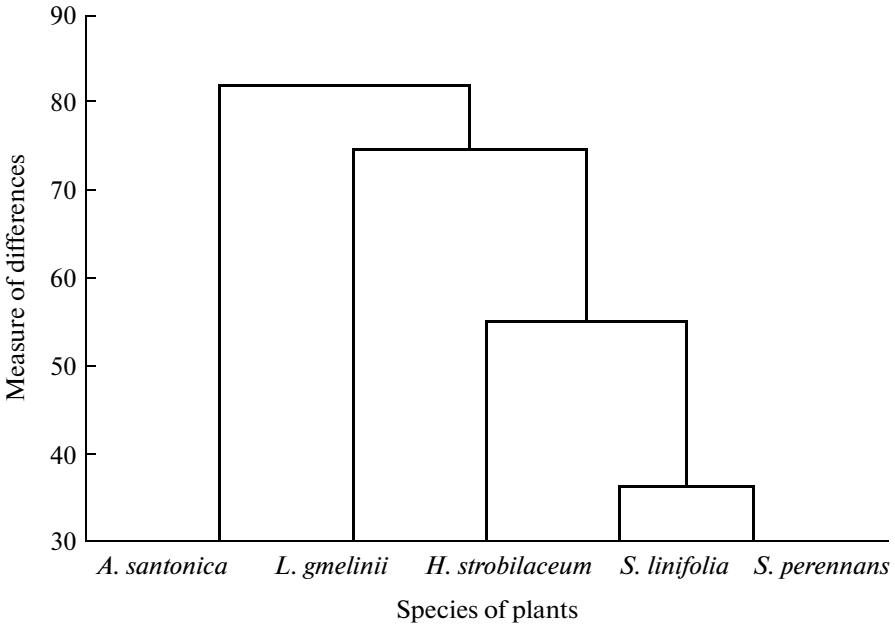

Fig. 6. Degree of relationship of biochemical signs of halophytes in Prieltonye according to the cluster analysis.

cides with the type of regulation of salt exchange, which means active and specific inclusion of lipids, pigments, and proteins of cells in mechanisms of adaptation of euhalophytes, crynohalophytes, and glycohalophytes to extreme environmental conditions, in particular, to a high level of soil salinity.

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