

## Halophyte Adaptation to the Gradient of Conditions at the Intertidal Zone of the White Sea Coast (with *Triglochin maritima* L. as an example)

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### Abstract

The comparative study of structural and functional leaf features of *Triglochin maritima* L. growing under gradient intertidal zone conditions of the Pomorsky coast of the White Sea was carried out. It is shown that under natural CO<sub>2</sub> concentration the leaves of plants growing near the coastline have higher values of photosynthetic intensity, transpiration and stomatal conductance, but there is the converse trend under increased CO<sub>2</sub> concentration. We suggested the hypothesis that the plants, which were under water for a long period of time (near the coastline), have to use the additional source of carbon - bicarbonate (HCO<sub>3</sub>). The phenomenon of structural and functional adaptation of halophytes of intertidal zone to the set of stress factors is discussed. The hypothesis of the existence of systemic reaction of the organism and its involvement in the daily rhythm of physiological processes as response on ecological factors rhythmicity at intertidal zone is suggested. It is connected with high plasticity of halophytes on this territory.

**Keywords:** Daily rythm; Ecological factors; Intertidal zone; Stress resistance; *Triglochin maritima* L.

**Abbreviations:** CVC: Cell Volume per Chloroplast, RBP: Ribulose Bisphosphate, RuBisCO: Ribulose-1,5-Bisphosphate Carboxylase/Oxygenase, LHC: Light-Harvesting Complex, CCM: CO<sub>2</sub>-Concentrating Mechanism, TPU: Triose-Phosphate Utilization Rate, CCP: CO<sub>2</sub> Compensation Point.

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### Introduction

*Triglochin maritima* is a member of *Juncaginaceae* family. This species is dominating at the saline types of habitats (maritime and continental) in the boreal region of North hemisphere. The majority of works are devoted to the analysis of the geographic distribution of *T. maritima* and investigation of ecological conditions of its vegetation in plant communities with different ecology [1]. This dominant species has the wide ecological range and takes different ecological niches at the west coast of the White Sea throughout littoral and supralittoral from coastline to valley side [2]. It propagates with seeds and vegetatively [3].

The habitat conditions of higher vascular plants in the intertidal zone are complicated due to its high level of substrate-relief

heterogeneity and variability of ecological factors [4]. The main process defining the instability of ecological conditions is the cyclical nature of tides, which change the habitat conditions of plants twice a day. This periodicity leads to the appearance of stress situations [5]. First of all, this is the exchange of ground-air environment to water one, that results in fast (minutes) and sharp decrease of illumination (at the depth of 1 meter only about 20% remains); the decrease of oxygen and carbon dioxide content [6] and the disturbance of water regime [7,8]. In water environment HCO<sub>3</sub> prevails, which cannot be assimilated by terrestrial plants, and CO<sub>2</sub> concentration is lower and the low diffusion rate decreases its availability for plants. In water, the boundary layer at the leaf surface which operates only under conditions of stagnation or slow motion of water flow increases

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[9]. The extent of flooding (partial or complete) and its duration (hours) depend on plant position on the littoral territory. During the low tide, when plants are completely exempt from water (hours), they are subjected to intensive illumination and can experience water deficiency. Every organism must be adapted to unstable ecological conditions during tidal cycle twice a day. It should be noted that all higher plant species inhabiting the littoral successfully undergo complete ontogenesis, which suggests that they managed to adapt to these unstable stress conditions. In literature, there are numerous works connected with the investigation of mechanisms of salt tolerance of halophytes [10,11], which grow under different salinity conditions, but the role of periodicity in the interaction of factors and their joint influence on the growth and development of higher plants are factually not investigated. It should be added that these phenomena are difficult for studying, and field researches are necessary in addition to cameral experiments.

The comparative investigation of structural and function leaf features of *T. maritima* growing in the gradient of conditions on coastal littoral of the Pomorsky coast of the White Sea was included in the objective of this study.

## Views on *Triglochin maritima*

*The object of investigation.* *Triglochin maritima* L., *Juncaginaceae* family, is a perennial herbaceous plant with erected stems 10-18 cm in height. The leaves are radical, narrowly linear, semi-cylindrical up to 60 cm in length. The rhizome is horizontal or oblique, short, strong. The inflorescence is racemose, many-flowered; the flowers are inconspicuous, greenish; the tepals are reddish on top; the fruits are ovate and consist of six fruitlets. The plant grows on the littoral of sea coasts, on wet salt-marsh meadows, peat bogs and shores of salt lakes. It is polyzonal species and has circumboreal areal. It can be met ubiquitously at the White Sea coast; it is the dominant and co-dominant in communities at zone of daily salt sea waters flooding. Also, *T. maritima* can grow and be dominant in regions higher than the daily flooding zone (especially in lowlands with clay substrate, where the sea water can stagnate since spring flooding) [2]. In coenopopulation, rather big groups with high value of dead central part of maternal individual are observed.

*The work was carried out* on the Pomorsky coast of the White Sea near the settlement Kolezhma in June, 2015. At the intertidal coastal zone there were laid two sample plots (SP) with the area of 0.25 m<sup>2</sup> near the shore (SP1) and near the coastline (SP2) during maximum low tide. The general projective cover of the species at SP1 was about 40%, including about 30% *Tripolium vulgare* and 10% *Triglochin maritima*. The maximum time of plants being under water with partial submersion (the half of stem was in the air) was approximately 1.5 hours at SP1 and 3 hours with complete submersion at SP2 per one intertidal cycle. The maximum height of the water column above the substrate was 42 cm. At SP2 projective cover of the species was 60%, including about 30% of *Plantago* species, small amount of *Glaux maritima* (about 5%) and about 25% of *T. maritima*.

*Anatomical and morphological methods.* 10 healthy well developed and illuminated plants were collected from each

sample plot; 5 formed leaves from each plant were taken for the fixation in 70% ethanol. The area was defined on 50 leaves taken from 10 plants; biometric measurements of anatomic structures (stomata, cells of epidermis and mesophyll) were conducted on samples from 10 leaves from each SP. The leaf anatomy structure was investigated on temporal preparations by means of light microscope with 100x magnification. The measurements of anatomical and morphological indexes and the calculations are described in work [12].

*Physiological methods.* For the detection of photosynthesis and transpiration rate, 3-4 leaves of plants from each sample plot were taken and the measurement was conducted at once by means of portable gas analyzer LCPro+ of company ADC BioScientific Ltd (United Kingdom). The repetitiveness of the experiments was 3-4-fold. In the leaf chamber, the middle part of 2-3 leaves was put in and under stationary values the rate of CO<sub>2</sub> gas exchange, transpiration, stomatal conductivity and CO<sub>2</sub> concentration in leaf intercellular spaces were indicated. All measurements were conducted from 11 to 15 o'clock in the period, when the plants were in air, under natural light intensity of 1000-1200 μmol quants m<sup>-2</sup>s<sup>-1</sup> and air temperature of 22-25°C. CO<sub>2</sub>-dependences of photosynthetic rates were made by changing the CO<sub>2</sub> concentration in the air supplied to the chamber of gas analyzer in the range of 0-1600 μmol CO<sub>2</sub> mol<sup>-1</sup> under saturating intensity of light. To do this, the levels of CO<sub>2</sub> concentration supplied to leaf chamber were made using microprocessor of analyzer and changed successively: 400, 200, 100, 50, 400, 800, 1200, 1600 μmol mol<sup>-1</sup>. The analysis of carbon dioxide curves of CO<sub>2</sub> gas exchange was carried out by model of Farquhar et al. [13], modified by [14] using Photosyn Assistant Ver. 1.1.2 programmes [15]. According to the equations of authors, the model allows to detect the maximum carboxylation rate (V<sub>c<sub>max</sub></sub>), the electron transport rate under light saturation (J<sub>max</sub>), the triose phosphate utilization rate (TPU) and a number of the other parameters. Each value in tables is an arithmetic average for 3-4 plants and its standard errors.

## Representation of Physiological Processes of *Triglochin maritima*

Conducted anatomical and morphological investigations showed that *T. maritima* plants growing near the shore (SP1) had the area of experimental leaves by 30% higher than that near coastline (SP2), where the leaf thickness was by 20% higher than these values at SP1 (near the shore) (**Table 1**).

The analysis of the *T. maritima* leaf mesostructure conducted recently has shown that the size of upper and lower epidermis cells, of palisade and spongy mesophyll appeared to be similar [16]. The increase of the leaf area of plants at SP1 is connected with the increase of cell amounts, but not of their size.

The amount of stomata on 1 mm<sup>2</sup> of leaf area of studied species increases 2-fold from SP1 to SP2, where it reaches its maximum value. The stomata area decreases by 20% and area of stomatal slit is lower by 10% in plants at SP2 - near the coastline. The plant leaves on both sample plots have negligible difference in chloroplast amounts (**Table 2**).

**Table 1.** Biometric parameters of *Triglochin maritima* plants grown in different habitats.

Conditions	Leaf morphology parameters	
	Leaf area, mm <sup>2</sup>	Leaf thickness, μm
At the shore, PP1	1377 ± 46	232.60 ± 3.50
At the low tide line PP2	994 ± 46	267.60 ± 3.80

**Table 2.** Quantitative parameters of stomata in the leaf epidermis of *Triglochin maritima* L. plants grown in different habitats.

Conditions	Epidermis	Stomatal parameters		
		Frequency of stomata	per 1 mm <sup>2</sup> leaf area	Stomatal aperture, μm <sup>2</sup>
At the shore, PP1	Upper	32 ± 1	179,00 ± 5,10	975,00 ± 19,00
At the low tide line PP2	Upper	60 ± 1	135,80 ± 3,60	862,00 ± 10,00

Thus, the analysis of morphological and anatomical structures of plants growing at sample plots different in transect has shown that the leaves of *T. maritima* differ mostly in assimilating surface area, which is higher in shore plants, and in amount of stomata per area unit, that is higher in leaves of coastline plants.

The investigation of different physiological processes detected that the leaves of plants growing at SP2 (the coastline) had higher (almost 2-fold) values of all parameters of gas exchange (photosynthesis intensity, transpiration and stomatal conductivity), that may indicate their higher functional activity. CO<sub>2</sub> concentrations in intercellular spaces of mesophyll were slightly lower in shore plants, but, however, within experimental error (Table 3).

Experimental increase of CO<sub>2</sub> concentration in the chamber allowed estimating the activity of individual reactions of light and dark steps of photosynthesis by the carbon dioxide curves analysis (Figure 1) using the model.

Photosynthesis is limited by RuBisCO activity (Wc), rate of electron transport (Wj), and triose-phosphate utilization or Pi availability (Wp). The curves were obtained by direct CO<sub>2</sub> uptake measurement (symbols) or by approximation of curves according to the model of Farquhar et al. [13].

First of all, it should be noted that the rate of all investigated processes was higher in plants at SP1. The limiting factor of CO<sub>2</sub> uptake by coastline plants was presented by RuBisCO activity at the range of all investigated concentrations. In coastal plants thus being under water for a short period of time the enzyme activity (Wc) was the limiting factor only in low CO<sub>2</sub> concentrations, that is typical for C<sub>3</sub> plants growing under natural CO<sub>2</sub> concentration in the air. Subsequently, the electron transport rate was the limiting factor. In plants subjected to prolonged flooding (SP2) photosynthesis was limited by RuBisCO activity in all range of CO<sub>2</sub> curve. Triose phosphate utilization rate and thus availability of inorganic phosphate (Wp) were not the limiting factors of photosynthetic CO<sub>2</sub> uptake.

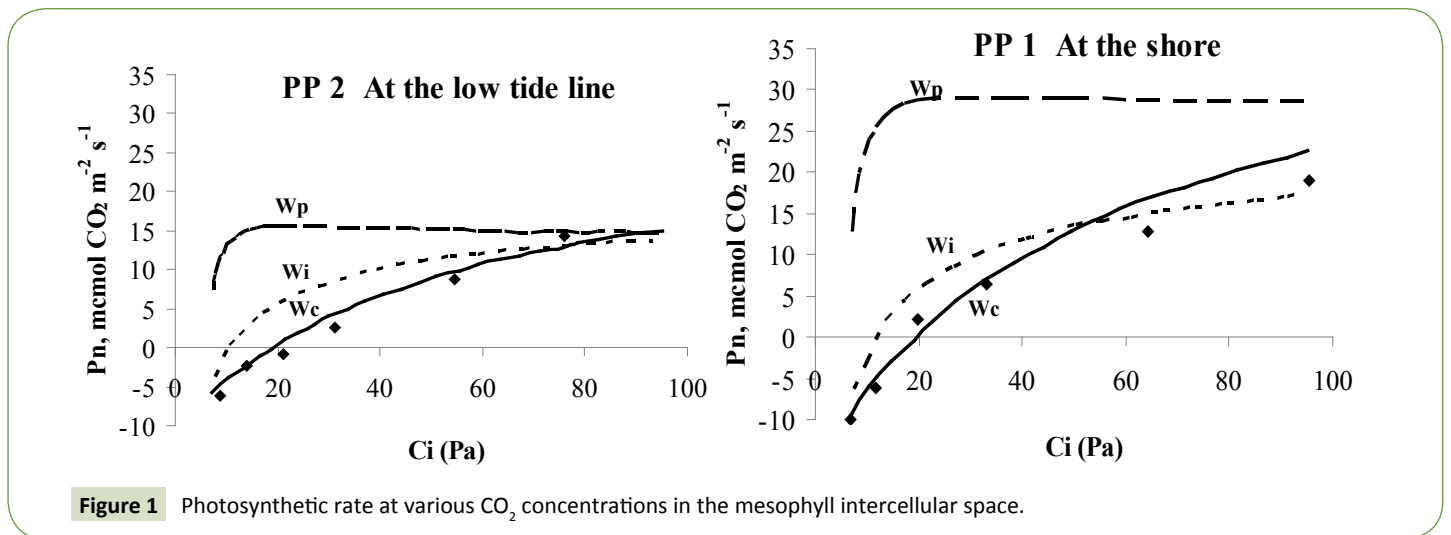
The maximum CO<sub>2</sub> uptake rate in plants at SP1 increased almost 30-fold as compared to data obtained under natural concentration, and this at SP2 increased only 10-fold (Table

4). The maximum uptake rate values at SP2 were lower only by 40% than at SP1 (the difference was 2-fold under natural concentration). Higher photosynthesis intensity values in plants at the shore (SP1) were accompanied by higher carboxylation rate, triose phosphate utilization (2-fold) and ETP values (by 70%) in comparison with plants growing near the water (SP2). The same plants had the dark CO<sub>2</sub> release intensity higher almost by 30% and CCP that was slightly higher. There was no difference in carboxylation efficiency between leaves of plants on both SP. The obtained data allow considering the coherence extent of dark and light photosynthesis steps operation. The ratio  $J_{max}/V_{max}$  could be the important indicator of this coherence. For *T. maritima* shore and coastline plants, this ratio appeared to be rather similar and was 2.83 and 2.72, which is indicating the absence of alterations in correlation of reaction ratios. That means that simultaneously with the decrease of light step activity (the rate of electron transport and energy equivalents generation - ATP and NADPH) the "tune-up" of dark step reactions occurs - the carboxylation rate ( $V_{max}$ ) decreases, and in this case the decrease of potential photosynthesis is caused by changes in both the electron transport chain activity of photosynthetic apparatus and enzyme RuBisCO activity. Observed converse of higher maximum photosynthesis rate values in plants at SP1 compared to the data obtained under natural CO<sub>2</sub> concentration can be caused by a number of factors. Thus, low values of SP1 plant gas exchange, compared to plants at SP2, can be connected with lower extent of stomatal conductivity (Table 3). As it is obvious from CO<sub>2</sub> curves analysis (Figure 1 and Table 4), under saturating CO<sub>2</sub> concentration the photosynthesis rate of plants growing at SP1 was higher by 40% in comparison with coastline plants.

This is the case due to both higher carboxylation reaction potential activity values ( $V_{max}$ ) of these plants and higher light reactions activity ( $J_{max}$ ) (by 40%) compared to coastline plants. As it is known from literature, there is the inverse relation of carboxylation reaction activity and the plant leaves thickness [17], and this is confirmed in our experiments (Tables 1 and 4). On the other hand, the converse of photosynthesis rate of plants at SP2 (the coastline) and SP1 at the shore under the natural and increased CO<sub>2</sub> concentration may be the case as the plants being under water for a long period of time have to use another carbon source - bicarbonate. If one supposes the presence of this mechanism in *T. maritima*, then on air under the natural CO<sub>2</sub> concentration the photosynthesis rate in coastline plants will be higher than that in plants growing at the shore. Recently, according to the similar data obtained on *Aster tripolium* growing at the White Sea coast as well, it was hypothesized that this plant has CO<sub>2</sub>-concentrating mechanism (CCM) [2]. Preliminary investigations have shown that for flooding period stomata of *A. tripolium* and *T. maritima* are open during light period of a day, which means their functional activity under water in slightly alkaline pH, when the main part of carbon is in the form of bicarbonate ion. As it is known, sea algae and vascular plants have CCM functioning under flooding conditions with involvement of carbonic anhydrase, which enhances bicarbonate degradation to CO<sub>2</sub> and optimizes activity of RuBP-carboxylase [18]. If we suggest the presence of this mechanism in SP2 seaside halophytes being under water for a long period of time (more than 6 hours a day),

**Table 3.** Gas exchange parameters of *Triglochin maritima* grown in different habitats.

Conditions	Gas exchange parameters			
	Photosynthetic rate, $\mu\text{mol CO}_2/(\text{m}^2 \text{ s})$	Transpiration rate, $\text{mmol H}_2\text{O}/(\text{m}^2 \text{ s})$	Stomatal conductance, $\text{mol H}_2\text{O}/(\text{m}^2 \text{ s})$	Internal $\text{CO}_2$ concentration, $\mu\text{mol CO}_2/\text{mol}$
At the shore, PP1	$4,7 \pm 0,7$	$1.4 \pm 0.2$	$0.06 \pm 0.01$	$188 \pm 15$
At the low tide line PP2	$7.9 \pm 0,9$	$2.9 \pm 0.4$	$0.12 \pm 0.02$	$207 \pm 13$



**Figure 1** Photosynthetic rate at various  $\text{CO}_2$  concentrations in the mesophyll intercellular space.

**Table 4.** Fitting parameters for the plots of  $\text{CO}_2$  exchange versus carbon dioxide content in *Triglochin maritima* leaves, as obtained from the model of Farquhar et al.

Parameters	Growth conditions	
	At the shore, PP1	At the low tide line, PP2
Maximal rate of $\text{CO}_2$ uptake, $\mu\text{mol CO}_2/(\text{m}^2 \text{ s})$	$143.2 \pm 7.6$	$87.9 \pm 8.1$
Maximal rate of carboxylation, $\mu\text{mol}/(\text{m}^2 \text{ s})$	$60.13 \pm 4.3$	$37.3 \pm 1.8$
Effectiveness of carboxylation, $\mu\text{mol CO}_2/(\text{m}^2 \text{ s Pa})$	$0.45 \pm 0.05$	$0.59 \pm 0.13$
Rate of electron transport at light saturation, $\mu\text{mol}/(\text{m}^2 \text{ s})$	$170 \pm 16$	$101 \pm 14$
Rate of triose-phosphate utilization, $\mu\text{mol}/(\text{m}^2 \text{ s})$	$17.2 \pm 1.2$	$7.4 \pm 0.8$
Rate of dark respiration in the light, $\mu\text{mol CO}_2/(\text{m}^2 \text{ s})$	$-10.9 \pm 0.8$	$-7.7 \pm 1.0$
Carbon dioxide compensation point, $\mu\text{mol CO}_2/\text{mol}$	$223.6 \pm 8.4$	$204.4 \pm 6.3$

then under natural  $\text{CO}_2$  concentration photosynthesis efficiency in coastline plants must be higher than that in shore plants, which is confirmed by our experimental data.

Also,  $\text{CO}_2$  compensation point, lower than this in SP1 plants, is the evidence of CCM functioning possibility in plants, which grow at the coastline and are subjected to more prolonged flooding. However,  $\text{CO}_2$  compensation point of *T. maritima* growing in different conditions are rather similar (the differences are about 10%), but in *A. tripolium* CCP value at the coastline is lower approximately by 30% compared to shore plants. These differences between two species may indicate the different CCM contribution in daily carbon metabolism: it is more significant for *A. tripolium* than for *T. maritima*.

CCM is related to inducible processes [18] and activates in case of  $\text{CO}_2$  deficiency for carboxylation reaction implementation. However, two halophytes of intertidal zone (*A. tripolium* and *T. maritima*.) inhabit different range of ecotopes. Thus, *T. maritima* can grow in wide range of ecotopes: swamps, alkali soils, but its favorite habitat is the banks of brackish ponds; *A.*

*tripolium* inhabits narrower range of ecotopes connected with only saline habitats [2]. If in halophylity both species are obligate halophytes, then in ecological valence width *T. maritima* is closer to eurybionts, and *A. tripolium* is closer to stenobionts, thus, the CCM contribution to carbon metabolism as well as that of optional carbon fixation mechanism can be different. The CMM contribution can be of special importance for plants inhabiting the littoral at high latitudes, where photosynthesis occurs during long polar day, and additional  $\text{CO}_2$  source should be more significant than that for plants of lower latitudes.

Obtained data allow considering another problem - simultaneous effect of several environmental stress factors in intertidal zone [19,20]. All halophytes of the White Sea coast intertidal zone growing along transects are perennials and accumulate sufficient biomass during the vegetation period that provides their successful ontogenesis. It assumes that for halophytes the conditions of intertidal zone are not stressful, and even under conditions of complete flooding the plants are more active than in low tide (Table 3). As it is known from literature, there is an interaction effect of different factors, that can influence vital

functions of organism both positively and negatively [21]. Thus, in our study, we marked two different states of tidal dynamic cycle in plants. Hence, environmental factors combination in SP1 shore halophytes of intertidal zone at low tide (air environment is coupled with higher CO<sub>2</sub> and O<sub>2</sub> values and high temperature for a long time) does not inhibit plant vital functions that is consistent with literature data, in which this interaction is interpreted as potentially positive [21]. The same positive effect was detected in SP2 plants at high tide (prolonged flooding is coupled with low illumination, changed gas environment in CO<sub>2</sub> and O<sub>2</sub> and lower temperatures). In literature, this combination is attributed to interactions that are not studied well [21]. Gradient short (for hours) multi day influence of low temperature, which provides consequently decrease of linear plant size and the increase of productivity, resistance and development enhancement, was referred to as "DROP-technology" and is widely used [22]. Certain parallel is the case also in the influence of different factors on the intertidal plants: the gradient conditions, short effect of factors which have level of values beyond the limits of optimum region, and its daily rhythm.

## Conclusion

This allows supposing that the intertidal halophytes have formed system feedback not to individual factors, but to its combination, that induces vital processes stimulation, and this ability is included in semidiurnal and circadian rhythm of organism vital functions. This research direction will allow better understanding of plant life on this unique natural area and deserves special attention. Contemporary studies have shown that under prolonged reaction of plants on the factors interaction the increase of plant resistance is indicated, that, according to the authors, is consistent with higher antioxidant ability and low level of reactive oxygen species

accumulation. In addition to that, transcriptome, metabolomic and proteomic analyses have demonstrated that various factors combinations can induce specific signaling pathways, which provide the feedback reaction of organism. The assumption about the presence of sensors, which are sensitive to alterations of physical features of membranes disregarding nature of the stress influence, is one of such hypothesis. These sensors should be either transmembrane or associated with membranes (Hik33, Sln1p or mechanosensitive calcium and potassium channels). Due to the fact that the cyclical tides are the leading processes determining the variability and instability of ecological conditions, attention should be paid to the mechanosensitive calcium and potassium channels for the ecological situation at intertidal zone.

The conducted study has shown that the plants of intertidal zone within the populations of one species have the differences in leaf morpho- and mesostructures and functional activity of light and dark reactions of photosynthesis depending on the position at the littoral. The halophyte capability of growing in the wide range of ecotopes in various seaside ecosystems indicates the presence of systemic reaction at the level of organism, and its involvement in daily rhythm of physiological processes as a response on the rhythm of ecological factors at intertidal zone. Adoptive facilities of intertidal halophytes are connected with the high level of their structural and functional flexibility.

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## References

- 1 Siira J (1987) On the vegetation and ecology of saline and brackish marshes in Finnmark (Norway). *Aquilo. Ser. Bot. Oulu* 24: 15-17.
- 2 Markovskaya EF, Sergienko LA, Shklyarevich GA, Sonina AV, Starodubtseva AA, et al. (2010) *The Natural Complex of the White Sea Coastlines: a Study Guide*. Petrozavodsk: the KarRC of the RAS.
- 3 Kirillova NR (2013) The Populations of *Triglochin maritima* L. (Yuglandaceae) in Limnodioms of the Murmansk Region. *Biodiversity and Cultural Cenosis in Extreme Conditions. Proceedings of the II All-Russian Scientific Conference with International Participation. Apatity*.
- 4 Dregelyi-Kiss A, Dregelyi-Kiss G, Hufnagel L (2008) Ecosystems as climate controllers - biotic feedbacks. *Applied ecology and environmental research* 6: 111-134.
- 5 Armstrong W, Brandle R, Jackson MB (1994) Mechanisms of flood tolerance in plants. *Acta Botanica Neerlandica* 43: 307-310.
- 6 Makarov MV, Ryzhik IV, Voskoboinikov GM (2012) The Effect of *Fucus vesiculosus* L. Depth of Vegetation in the Barents Sea on Its Morpho-Physiological Parameters. *Algology* 4: 345-348.
- 7 Maricle BR, Koteyeva NK, Voznesenskaya EV, Thomasson JR, Edwards GE (2009) Diversity in leaf anatomy, and stomatal distribution and conductance, between salt marsh and freshwater species in the C4 genus *Spartina* (Poaceae). *New Phytologist* 184: 216-220.
- 8 Mommer L, Visser EI (2005) Photosynthesis in Flooded Terrestrial Plants: A Matter of Leaf Plasticity. *Annals of Botany* 96: 581-585.
- 9 Smith FA, Walker NA (1980) Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO<sub>2</sub> and HCO<sub>3</sub> and to carbon isotopic discrimination. *New Phytologist* 86: 245-248.
- 10 Anderson U, Samson I, Levinsh G (2012) Protection of photosynthesis in coastal salt marsh plants *Aster tripolium* and *Hydrocotyle vulgaris* in conditions of increased soil salinity. *Environmental and Experimental Biology* 10: 89-91.
- 11 Flowers T, Galal H, Bromham L (2010) Evolution of halophytes: multiple origins of salt tolerance in land plants. *Functional Plant Biology* 37: 604-608.
- 12 Mokronosov AT, Borzenkova RA (1978) Method of Quantitative Assessment of the Structure and Functional Activity of Photosynthesizing Tissues and Organs. *Works on Applied Botany, Genetics and Selection* 61: 119-221.
- 13 Farquhar GD, Von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> plants. *Planta* 149: 78-80.
- 14 Harley PC, Sharkey TD (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. *Photosynthesis Research* 27: 169-173.
- 15 Parsons R, Ogston S (1999) *Photosynthesis Assistant: Tools for analysis of photosynthetic data (Ver 1.1.2.)*. Dundee Scientific, United Kingdom.
- 16 Morozova KV, Anisimova DI (2015) Anatomic-Morphological Characteristics of Arrow Grass Leaves (*Triglochin maritima* L.) in Seacoast Communities on the White Sea Coast (Karelia). *Modern Problems of Science and Education. Scientific and Methodological Journal* 7: 40-43.
- 17 Walker AP, Beckerman AP, Gu L, Kattge J, Cernusak LA, et al. (2014) The relationship of leaf photosynthetic traits - V<sub>cm</sub> and J<sub>max</sub> - to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution* 4: 3218-3221.
- 18 Pederson O, Colmer TD, Sand-Jensen K (2013) Underwater photosynthesis of submerged plants-recent advances and methods. *Front. Plant. Sci.* 140: 20-24.
- 19 Levinsh G (2006) Biological basis of biological diversity: physiological adaptation of plants to heterogeneous habitats along a sea coast. *Acta Universitatis Latviensis* 710: 53-56.
- 20 Leysan R, Kayumova LR, Zakirova VG (2016) Educational Environment Risks: Problems of Identification and Classification. *International Journal of Environmental and Science Education* 11: 1013-1019.
- 21 Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R (2016) Abiotic and biotic stress combinations. *New Phytologist* 203: 32-34.
- 22 Markovskaya EF, Sysoeva MI, Sherudilo EG (2013) *Short-Term Hypothermia and Plants*. Petrozavodsk: the KarRC of the RAS.