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Membrane-forming lipids of wild halophytes growing under the conditions of Prieltonie of South Russia

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ABSTRACT

The composition of membrane-forming lipids has been examined for 10 wild halophyte species growing in southern Russian on alkaline soil. The plants belong to seven taxa of family rank: by their life form, which are semi-shrubs, herbaceous annuals, and perennial plants; their salt tolerance, which are classified as the euhalophytes, crynohalophytes, and glycohalophytes; and by their sensitivity to water, classifications of mesoxerophytes and xeromesophytes. Parallels have been found between the lipid composition and the ecological status of the plants. It has also been revealed that the similarity in the glyco- and phospholipid composition of different plant groups relates to the water factor and the type of salt accumulation, respectively. The fatty acid compositions of the examined plants is determined at the species level.

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1. Introduction

Halophytes comprise an ecological–physiological group of plants with high biological potential to resist salinisation (Lokhande and Suprasanna, 2012; Parida and Das, 2005). The halophytes of wild flora are used as a source of medicinal and oily raw material and as biomeliorative agents in agricultural practice in arid territories (Ashfar and Harris, 2004; Kirichenko et al., 2008; Rahdari and Hoseini, 2011; Wang et al., 2011; Weber et al., 2007).

Halophytes are extremely diverse in their ecological, physiological–biochemical, morphological, and anatomical properties. Depending on the type of salt accumulation in the plant tissues, halophytes are classified as euhalophytes, crynohalophytes, and glycohalophytes (Strogonov et al., 1989). The differences in morphological and anatomical features relate to the presence or absence of leaf salt glands, xeromorphic, or succulent type of leaf structure and, in some species, to the Kranz anatomy of chlorenchyma cells (Shepherd et al., 2005; Voznesenskaya et al., 2007).

Abbreviations: Al, alcohols; DAG, diacylglycerols; DGDG, digalactosyl diacylglycerol; ES, steryl esters; FA, fatty acids; FFA, free fatty acids; FAME, fatty acid methyl esters; GL, glycolipids; MGDG, monogalactosyl diacylglycerol; NL, neutral lipids; PA, phosphatidic acid; PL, phospholipids; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; DPG, diphosphatidylglycerol; ST, sterols; SQDG, sulfoquinovosyl diacylglycerol; TAG, triacylglycerols; TLC, thin-layer chromatography; USFA, unsaturated fatty acids.

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According to modern views, tolerance of plants to soil salinisation is based on the following mechanisms: (1) accumulation or exclusion of ions (Strogonov et al., 1989); (2) control for the uptake of ions by roots and their transport into leaves (Balnokin et al., 2005); (3) compartmentalisation of ions at the cellular level or entire plant (Glenn and Brown, 1999; Lv et al., 2012); (4) synthesis of compatible soluble compounds (Kreslavsky et al., 2007); (5) change of the photosynthetic rate (Sivakumar and Panneerselvam, 2011); and (6) induction of the synthesis of antioxidant enzymes and hormones (Guan et al., 2011; Sivasankaramoorthy et al., 2011). The salt adaptation of higher plants is often noticeable at the cellular level (e.g., plant cells may react to a salt stress by increased vesiculation of plasma membranes and tonoplasts or by an increased level of rough endoplasmic reticulum) (Hirayama and Mihara, 1987). The membrane lipids and transport proteins play a fundamental role in the regulation of membrane permeability and trigger responses to the primary effect of salinity (Lopez-Perez et al., 2009).

It is known that the membranes of halophytes and glycophytes were shown to differ by the content of lipids of certain classes (Hirayama and Mihara, 1987; Wu et al., 2005) and by the fatty acid (FA) composition, especially by the content of FA with more than 20 carbons (Ivanova et al., 2009). Many studies have shown that in response to increasing concentrations of sodium chloride (NaCl) in the medium, lipid content of free sterols (FS) (Kerkeb et al., 2001; Wu et al., 2005), the ratio of sterols (ST) to phospholipids (PL) (Lüttge, 1993; Mansour et al., 2002), the content of phospho-

tidylcholine (PC) and phosphatidylethanolamine (PE) in the plasma membrane (Blits and Gallagher, 1990; Brown and Dupont, 1989), and the total content and individual glycolipids (GL) in the lipid pool (Okonenko et al., 2011) are affected.

In this paper, we investigate the features of membrane lipids of wild halophytes depending on the systematic position, life form, and type of salt accumulation. The region of study, Prieltonie, is characterised by soil salinisation, which resulted in the formation of brackish and solonchic soils.

2. Results and discussion

The halophyte species studied belong to the phylum Magnoliophyta, class Magnoliopsida and represent three orders, three families, and seven genera (Table 1). Nine out of 10 species are obligate halophytes, which can only be found in saline ecotopes, and one species (*Artemisia santonica*) is a facultative halophyte, which adapts to salinisation or its absence. The life forms of the halophytes studied are semi-shrubs, annual, and perennial herbs. The largest group in our study was the euhalophytes. According to the ecological regime related to the water factor, all the species examined were divided into xeromesophytes and mesoxerophytes (on the basis of our own observations).

In the euhalophyte group, water content varied from 70% to 86% of fresh weight and in glycohalophytes and crynohalophytes from 40% to 72% (Fig. 1). Therefore, euhalophytes were characterised by higher water content of plant tissues compared with glyco- and crynohalophytes.

The total lipid content in the leaves varied from 15 to 90 mg g⁻¹ dry weight (Fig. 2). Polar lipids (PL and GL) amounted to 54–70% of total lipids in euhalophytes, 62% and 84% in semi-shrubs, and 60–75% in perennial crynohalophytes. The highest percentage of membrane lipids in the total lipid pool was observed in the euhalophyte *Halocnemum strobilaceum* (84%) and crynohalophyte *Limonium gmelinii* (75%). As expected, dominating among polar lipids were GL. An especially high content of GL was registered in the euhalophyte *A. santonica*, which can be related to a large number of thylakoids or chloroplasts in this plant (and, correspondingly, a large network of photosynthetic membranes, for which GL are major structural components).

It is known that, apart from GL and PL, membranes contain ST which, being incorporated in the membrane bilayer, can regulate its fluidity and thereby affect the functions of membrane-bound proteins: enzymes, channels, receptors, or components of the signal transduction system (Schaller, 2004). Analysis of the PL/ST ratio showed that it was 3.9–5.6 and 4.4–5.4 in the *Suaeda* and *Limonium* plants, respectively, and 2.2–3.7 in other species (Fig. 3). The role of free ST in the tolerance of plants to salts was investigated quite thoroughly. For example, the PL/ST ratio is used as an indicator

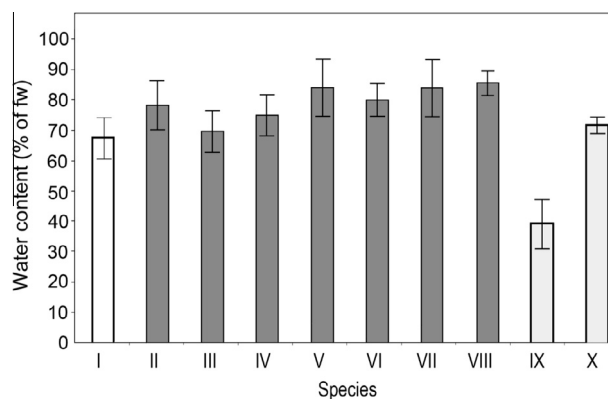


Fig. 1. The water content in overground part of halophyte (mg g⁻¹ fw): I – *Artemisia santonica*; II – *Halocnemum strobilaceum*; III – *Halimione verrucifera*; IV – *Petrosimonia oppositifolia*; V – *Salicornia perennans*; VI – *Suaeda acuminata*; VII – *Suaeda linifolia*; VIII – *Suaeda salsa*; IX – *Limonium caspium*; X – *Limonium gmelinii*.

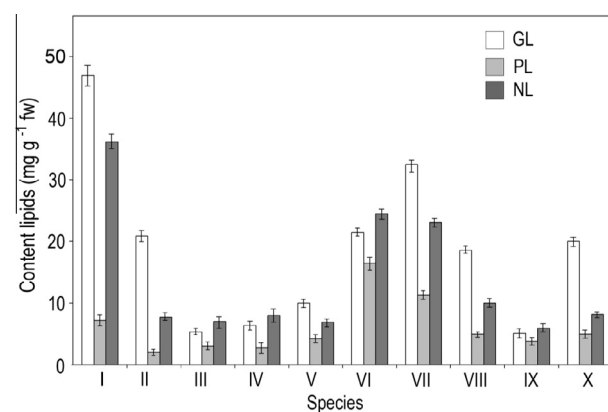


Fig. 2. The content of glycolipids (GL), phospholipids (PL), and neutral lipids (NL) in overground part of halophytes (mg g⁻¹ fw). I to X – species.

of the plant sensitivity to salt treatment. The plasma membrane vesicles isolated from calli of salt-tolerant tomatoes had a lower PL/ST value than those of salt-sensitive species (Kerkeb et al., 2001). The content of ST in the plasmalemma of *Spartina patens* callus cells (Wu et al., 2005) and the ST/PL ratio in the plasma membrane of wheat root cells (Mansour et al., 2002) were shown to rise as the concentration of NaCl in the medium increased. It is believed that a high value of ST/PL in the plasma membrane helps to maintain integrity and structure of the membrane bilayer but decreases its permeability. It seems that plant species of genera *Suaeda* and *Limonium* have more rigid and, hence, less-permeable membranes.

Table 1
The systematic and environmental classification of wild halophytes.

Taxon				Life-form	Ecological group in relation to factors	
Order	Family	Genus	Species		Soil salinity	Moisture
Asterales	Asteraceae	<i>Artemisia</i>	<i>Artemisia santonica</i>	Semishrub	Glycohalophyte	Xeromesophyte
Caryophyllales	Chenopodiaceae	<i>Halocnemum</i>	<i>Halocnemum strobilaceum</i>	Semishrub	Euhalophyte	Xeromesophyte
		<i>Halimione</i>	<i>Halimione verrucifera</i>	Annual herbs	Euhalophyte	Xeromesophyte
		<i>Petrosimonia</i>	<i>Petrosimonia oppositifolia</i>	Annual herbs	Euhalophyte	Xeromesophyte
		<i>Salicornia</i>	<i>Salicornia perennans</i>	Annual herbs	Euhalophyte	Mesoxerophyte
		<i>Suaeda</i>	<i>Suaeda acuminata</i>	Annual herbs	Euhalophyte	Mesoxerophyte
		<i>Suaeda eltonica</i>	Annual herbs	Euhalophyte	Mesoxerophyte	
		<i>Suaeda linifolia</i>	Annual herbs	Euhalophyte	Mesoxerophyte	
		<i>Suaeda salsa</i>	Annual herbs	Euhalophyte	Mesoxerophyte	
		<i>Limonium</i>	<i>Limonium caspium</i>	Perennial herbs	Crynohalophyte	Xeromesophyte
			<i>Limonium gmelinii</i>	Perennial herbs	Crynohalophyte	Xeromesophyte

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