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## **Adaptive strategy of halophytic plants *Polygonum maritimum* and *Euphorbia paralias***

*Presented by Corresponding Member of the NAS of Ukraine Ya. P. Didukh*

*The leaf surface microstructure, pigments spectrum, phytohormones content, and lipids composition of halophytes with various metabolic and physiological strategies of adaptation to salinity of *Polygonum maritimum* L. and *Euphorbia paralias* L. grown under natural conditions on dunes of the Pomorie Lake (Bulgaria) are compared. *P. maritimum* stomata are located on the leaf both sides below the cuticle level, whereas, in *E. paralias*, stomata are present only on the abaxial side, and they are surrounded with hump-shaped cuticle constructions. A high amount of carotenoids (as compared with chlorophylls) in *P. maritimum* leaves indicates that these pigments have a light-collecting function and could transfer an additional energy to chlorophylls. In leaves of *E. paralias* and *P. maritimum*, free abscisic acid and conjugated indole-3-acetic acid prevailed. The inactive cytokinins (cis-zeatin and zeatin-O-glucoside) dominated in *E. paralias* leaves, whereas *P. maritimum* leaves contained a significant quantity of isopentenyl-type cytokinins. The presence of a large amount of saturated fatty acids provides a decrease of membrane permeability and better resistance against soil salinity. It is concluded that the ecological strategy of halophytes involves the complex of structural and functional adaptations and determines a successful existence under salinity conditions.*

**Keywords:** *Euphorbia paralias* L., *Polygonum maritimum* L., microstructure, photosynthetic pigments, phytohormones, lipids.

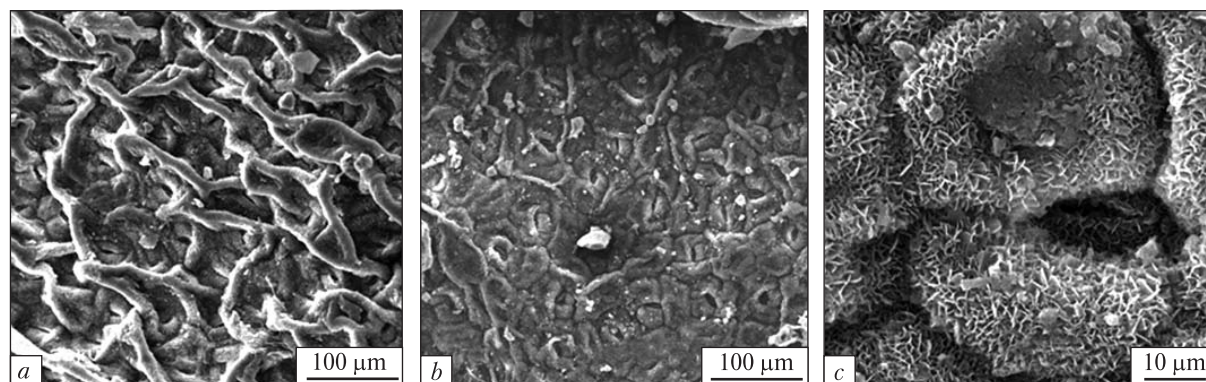
Soil salinity is one of the major ecological factors that limit plant growth and productivity. High concentrations of salt ions are known to cause disturbances in cell division, disintegrate the cytoplasm membrane structure, inhibit enzyme activity, have a negative effect on carbon assimilation, absorption of mineral nutrients, etc. Adaptation to the existence in saline soils results from the implementation of various metabolic and physiological strategies. It occurs at the different hierarchy levels from the molecular to population one. Halophytes are a heterogeneous group of plants that unites representatives of various taxa, living forms, and ecological types. Thus, euhalophytes accumulate salts in the middle of the plant. Krinohalophytes, on the contrary, remove salts

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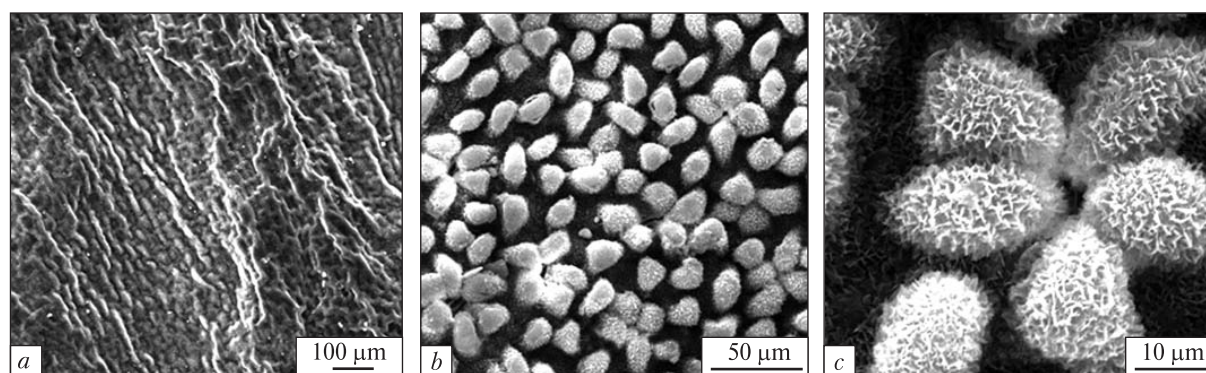
out, while glycohalophytes are salt-impermeable. Existence in saline soils affected the halophyte phenotypic characteristics. Succulence is typical of euhalophytes, whereas glycohalophyte leaves have a xeromorphic structure. Krinohalophytes excrete salts through special salt glands. Euhalophytes are characterized by a great size of photosynthesizing cells, while chlorenchyma cells are much smaller in krino- and glycohalophytes. A successful adaptation to the environment depends substantially on the optimal functioning of the assimilation machinery, and indicators of its state are the photosynthetic pigments content and ratio and the chloroplast ultrastructure [1]. The photosynthetic apparatus efficiency depends on the compliance of its structural and functional characteristics with climatic and ecological conditions. Plants salt tolerance is regulated by phytohormones. The contents of endogenous abscisic acid (ABA), indole-3-acetic acid (IAA), and cytokinins are changed under salinity. The salt-tolerant crops varieties and halophytes differ in their hormonal balance from non-tolerant plants and glycophytes. The treatment of plants with exogenous ABA and cytokinins has a positive effect on salt tolerance, which is associated with maintaining a certain content of endogenous phytohormones [2]. However, exact functions of different phytohormones in mechanisms of halophytes survival and growth under salinity and their connections with morphological features and pigments content are not established. A widespread cation of the salt stress is  $\text{Na}^+$  that is toxic to plants. Permeability of the plasmatic membrane – the first barrier on the way of  $\text{Na}^+$  – depends on the lipid bilayer state that is conditioned by the ratio between sterols and phospholipids and the saturation of fatty acid residuals [3].

Moreover, the majority of researches focus on the study of the salt tolerance of glycophytes and facultative halophytes, whereas the peculiarities of plants that have different mechanisms of adaptation to salt effects are almost unstudied. The aim of our study was to examine the microstructure of the leaf surface, pigment spectrum, phytohormonal balance, and lipids composition of euhalophyte *Euphorbia paralias* L. and glycohalophyte *Polygonum maritimum* L. that grow under natural conditions. We suggested that the adaptation strategy formation in halophytes involves the complex of structural and functional reconstructions that cover specific features in all above characteristics and determine a successful plant existence under salinity.

**Material and methods.** We studied halophyte plants *Polygonum maritimum* L. and *Euphorbia paralias* L. that grew on dunes under natural conditions of the Pomorie Lake (Bulgaria), whose high salinity (60–80 %) contributed to the formation of a unique ecological environment. The glycohalophyte *P. maritimum* (sea knotgrass) is a perennial herb characterized by an increased salt content and high cell pressure that enable it to absorb moisture from rather concentrated soil solutions. It occurs in the Mediterranean region and is also found in Northern England and on Channel Islands. Its 50 cm long trailing stalk is weak and xeromorphic, grew. The euhalophyte *E. paralias* (sea spurge) is a 25–70 cm long (sometimes, its length reaches 100 cm) perennial herb, hemicryptophyte is adapted to saline soils and tolerant to salty water splashes effects. It has a long branchy root, 3–5 mm long stalk, relatively numerous, strong, upright leaves. Leaves and shoots color is bluish-green, stalk lower parts often redden. *E. paralias* leaves are assidenous, naked, no dissected 30 mm long, 15 mm wide. Leaf shape in the lower stalk part is prolate-ellipsoidal with a blunt tip, and there is lanceolate with a sharp tip above that part. The species is widespread in Western Europe and the Mediterranean. The samples of plants were collected in August 2015 from the sand dunes near the Pomorie Lake (soil salinity was 330–350 mg of salts per 100 g of soil). The average temperature of air was 25–28 °C. The plants were collected during the flowering



**Fig. 1.** Microstructure of the leaf lamina adaxial surface in *P. maritimum* (a); Microstructure of the leaf lamina abaxial surface (b); Stomata pores on the leaf lamina abaxial surface (c)



**Fig. 2.** Microstructure of the leaf lamina adaxial surface in *E. paralias* (a); Microstructure of the leaf lamina abaxial surface (b); Stomata pores surrounded by hump-shaped cuticle constructions on the leaf lamina abaxial surface (c)

phase. Plant material for the scanning electron microscopy was fixed in 70° ethanol. Fixed samples were dehydrated in ethanol solutions at increasing concentrations. Following the treatment with absolute alcohol, samples were placed on brass objective tables and adhered there using adhesive tape, kept there for some time to reach an air-dry condition, and covered with a layer of gold in the ion coating chamber to provide conductivity. The surfaces of *P. maritimum* and *E. paralias* leaves are studied by means of a scanning electron microscope JEOL JSM-6060 LA. Structure dimensions on microphotographs were measured using the program ImageJ 1.49v, involving a scale bar set up by the instrument on pictures. Photosynthetic pigments were extracted with 80 % aqueous acetone [4]. Spectra were recorded using a spectrophotometer Specord M-40. For lipid analysis, small peaces from the aerial parts were extracted consecutively with chloroform—methanol (2 : 1) to obtain the total lipophilic extracts. The isolation of the main lipid classes and the analysis of their fatty acid composition were performed using thin-layer and gas chromatographic techniques [5]. Extraction of hormones and determination of free and conjugated forms of ABA, IAA, and cytokinins were performed according to the method in [6]. Qualitative and quantitative analyses

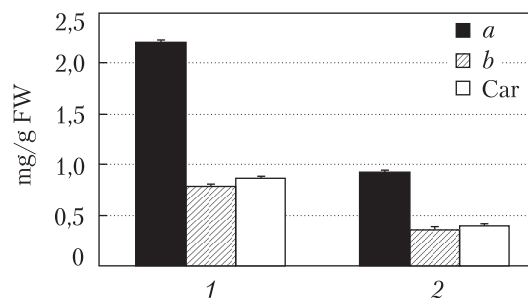
of phytohormones were performed using high performance liquid chromatography (HPLC) on a chromatograph Agilent 1200 LC system with a diode array detector G 1315 B (USA), column Eclipse XDB-C 18, with the parameters  $4.6 \times 150$  mm, size of particles – 5 microns. Chromatograms were calculated using the software ChemStation (version 3.1 V.) in the offline mode.

Experiments were carried out in three biological and five analytical replicates. Digital materials were processed statistically using the programs MS Excel 2003 and Origin 6.0. Significant differences were assessed by Student's criterion, using a 5 % level of significance ( $P < 0.05$ ).

**Results and discussion. Microstructure.** The adaxial surface of *P. maritimum* leaves is green-colored, smooth by touch. The epidermis is covered by a dense cuticle layer. Adaxial surface microphotographs obtained using the scanning electron microscopy show that a thick cuticle layer forms a network of large folds (Fig. 1, a). Stomata pores are located below the cuticle surface (see Fig. 1, b). Stomata number per  $1 \text{ mm}^2$  –  $156.6 \pm 8.4$ , length of stomata pores in dry substance –  $11.2 \pm 2.1 \mu\text{m}$ . The microstructure of leaf lamina abaxial surface is similar to that of adaxial one. The lower surface also has clear-cut stomata (see Fig. 1, c). Stomata pores are under the epidermis level. The number of stomata per  $1 \text{ mm}^2$  reaches  $158.3 \pm 4.5$ . An average length of stomata pore opening is close to that of the adaxial side. Thus, the adaxial and abaxial surfaces of the leaf lamina in glycohalophyte *P. maritimum* are characterized by a practically similar number of stomata and similar values of stomata pores sizes. In many flowering plants, stomata are known to be located on the leaf both sides [7]. However, in xeromorphic plants, the location of stomata pores below the basic cuticle level might be regarded as adaptation to droughty conditions.

Euhalophyte *E. paralias* leaves are sessile, 30 mm long and 15 mm wide. Scanning electron microphotographs of the leaf adaxial surface show that the epidermis is covered with a layer of very dense cuticular wax that results in a glossy surface effect. The cuticle produces an extensive network of small folds. The wax layer is homogeneous and smooth. No stomata are seen on the adaxial side (Fig. 2, a). The leaf abaxial surface of *E. paralias* contains stomata. The epidermis is covered with a substantial cuticle layer that, along with hump-shaped protrusions, cause some roughness of the leaf lower side (see Fig. 2, b). Stomata pores are below the epidermis level and surrounded by several hump-shaped constructions (see Fig. 2, c). The number of stomata per  $1 \text{ mm}^2$  reaches  $124.1 \pm 2.3$ . The average length of stomata pores does not exceed  $10 \mu\text{m}$ . Lack of stomata on the adaxial surface and their insignificant number on the abaxial surface of the leaf lamina, a well-developed cuticle, and a large leaf thickness belong to the structural components that enable *E. paralias* to adapt to specific conditions of growing. Our previous studies have indicated that the adaxial and abaxial leaf surfaces of euhalophytes *Eryngium maritimum* L. have well-developed cuticle and stomata pores placed below the surface of the epidermis [8].

**Photosynthetic pigments.** It was shown that, in leaves of glycohalophyte *P. maritimum*, the contents of chlorophylls *a* and *b* and carotenoids were higher than that of euhalophyte *E. paralias*. The level of carotenoids in both species exceeded the chlorophyll *b* content (Fig. 3). The level of chlorophylls was lower as compared with that in mesophyte plant



**Fig. 3.** Pigments content in leaves of *P. maritimum* (1) and *E. paralias* (2)

*Triticum aestivum* L., the content of carotenoids was also two times lower than in winter wheat leaves [9]. Carotenoids are known to protect the reaction sites from chlorophyll photoinhibition and photooxidation and improve light-collecting characteristics of the photosynthetic mechanism [10]. The ratio of chlorophylls *a/b* in the studied species was within the range of 2.7–2.8. In general, the ratio between pigments was similar to that in winter wheat [9]. Thus, the key role in a photosynthetic activity in glycohalophyte *P. maritimum* and euhalophyte *E. paralias* is played by chlorophyll *a*. However, a high amount of carotenoids (as compared with an amount of chlorophylls) indicates that these pigments have a light-collecting function and could transfer an additional energy to chlorophylls. *P. maritimum* leaves, which are much smaller in their size than those of *E. paralias*, were characterized by a higher carotenoid content that contributes to an effective application of solar light.

**Phytohormones.** We have shown that, in leaves of *E. paralias* and *P. maritimum*, the content of a free form of ABA exceeded that of conjugated form by 3.5–4 times. The level of a free form of ABA was higher in leaves of glycohalophyte *P. maritimum* (Table 1).

It was previously shown that, as compared to *Arabidopsis thaliana* L., the expression of genes responsible for ABA biosynthesis and metabolism was more intensive in a salt-tolerant plant *Thellungiella halophylla* L. [11]. ABA-deficient mutants are more sensitive to salt stresses than wild species [11]. This suggests that high levels of free active ABA in *E. paralias* and *P. maritimum* may be a regulatory basis of the wild plant salt tolerance. It is confirmed by information that ABA treatment enhances the endogenous ABA content, improves viability, and decreases the level of oxidative stress in facultative halophyte *Mesembryanthemum crystallinum* L. under salinity [2]. It should be noted that, in contrast to *E. paralias*, a higher content of ABA in *P. maritimum* coincides with a pigment higher content in leaves. Under stress conditions, ABA is synthesized from carotenoids through xantoxin. It appears that there is a close relationship between the pigment and hormone systems in the studied plants. So, a physiological significance of higher ABA levels that we have discovered in halophytes, having different mechanisms of salt tolerance, consists probably in a defense effect of this hormone and maintaining the normal functions of plants growing on saline soils.

In both studied species, the conjugated form of IAA prevailed. As compared to euhalophyte *E. paralias*, glycohalophyte *P. maritimum* contained large amounts of conjugated and free forms of IAA. In a bound state, IAA loses activity and could be used as a transport form or be a depot of the phytohormone. The predominance of conjugated IAA demonstrated that the activity of the hor-

Table 1. The content of phytohormones (ng/g FW) in the leaves of *E. paralias* and *P. maritimum*

ABA free	ABA bound	IAA free	IAA bound	<i>t-Z</i>	<i>c-Z</i>	ZR	ZOG	iPa	iP
<i>Euphorbia paralias</i>									
152 ± 6	44 ± 2	91 ± 4	180 ± 9	82 ± 3	250 ± 12	219 ± 10	163 ± 7	25 ± 1	23 ± 1
<i>Polygonum maritimum</i>									
190 ± 8	47 ± 2	145 ± 6	212 ± 11	37 ± 1	33 ± 1	129 ± 6	289 ± 14	124 ± 6	330 ± 16

Note. ABA – abscisic acid, IAA – indole-3-acetic acid, *t-Z* – *trans*-zeatin, *c-Z* – *cis*-zeatin, ZR – zeatin riboside, ZOG – zeatin-O-glucoside, iPa – isopentenyladenosine, iP – isopentenyladenine.

mone in *P. maritimum* and *E. paralias* is limited. Therefore, a regulatory function of IAA in these plants salt tolerance is questionable.

*P. maritimum* and *E. paralias* plants differ considerably in their contents of endogenous cytokinins. *P. maritimum* leaves contained significant amounts of isopentenyl forms – isopentenyladenosine and isopentenyladenine. Among zeatin forms, zeatin-O-glucoside prevailed (see Table 1). In leaves of *E. paralias*, the zeatin forms are predominant, but the level of inactive cytokinins (*cis*-zeatin and zeatin-O-glucoside) is considerably higher than that of active ones (*trans*-zeatin and zeatin riboside).

Cytokinins are known to be an important regulatory factor of plant stress tolerance. Many plants pretreated with cytokinins or mutants lacking some specific cytokinin signalling components enhanced tolerance to drought and salt stresses. As our experiments show, halophytes, having different salt tolerance patterns, differ considerably in the cytokinins metabolism. Glycohalophyte *P. maritimum* impermeable for salts accumulates cytokinins of the isopentenyl type that is not typical of higher plants under normal conditions. Some increase in the contents of isopentenyladenosine and isopentenyladenine occurred in glycophyte *Ph. vulgaris* and facultative halophyte *M. crystallinum* affected by NaCl [12]. In euhalophyte *E. paralias* that can congest salts, inactive cytokinins forms were dominant as in plants, whose growth intensity is low. Furthermore, in contrast to *E. paralias*, an increased content of pigments in *P. maritimum* leaves coincides with a higher total concentration of cytokinins and their active forms. Cytokinins are known to play some role in preserving the structure and function of the photosynthetic machinery under stress conditions. Cytokinin treatment retains higher transcript levels of photosystem II-related genes and maintains the chlorophyll *a/b* ratio resulting in the stability of photosynthetic pigment complexes and functional stay-greenness in rice [13]. Thus, the species specificity of the cytokinin status of the studied halophytes may be associated with the type of their strategy concerning survival in saline soils.

**Lipids composition.** It was shown that the main fatty acids in *E. paralias* leaves were palmitic, linoleic, and linolenic ones (Table 2). The content of 16:1 acid is low. In *P. maritimum*, the amount of saturated fatty acids was higher than that of *E. paralias*. There are same significant differences in the proportion of linoleic and linolenic acids in these halophyte plants. In *E. paralias*, the amount of linolenic acid is higher than that in *P. maritimum*. In general, the amount of saturated fatty acid in both plants is high in comparison with other terrestrial plants. The similar phenomenon was observed in other halophyte plants and seems to be typical of salt-stressed plants [3]. A high content of saturated fatty acid leads to some decrease in the membrane permeability and a better resistance of halophytic plants to soil salinity. The plant membrane fluid-

Table 2. Fatty acids in *P. maritimum* and *E. paralias* leaves

Plant	Fatty acids (wt % of total)								
	Lipid class								
	12:0	14:0	16:0	16:1	18:0	18:1	18:2	18:3	20:0
<i>P. maritimum</i>	3.15	2.93	21.87	1.49	3.24	8.32	16.04	39.14	3.82
<i>E. paralias</i>	0.67	3.43	21.20	1.12	3.34	2.10	12.21	51.71	4.22

ity depends also on the content of unsaturated linoleic (18 : 2) and linolenic (18 : 3) acids. An increase in salinity involves some growth of the amount of 18 : 2 (see Table 2). Studies on wheat seedlings demonstrated that environmental salinity enhanced fatty acids saturation [14]. It was also shown that, in contrast to a salt-sensitive tomato variety, the fatty acids saturation in cell plasmatic membranes of a salt-tolerant tomato variety was higher [15]. However, a high content of unsaturated fatty acids, as well as fatty acids with a long carbon chain, affects the functioning of membrane-bound enzymes, particularly those that are components of the ion active transport. These findings give reason to suggest that the regulation of the plasmatic membrane transport function that involves unsaturated fatty acids is a component of the salt defense mechanism in euhalophyte and glycohalophytes.

Thus, the growing in saline and dry soils of glycohalophyte *P. maritimum* and euhalophyte *E. paralias* provides, among other adaptive mechanisms, a specific microstructure of the leaf, adaxial and abaxial surfaces of which have well-developed cuticle and pores of stomata placed below the surface of the cuticle. A specific feature of euhalophyte *E. paralias* is the presence of stomata pores only on the leaf lamina abaxial surface. Each stoma is surrounded by hump-shaped cuticle constructions. In contrast to euhalophyte *E. paralias*, glycohalophyte *P. maritimum* is characterized by a higher content of photosynthetic pigments in leaves. Chlorophyll *a* plays a key role in photosynthetic activity. However, a high amount of carotenoids (as compared with the amount of chlorophylls) indicates that these pigments have a light-collecting function and could transfer an additional energy to chlorophylls. The analysis of the phytohormone system indicated that the salt tolerance formation involves ABA, a free form of which in leaves of both halophytes prevailed. Moreover, *P. maritimum* leaves had higher concentrations of endogenous phytohormones (ABA, IAA, and cytokinins). A high level of the conjugated form of IAA demonstrated that the activity of the hormone is limited. The content of isopentenyl-type cytokinins in glycohalophyte *P. maritimum* was considerably higher than that of euhalophyte *E. paralias*. The presence of a large amount of saturated fatty acids causes a decrease in membrane permeability and better resistance to soil salinity.

The results of our study demonstrate that the formation of adaptation strategy in halophytes involves the complex of structural and functional reconstructions that covers specific features in the phytohormone system, pigment complex, lipid composition, and surface microstructure of leaves and determines a successful existence in saline conditions.

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#### АДАПТИВНА СТРАТЕГІЯ ГАЛОФІТІВ *POLYGONUM MARITIMUM* І *EUPHORBIA PARALIAS*

Проведено порівняння мікроструктури листової поверхні, пігментного спектра, вмісту фітогормонів і складу ліпідів у галофітів з різною метаболічною і фізіологічною стратегіями адаптації до засолення *Polygonum maritimum* L. та *Euphorbia paralias* L., які зростали у природних умовах на дюнах Поморійського озера (Болгарія). У *P. maritimum* продири знаходяться по обидва боки листка нижче рівня кутикули, тоді як у *E. paralias* — лише на абаксiальному боці й оточені складками кутикули. Значна кількість каротиноїдів (порівняно з хлорофілами) у листках *P. maritimum* указує на те, що ці пігменти виконують світлозбиральну функцію і можуть передавати додаткову енергію на хлорофіли. У листках *E. paralias* і *P. maritimum* переважають вільна абсцизова кислота і кон'югована індоліл-3-оцтова кислота. Неактивні цитокініни (цис-зеатин і зеатин-О-глюкозид) домінують у листках *E. paralias*, тоді як у листках *P. maritimum* міститься значна кількість ізопентенільних форм цитокінінів. Наявність великої концентрації насичених жирних кислот забезпечує зменшення проникності мембран і кращу солестійкість. Зроблено висновок, що екологічна стратегія галофітів поєднує комплекс структурних та функціональних пристосувань і визначає успішне існування в умовах засолення.

**Ключові слова:** *Euphorbia paralias* L., *Polygonum maritimum* L., мікроструктура, фотосинтетичні пігменти, фітогормони, ліпіди.



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#### АДАПТИВНАЯ СТРАТЕГИЯ ГАЛОФИТОВ *POLYGONUM MARITIMUM* И *EUPHORBIA PARALIAS*

Проведено сравнение микроструктуры листовой поверхности, пигментного спектра, содержания фитогормонов и состава липидов у галофитов с различной метаболической и физиологической стратегиями адаптации к засолению *Polygonum maritimum* L. и *Euphorbia paralias* L., произрастающих в естественных условиях на дюнах Поморийского озера (Болгария). У *P. maritimum* устьица находятся по обе стороны листа ниже уровня кутикулы, тогда как у *E. paralias* — только на абаксиальной стороне и окружены складками кутикулы. Значительное количество каротиноидов (относительно хлорофиллов) в листьях *P. maritimum* указывает на то, что эти пигменты выполняют светособирающую функцию и могут передавать дополнительную энергию на хлорофиллы. В листьях *E. paralias* и *P. maritimum* преобладают свободная абсцизовая кислота и конъюгированная индолил-3-уксусная кислота. Неактивные цитокинины (цис-зеатин и зеатин-О-глюкозид) доминируют в листьях *E. paralias*, в то время как в листьях *P. maritimum* содержится значительное количество изопентенильных форм цитокининов. Наличие высокой концентрации насыщенных жирных кислот обеспечивает уменьшение проницаемости мембран и улучшает солеустойчивость. Сделан вывод, что экологическая стратегия галофитов объединяет комплекс структурных и функциональных приспособлений и определяет успешное существование в условиях засоления.

**Ключевые слова:** *Euphorbia paralias* L., *Polygonum maritimum* L., микроструктура, фотосинтетические пигменты, фитогормоны, липиды.