



# STRUCTURAL AND FUNCTIONAL FEATURES OF THE LEAVES OF THE DOMINANT PLANTS IN THE TIDAL ZONE OF THE WHITE SEA

Evgenia F. Markovskaya<sup>1</sup>, Elena N. Gulyaeva<sup>1</sup>, Anatoly A. Kosobryukhov<sup>2</sup>, Kira V. Morozova<sup>1</sup>  
and Lyudmila A. Sergienko<sup>1</sup>

<sup>1</sup>Petrozavodsk State University, Institute of Biology, Ecology and Agrotechnology, Department of Botany and Plant Physiology, Petrozavodsk, Russia.

<sup>2</sup>Institute of Basic Biological Problems Russian Academy of Sciences, Group of Ecology and Physiology of Phototrophs, Pushchino, Russia.

## Abstract

The research was performed on the dominant halophyte species (*Plantago maritima* L., *Triglochin maritima* L., *Glaux maritima* L., *Tripolium vulgare* Ness) in 2012–2015 at the western coast of the White Sea, in the estuaries of the rivers (Kolezhma, Vyg, Kieretti). At the experimental plots over the transect from the coast to the line of mean low water neaps, the leaf area decreases, while the leaf thickness and number of stomata per unit area increase, as the tidal level and the flooding period increase. The studied species possess special adaptive structures: *P. maritima* has water storage tissue and large number of stomata, *T. vulgare* – aerenchyma, water storage tissue and smaller number of stomata; in *T. maritima* aerenchyma constitutes a large proportion of the inner structure, thus decreasing the proportion of photosynthetic tissue in the leaves, whereas in *G. maritima* specialized tissues are almost absent and this species is marked by the lowest biometric plant size in the tidal zone. A hypothesis about the correlation between structural and functional features of the dominant species and their survival strategy and the patterns of distribution under various eco-coenotic conditions of the coastal habitats of the White Sea coast was proposed.

**Key words:** halophytes, adaptation, leaf anatomical structure, photosynthesis, pigments, water regime, White Sea coast

## Introduction

The tidal zone of the Holarctic seas is highly heterogenic, providing a wide range of local conditions for the biota and the plants inhabiting this zone constitute the azonal floristic complex (Sergienko, 2008; Markovskaya *et al.*, 2010) and possess certain adaptations to the unstable environmental conditions with the diurnal and the seasonal changes (gradient of temperature, lighting intensity, and humidity, seasonal photoperiodic changes, diurnal gradual effects of flooding, variations in the substrate salinity). Only a limited number of species can live under such conditions. The coastal flora of Russian Arctic includes 113 species of vascular plants (12% of the flora of the whole Arctic), belonging to 62 genera and 31 families. The partial coastal flora of the White Sea coasts includes 56 species and subspecies, belonging to 21 families and 42 genera. 4 species of those are halophytes, dominating the tidal zone of the White Sea

(inhabiting muddy derelictions of the deltas and estuaries of the rivers, and tolerating high levels of soil salinity): *Triglochin maritima* L., *Tripolium vulgare* Ness, *Glaux maritima* L. and *Plantago maritima* L. (Markovskaya *et al.*, 2010).

Examination of the anatomical structure of leaves is a common method for identifying the ability of plants to adapt to various ecological conditions. Changes in the number, size and shape of the tissue cells provide particular ways to create an optimal leaf structure, depending on the ecological conditions (Mokronosov and Borzenkova, 1978). The features reflecting functions of the photosynthetic apparatus, such as photosynthesis rates and pigment content, are the most informative from the perspective of assessment of the plant functional state (Pyankov, Mokronosov, 1993; Maslova, Popova, 1986; Golovko, 2007) and others.

The analysis of literature on the topic has shown that,



**Fig. 1 :** Sampling areas. 1 – Pomorskiy coast (Kolezhma settlement); 2 – Pomorskiy coast (Rastnavolok settlement); 3 – Karelian coast (Keret (Kieretti) settlement).

in spite of the growing number of studies on biology and physiology of plants of the sea coastal territories, the issues of structural and functional adaptation of the plants to the tidal regime are still understudied, particularly concerning the sea coastal territories of Russia. The dominant halophytic species of the tidal zone inhabiting the certain range of ecotopes within this territory deserve particular attention.

The aim of the study was to perform the comparative analysis of structural and functional features of the leaves of the dominant halophytic species growing in different habitats of the White Sea coast.

## Materials and Methods

### Study area

The research was performed in 2012–2015 during summer field seasons at the coastal territories of the western coast of the White Sea, varying in the geomorphological structure of the shore and its position, relative to the open sea area, slope exposition, lithological composition of the major rocks, mechanical soil composition, the size of the tidal zone. Three model transects were set on the Pomorskyskiy coast: near Rastnavolok settlement (64°58'N, 34°91'E, Belomorskiy District), on the shore consisting of the exposed monolithic bedrock (granite gneiss, gneiss granites) and marked by

the presence of muddy and sandy sites; the coast near Kolezhma settlement (64.22°N, 35.93°E, Belomorskiy District) with flat sandy shore. Two transects were set on the Karelian coast: on the coast near Keret (Kieretti) settlement, Nikolskaya bay (66°16'N, 33°33'E, Loukhskiy District), located at the right shore of the Kieretti River, is a small semi-enclosed bay of the estuarine type with lower waving (the mouth of the bay is relatively narrow) and flat accumulative coast. The major part of studies was carried out at the eastern coast, marked by muddy and rocky substrate.

Two sampling plots (SPs) were set at each transect from the line of mean low water neaps to the foot of the plane: at the foot of the plane (SP1) and at the line of mean low water neaps (SP2).

### Subject of studies

The subjects of the research included the dominant halophytic species – euhalophytes: *Plantago maritima* L. (*Plantaginaceae* family) – subarctic Eurasian species, *Triglochin maritima* L. (*Juncea ginaceae* family) – boreal Eurasian circumpolar species, *Tripolium vulgare* Ness – subarctic Eurasian species (*Asteraceae* family), and crynohalophyte *Glaux maritima* L. – subarctic Eurasian species (*Primulaceae* family). These species migrated from Central Asia to the shores of the White and the Barents Sea during the late Cainozoic, became widespread

in the evolutionary “new” environment (Tolmachev and Yurtsev, 1970) and reached the limits of their distribution area at high latitudes (Chernov, 2008).

### Sampling

Flowering plants were collected for morphological, anatomical and physiological analysis. 10 healthy, well-developed and well-illuminated plants were collected at each sampling plot for the anatomical studies. Three leaves of the middle part of the stem of each plant were collected and fixed in 70% ethanol.

All physiological experiments were performed in fine weather, at high levels of incoming solar radiation (1200–1400  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ), and air temperature of 22–25/18–22°C in the day/at night. The studies were performed in 3–4 biological replicates. The samples of the mature leaves were put in a humidified box and transferred (in 2–5 minutes) to the place of examination.

### Methods of study

**Morphological and anatomical methods :** The area of the leaves of *P. maritima*, *T. vulgare* and *G. maritima* was measured in 30 replicates, according to the following equation:

$$S = a * b,$$

Where, *a* is leaf width, *b* is leaf length.

The area of the leaves of *T. maritima* was calculated in 30 replicates, according to the following equation:

$$S = \pi * r * l,$$

Where, *r* is 1/2 of cross-section width in the central part of the leaf, *l* is leaf length.

The anatomical structure of the leaves was studied on the cross-sections using the MIKMED-6 optical microscope (LOMO, Russia) at 40× and 100× magnifications. The histological slides were prepared according to the standard protocols (Mokronosov and Borzenkova, 1978), the sections were stained with saphranine. WF10X/22 mm ocular micrometer was used for the measurements. The measurements were performed in 100 replicates. The stomata seen in 1 field of view were counted, and the number of stomata per 1 mm<sup>2</sup> of the leaf surface was calculated. The area of an individual stoma was obtained, according to the equation:

$$S_{\text{stn}} = \pi * D * L/4,$$

Where, *D* is length of the stoma, *L* is width of the stoma.

**Physiological methods :** The rate of CO<sub>2</sub> assimilation and plant transpiration were measured in field with LCPro+ transportable gas analyzer (ADC BioScientific

Ltd.) in the middle of the day, under the natural conditions. Stomatal conductance and the intracellular concentrations of CO<sub>2</sub> were calculated automatically with the gas-analyzer microprocessor. The correlations between the photosynthesis rate and the CO<sub>2</sub> content were assessed at the different concentrations of CO<sub>2</sub> (in the range of 0–1600  $\mu\text{mol CO}_2 \text{ mole}^{-1}$ ) in the air conveyed to the assimilation chamber of the gas analyzer at saturating light intensity. The levels of CO<sub>2</sub> injected into the leaf chamber were set with the gas-analyzer microprocessor and consequently changed in the following order: 400, 200, 100, 50, 400, 800, 1200, 1600  $\mu\text{mol mole}^{-1}$ . The curves of CO<sub>2</sub> gas exchange were analyzed according to the model by Farquhar *et al.* (1980), modified by Caemmerer and Farquhar (1981) and Harley and Sharkey (1991), with the software Photosyn Assistant Ver. 1.1.2 (Parsons and Ogston, 1999). The model implementing the equations of the authors provides an opportunity to calculate the maximal rate of CO<sub>2</sub> consumption,  $\mu\text{mol CO}_2 \text{ m}^{-2}\text{c}^{-1}$  (Pn max) under the CO<sub>2</sub> saturation conditions.

The concentrations of chlorophylls (chl) and carotenoids (car) were determined spectrophotometrically (SF-26, Russia) in the alcohol extraction by the values of the optical density at the absorption maxima of chlorophylls *a*, *b*, and carotenoids (Sapozhnikov *et al.*, 1978; Maslova *et al.* 1986). The proportion of chl in the light-harvesting complex (LHC) was calculated, assuming that almost all chl is located in the LHC and the chl *a/b* ratio is equal to 1.2 (Maslova *et al.*, 1986).

**Statistical methods :** Statistical analysis of the experimental data was performed with the software packages Microsoft Excel 7 and Statistica for Windows. Statistical significance was assessed with Student’s *t*-test at P = 0.95. Mean values and standard errors are shown in the tables. Each value represents the mean for 3–4 plants and corresponding standard errors.

Scientific names of plants are given according to the report by Kravchenko (2007).

## Results

The analysis of the leaf anatomy of the dominant plant species (*P. maritima*, *T. maritima*, *T. vulgare*, *G. maritima*) inhabiting the coastal areas of the White Sea, revealed the similarity of their anatomical structures to those of the plants of the same species growing at the salt marshes and the coastal territories of Europe at lower latitudes (Bavaru and Bercu, 2002; Evert, 2006; Bercu *et al.*, 2012; Grigore *et al.*, 2014) and others. This comparison is consistent with the idea of the azonal nature of the coastal zone (Walter, 1975 and Markovskaya *et al.*, 2010) and others. However, both the literature data

and our own research suggest that each of these species possesses its own adaptive features that either participated in or resulted from the exploration of the tidal zone. In *P. maritima*, these include isolateral leaf structure with the water storage tissue located in the center, with the cells, containing water and mucilage. Stomata are located within the upper and the lower epidermis, palisade mesophyll consists of 2–3 layers, mechanical tissues are well-developed. Specific features of *T. maritima* include the hypodermal layer underlying the epidermis, centric leaf structure, 2–3-layered palisade mesophyll, aerenchyma with the intercellular spaces filled with air, varying in diameter and located in leaves, stems and rhizomes. *G. maritima* has dorsoventral leaf structure, stomata located on both sides of leaves, aerenchyma with a small number of little intercellular spaces in stems. In *T. vulgare*, the adaptive features include isolateral leaf structure, stomata located on both sides of leaves, aerenchyma in stem and rhizomes, hypoderma in leaves. Water storage tissues of this species are described in the literature (Topa, 1954). These specific features have provided these species with almost equally successful growth in the coastal territories.

These species are marked with the halophyte-specific succulent leaf structure. Succulent leaves have high values of the leaf volume-to-surface ratio, which are more common in *T. vulgare* and *P. maritima* containing the water storage parenchyma in their leaves. Hence, the plants have relatively high transpiration rates at low rates of water consumption (Walter, 1975). Limited water flow is important to avoid rapid transfer of chlorides and sulfates abundant in the salinized soils to the plant tissues.

All four species are marked with presence of thick layer of cuticle. This structure is essential for halophytes, inhabiting the tidal zone, as the communities of this territory are at the initial stages of succession and have low projective cover, therefore, the plants are protected from overheating during the low tide.

Aerenchyma present in *T. maritima*, *T. vulgare*, *G. maritima* is also a part of the adaptation to the living conditions. The plants growing in the tidal zone, which is periodically flooded, are exposed to the hypoxic conditions and can use the gases (carbon dioxide and oxygen) stored in aerenchyma (Schulze *et al.*, 2005). Similar structure can be found in mangrove trees growing under the same conditions (Waisel, 1972).

These specific features of the studied species help them to struggle with “physiological drought” and hypoxia during the tidal changes, which is typical for the plants of the coastal territories, as well as with other stressing

factors.

Tidal dynamics determines heterogeneity of the examined territory, which results in various habitats related to different height of water column and duration of the submersed state of the plants. Analysis of the quantitative features of the leaf anatomical structure in all the studied plants over the transect has revealed no significant differences in such features as the size of epidermal cells, palisade and spongy mesophyll cells, and the number of chl per cell: these values were similar at SP1 near the coast and SP2 near the line of mean low water neaps within all the species. However, statistically significant changes (table 1) were observed in the leaf area and thickness in all the species: the leaf area was higher in the plants growing near the foot of the plane, whereas the leaf thickness – in the plants growing near the line of mean low water neaps. The plants growing near the line of mean low water neaps, undergo longer periods of flooding and high impact of tidal waves, which results in smaller, thicker leaves that are more tolerant to mechanical stress, as well as in lower height of the plant itself. It should be noted that, as the size of the cells does not depend on the growing conditions, higher leaf area in the plants at SP1 is related to larger number of cells.

Significant difference in the number of stomata per 1 mm<sup>2</sup> (table 2) was observed. It turned out that in two species (*T. vulgare* and *G. maritima*) the number of stomata progressively decreases from the line of mean low water neaps to the coast. The same correlation was observed in the study on *T. maritima* (Kosobryukhov and Markovskaya, 2016). Our large-scale research has revealed that all the species have open stomata during the period of flooding. This fact may indicate that these plants, being in water, are able to absorb carbon dioxide from water. Previously, a hypothesis on facultative involvement of the process of CO<sub>2</sub> uptake from bicarbonate during the flooding, *i.e.*, presence of a CO<sub>2</sub>-concentrating mechanism, was proposed based on the evidence of *T. vulgare* (Markovskaya *et al.*, 2015), as this mechanism would enable these plants to perform photosynthesis both in air and water. Sea grass *Zostera marina* L. was also shown to be able to uptake CO<sub>2</sub> through its surface tissues both from the atmosphere and from bicarbonate (Andersen *et al.*, 2007).

Comparative analysis of the functional activity of the plants at SP1 and SP2 during the low tide has revealed high CO<sub>2</sub> uptake rates, calculated per wet biomass of the leaf surface, in *P. maritima* and *G. maritima* and significantly (3–4 times) lower rates in *T. maritima* and *T. vulgare*. We observed high stomatal conductivity of

**Table 1** :Morphological parameters of the leaves in the dominant halophytes in different habitats (the case of the coast near Rastnavolok settlement).

Species	SP1 near the foot of the plane		SP2 near the line of mean low water neaps	
	Leaf area (mm <sup>2</sup> )	Leaf thickness (μm)	Leaf area (mm <sup>2</sup> )	Leaf thickness (μm)
<i>Tripolium vulgare</i>	1976.0±324.6	720.2±41.6	461.0±52.6	943.2±61.2
<i>Plantago maritima</i>	651.7±129.0	728.6±12.5	1506.4±974.4	688.4±76.6
<i>Glaux maritima</i>	53.7±16.3	415.8±70.1	51.2±7.8	458.7±58.1
<i>Triglochin maritima</i>	1199.4±346.6	428.1±53.7	637.7±145.9	527.4±58.3

**Table 2** :Features of the stomatal complex of the upper epidermis of the leaves in the dominant halophytes, growing in different habitats (by the example of the coast near Rastnavolok settlement).

Species	SP1 (coast)		SP2 (sea)	
	Number of stomata per 1 mm <sup>2</sup>	Stomatal area (μm <sup>2</sup> )	Number of stomata per 1 mm <sup>2</sup>	Stomatal area (μm <sup>2</sup> )
<i>Tripolium vulgare</i>	48 ±7	889.2 ±67.2	91 ±6	858.1 ±63.5
<i>Plantago maritima</i>	74 ±15	728.8 ±84.1	110 ±23	571.2 ±70.4
<i>Glaux maritima</i>	78 ±21	983.1 ±96.2	73 ±16	1126.5 ±146.2
<i>Triglochin maritima</i>	198 ±21	709.7 ±81.4	226 ±47	715.3 ±62.2

the gas flow in *P. maritima* and *T. vulgare*, whereas in *T. maritima* this value was almost 3-fold lower and *G. maritima* had intermediate values, being closer to *P. maritima*. Lower stomatal conductivity of the gas flow in *T. maritima* resulted in small transpiration rates and more efficient water use by this species (table 3).

The concentration of carbon dioxide in the intercellular spaces of *T. vulgare* and *T. maritima* was at equally high levels, which might indicate the absence of the stomatal limitation of photosynthesis in these species. However, lower values of the photosynthesis rate in these species, as compared to *P. maritima*, imply other limiting factors. In *G. maritima*, the average values of the internal concentration of carbon dioxide were observed, which, considering high rates of photosynthesis and transpiration, indicates the lack of the CO<sub>2</sub>-related limitations. High rates of the major physiological processes confirm that *G. maritima* belongs to the mesophyte ecological group (Goryshina, 1979). Assessment of potential photosynthesis under the elevated concentrations of carbon dioxide in the air has revealed the highest values in *G. maritima* and *P. maritima* and the lowest values in *T. maritima*. However, the comparison of the photosynthesis rates under the natural and the elevated concentrations of CO<sub>2</sub> revealed almost 6-fold increase in *T. vulgare* and *T. maritima*, whereas in *P. maritima* and *G. maritima*, only 2–3-fold gain was observed. These results may indicate different sensitivity of the species to the increasing concentrations of carbon dioxide and different limiting mechanisms, involved in this process,

in the C<sub>3</sub> plants.

Moreover, certain decrease in the total content of chlorophylls (table 4) was observed in the leaves of *T. vulgare* and *T. maritima*, as compared to *P. maritima* and *G. maritima*, but higher values of chl *a* / chl *b* ratio were revealed. This parameter is particularly high in *G. maritima*. There are four types of chlorophyll-protein complexes forming in the chloroplasts of embryophytes (Ladygin, 1998). The complexes of the reaction centers of photosystem I (PS-I) and photosystem II (PS-II) contain exclusively chl *a*, whereas the light-harvesting complexes related to PS-I (LHC-I) or PS-II (LHC-II) contain the short-wavelength forms of chl *a* and all the chl *b* (Ladygin, 1998). The lowest chlorophyll ratios were observed in *P. maritima*, which might indicate more significant protective function of car in this species or its higher shade tolerance. The results on the chlorophyll ratio and the minor differences observed in the LHC size may suggest that the photosynthetic units in *G. maritima* and *P. maritima* contain more LHCs per the reaction center than those of *T. maritima* and *T. vulgare*. The carotenoid content was almost identical in *P. maritima*, *T. maritima* and *T. vulgare*, whereas in *G. maritima*, higher concentrations were observed. This increase is believed to be related to the antioxidant function (Edge and Truscott, 2010), which should be more important for *T. vulgare* and *T. maritima*.

Comparative analysis of the studied species has showed that high photosynthetic rates in *P. maritima* combined with high stomatal conductivity allow it to

**Table 3** : Physiological characteristics of the dominant halophytes under the natural conditions (the case of the coast near Kolezhma settlement).

Study subjects	Photosynthetic rate, $\mu\text{mol CO}_2/(\text{m}^2\text{s})$	Rate of photosynthetic capacity at light saturation, $\mu\text{mol CO}_2/(\text{m}^2\text{s})$	Transpiration rate, $\mu\text{mol H}_2\text{O}/(\text{m}^2\text{s})$	Pn/E	Stomatal conductance, $\mu\text{mol H}_2\text{O}/(\text{m}^2\text{s})$	Internal $\text{CO}_2$ concentration, $\mu\text{mol CO}_2/\text{mol}$
<i>Tripolium vulgare</i>	11.5± 0.8	76.9 ± 4.6	4.7± 0.2	2.4	280±10	298±14
<i>Triglochin maritima</i>	8.4± 1.2	48.7 ± 3.4	2.8±0.2	3.0	80±10	207±15
<i>Glaux maritima</i>	38.7± 0.6	96.2±8.1	12.5±0.3	3.1	290±5	130±4
<i>Plantago maritima</i>	36.9±1.1	85.0 ± 4.8	9.4±0.4	4.0	255±6	64±4

**Table 4** : Pigment content in the leaves of the dominant halophytes (calculated per 1 mg of chlorophyll per 1 g of dry weight of the leaves) (the case of the coast near Kolezhma settlement).

Parameters	Plant species			
	<i>Plantago maritima</i>	<i>Tripolium vulgare</i>	<i>Glaux maritima</i>	<i>Triglochin maritima</i>
Chl <i>a</i> , mg/gDW	2.0±0.4	2.0±0.1	2.7±0.3	2.1±0.2
Chl <i>b</i> , mg/gDW	1.2±0.2	0.7±0.1	0.7±0.1	0.7±0.1
Chl <i>a+b</i> , mg/gDW	3.3±0.6	2.6±0.2	3.4±0.3	2.8±0.1
Car, mg/gDW	0.6±0.1	0.6±0.1	0.9±0.1	0.6±0.1
Chl <i>a/b</i>	1.6±0.6	3.0±0.3	3.8±0.6	3.0±0.6
Chl/Car	5.9±0.7	4.2±0.1	3.9±0.6	5.1±0.9
LHC, %	52.2±8.8	55.3±3.5	46.3±8.2	56.7±9.3

maintain high levels of both carbon-dioxide and water exchange. The same features are typical for *G. maritima*. However, this species, unlike the others, has the minimal height and lacks specialized tissues, which, apparently, may limit its participation in the plant communities under the deep flooding conditions. In *T. vulgare*, lower carbon-dioxide exchange, together with lower content of chlorophyll, is combined with high level of water regime, whereas *T. maritima* has lower rates of both photosynthesis and water exchange than the other species. At the same time, *T. maritima* is marked by more economic use of water. Extensive adaptation of *T. vulgare* to the water regime is confirmed by its ability of the underwater pollination (Bercu *et al.*, 2012).

## Discussion

The comparison of the structural data with the data on the functional activity of the leaves in the studied species reveals certain correlations. *P. maritima* plants can be qualified as more functionally active and better adapted, as they have the combination of water storage tissue and large number of stomata, providing high rates of both photosynthesis and water exchange. In *T. vulgare*, presence of aerenchyma and water storage tissue, combined with lower number of stomata, also results in relatively high functional activity, which is, however,

lower than in *P. maritima*. In *T. maritima* large fraction of aerenchyma decreases the proportion of photosynthetic tissue in the leaves, while the absence of the water storage tissue implies more economic use of water. Low stomatal conductivity and high values of the internal  $\text{CO}_2$  concentration are observed in this species. This combination provides lower rates of both carbon-dioxide and water exchange. *G. maritima*, being the only crynhalophytic species, has high levels of functional activity and an insignificant proportion of specialized tissues in the general structure of the plant, which makes it a highly specialized form restrained to the coastal habitats within the taiga zone, in contrast to other species (Kravchenko, 2007).

Comparative analysis of the structural and the functional features of the examined species explains their expansion to the north: the most northern habitats belong to *Triglochin maritima* and *Plantago maritima* (represented on the Barents Sea coast) (Ramenskaya and Andreeva, 1982), whereas the natural habitat of *Tripolium vulgare* and, to a greater degree, *Glaux maritima* is limited to the northern shore of the White Sea (Kravchenko, 2007). These results substantiate the hypothesis about the relation between structural and functional features of the dominant species and their

survival strategy and patterns of distribution under various eco-coenotic conditions of the coastal habitats of the White Sea coast.

During the preceding eras, when the temperature of the sea coasts was gradually decreasing due to ice formation in the Polar basin, the coastal meadows dominated by the euarctic species – arctic halophytes [*Puccinellia angustata* (R.Br.) E.L.Rand & Redfield, *Carex ursina* Dewey, *Carex subspathacea* Wormsk. ex Hornem., *Dupontia fisheri* R.Br.] have been forming in the Pliocene and the Pleistocene (Yurtsev, 1978). However, drying of the shelf areas, migration of the coastline and the absence of competitors at the unsodded coastal areas allowed certain allochthonous forms, obviously including all the studied species, to enter these territories, perhaps, at different times. The complex of the arctic flora is relatively new (Tolmachev and Yurtsev, 1970) and is still being established. Our research has revealed certain aspects of this process: the limited range of species, high rates of form creation and species creation, high variability of their structural and functional features, various specialized structures and inducible metabolic pathways in different species, providing the range of alternative ways of adaptation of the coastal halophytes (Sergienko, 2008; Markovskaya *et al.*, 2010; Kosobryukhov *et al.*, 2012; Markovskaya *et al.*, 2014).

### Conclusion

Our research has shown that extensive adaptation of the halophytes to the habitats of the White Sea coast is related to their structural and functional features. Combinations of these features vary from species to species. These facts can be of certain interest for genetic engineering, which commonly uses the plants adapted to the elevated salt content, yet the researchers almost never work with the halophytes of high latitudes (Shamsutdinov *et al.*, 2000). Our data on the high rates of actual and potential activity of the halophytes at the coastal territories of high latitudes, combined with various adaptive specialized structures and high tolerance to the temperature gradient and the elevated concentrations of carbon dioxide, prove potential value of certain species of the coastal flora of the northern regions for genetic engineering.

### Funding

Current study received support of the grant of the Government contract of the Ministry of Education and Science of Russia (project no. 6.724.2014/k).

### References

- Andersent, T., C. Christensen and O. Pedersen (2007). Light – the Driving Force for Growth of Aquatic Plants. *The Aquatic Gardener*, **20** : 26–35.
- Bavaru, A. and R. Bercu (2002). *Morfologia și anatomia plantelor*. Constanța, Ex Ponto.
- Bercu, R., M. Fagara and L. Broasca (2012). Anatomical features of *Aster tripolium* L. (Asteraceae) to saline environments. *Annals of RSCB*, **17(1)** : 271–277.
- Caemmerer, S. and G. D. Farquhar (1981). Some relationships between the biochemistry of photosynthesis and the gas exchange rates of leaves. *Planta*, **153** : 376–387.
- Chernov, Y. U. I. (2008). *Ekologiya i biogeografiya* [Ecology and biogeography]. Moscow, KMK.
- Edge, R. and G. Truscott (2010). Properties of carotenoid radicals and excited states and their potential role in biological systems. In: Landrum, J. T. (ed.). *Carotenoids: Physical, Chemical, and Biological Functions and Properties*. Dordrecht, Kluwer Academic Publishers, p. 283–307.
- Evert, R. F. (2006). *Esau's Plant anatomy: meristems, cells, and tissues of the plant body: their structure, function, and development*. 3rd ed. Hoboken, NJ, John Wiley and Sons.
- Farquhar, G. D., S. Caemmerer and J. A. Berry (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> plants. *Planta*, **149** : 78–90.
- Golovko, T. K., G. N. Tabalenkova and O. V. Dymova (2007). Pigmentnyy apparat rasteniy Pripolyarnogo Urala [Pigment systems of plants of the Nether-polar Urals]. *Botanicheskiy zhurnal.*, **92(11)** : 1732–1741.
- Goryshina, T. K. (1979). *Fotosinteticheskiy apparat rasteniy i usloviya sredy* [Photosynthetic systems of plants and environmental conditions]. Leningrad, Leningrad State University Press.
- Grigore, M. N., L. Ivanescu and C. Toma (2014). *Halophytes: an integrative anatomical study*. Heidelberg, New York, Dordrecht, London, Springer.
- Harley, P. C. and T. D. Sharkey (1991). An improved model of C<sub>3</sub> photosynthesis at high CO<sub>2</sub>: reversed O<sub>2</sub> sensitivity explained by lack of glycerate reentry into the chloroplast. *Photosynth. Res.*, **27** : 169–178.
- Kosobryukhov, A. E. Markovskaya and L. Sergienko (2012). Photosynthetic characteristics of three species of the family Plantaginaceae growing on high and low tide coastal areas of the White Sea. *Czech Polar Reports*, **2(2)** : 71–79.
- Kosobryukhov, A. and E. Markovskaya (2016). Halophyte Adaptation to the Gradient of Conditions at the Intertidal Zone of the White Sea Cost (with *Triglochin maritima* L. as an example). *Global Media Journal*. Approved for print.

- Kravchenko, A. V. (2007). *Konspekt flory Karelii* [Brief guide to Karelian flora]. Petrozavodsk: KarSC RAS.
- Ladygin, V. G. (1998). Strukturno-funktsionalnaya organizatsiya fotosistem v khloroplastakh Chlamydomonas reinhardtii [Structural and functional organization of photosystems Chlamydomonas reinhardtii chloroplasts]. *Russian Journal of Plant Physiology*, **45(5)** : 741–762.
- Markovskaya, E. F., L. A. Sergienko, G. A. Shklyarevich, A. V. Sonina, A. A. Starodubtseva and O. V. Smolkova (2010). *Prirodnyy kompleks poberezhnyy Belogo morya* [Natural complex of the White Sea coast]. Textbook. Petrozavodsk: KarSC RAS.
- Markovskaya, E. F., A. V. Sonina, L. A. Sergienko, K. V. Morosova and N. A. Elkina (2014). Morphological and functional peculiarities of saltmarsh plants and epilithic lichens in tidal conditions of Russian Arctic Seas. *Czech Polar Reports*, **4(2)** : 168–177.
- Iarkovskaya, E. F., A. A. Kosobryukhov, K. V. Morozova and E. N. Gulyaeva (2015). Photosynthesis and anatomic-morphological characteristics of sea aster leaves on the Whyte Sea coast. *Russian journal of Plant Physiology*, **62(6)** : 830–836.
- Maslova, T. G., I. A. Popova and O. F. Popova (1986). Critical assessment of the spectrophotometric method of carotenoid measurement. *Fiziologiya rasteniy*, **33** : 615–619.
- Mokronosov, A. T. and R. A. Borzenkova (1978). Metodika kolichestvennoy otsenki struktury funktsionalnoy aktivnosti fotosinteziruyushchikh tkaney i organov [Methods of quantitative assessment of structure and functional activity of photosynthetic tissues and organs]. *Trudy po prikladnoy botanike, genetike i seleksii*, **61(3)** : 119–133.
- Parsons, R. and S. Ogston (1999). Photosynthesis Assistant: Tools for Analysis of Photosynthetic Data, Version 1.1.2, Dundee, UK, Dundee Scientific.
- P'Yankov, V. I. and A. T. Mokronosov (1993). Osnovnye tendentsii izmeneniya rastitelnosti Zemli v svyazi s globalnym potepleniem klimata [Major trends in changes in the Earth vegetation, related to the global warming]. *Fiziologiya Rasteniy*, **40** : 515–531.
- Ramenskaya, M. L. and V. N. Andreeva (1982). Opredelitel vysshikh rasteniy Murmanskoy oblasti i Karelii [Identification guide for embryophytes of the Murmansk Region and Karelia]. Leningrad, Nauka.
- Sapozhnikov, D. I., T. G. Maslova, O. F. Popova, I. A. Popov and O. Ya Koroleva (1978). Metod fiksatsii i khraneniya listev dlya kolichestvennogo opredeleniya pigmentov plastid [Technique of fixing and storing the leaves for measurement of pigment content in plastids]. *Botanicheskiy Zhurnal*. **63(11)** : 1586–1592.
- Sergienko, L. A. (2008). *Flora i rastitelnost poberezhnyy Rossiyskoy Arktiki i sopredelnykh territoriy* [Flora and vegetation of the Russian Arctic coast and adjacent territories]. Petrozavodsk, Petrozavodsk State University Press.
- Shamsutdinov, Z. Sh., I. V. Savchenko and N. Z. Shamsutdnov : *Galofity Rossii ikh ekologicheskaya otsenka i ikh polzovanie* [Halophytes of Russia: ecological assessment and utilization]. Moscow, Nauka.
- Tolmachev, A. I. and B. A. Yurtsev (1970). *Istoriya arkticheskoy flory v ee svyazi s istoriey Severnogo Ledovitogo okeana. Severnyy Ledovityy okean i ego poberezhie v kaynozoe* [History of the Arctic flora and its connection to the history of the Arctic ocean. The Arctic ocean and its coast during the Cenozoic Era]. Leningrad, Gidrometeoizdat.
- Schulze, E. D., E. Beck and K. Muller-Hohenstein (2005). *Plant ecology*. Berlin, Springer.
- Topa, E. (1954). Vegetația terenurilor sărate din R.P.Romnă. *Natura*, **6(1)** : 57–76.
- Walter, H. (1975). *Rastitelnost zemnogo shara. Ekologo-fiziologicheskaya kharakteristika* [Vegetation of the Earth. Ecological and physiological characteristics]. Vol. **3**. Moscow, Progres.
- Waisley, Y. (1972). *Biology of halophytes*. New York, Academic Press.
- Yurtsev, B. A. (1978). *Arkticheskaya floristicheskaya oblast* [Arctic floristic region]. Moscow, Nauka.