

Ecological and biological features of *Triglochin maritima* L. in the biotopes of the littoral zone with different degree of flooding on the coast of the White Sea

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Abstract

The study of *Triglochin maritima* L. was carried out on the Pomor (western) coast of the White Sea, in the Republic of Karelia (64°22'81"N, 35°93'14"E). Morphological analysis of aboveground and underground parts of the clones was performed on virginal plants. Anatomical analysis of leaf sheaths of the current year shoots, rhizomes and adventitious roots was carried out. The viability of pollen was assessed by determining the relative share of normally developed and malformed pollen grains. The content of heavy metals was determined in the soil, sea water and plant samples. The study was carried out on a model transect in the littoral zone on three test plots representing the lower littoral; the middle and the upper littoral zones. Adaptation to wave and storm impact was manifested in a well-developed system of underground organs. In the lower littoral, underground part surpasses the aboveground vegetative organs in terms of the mass and the formation of mechanical tissues. This allows the plants to anchor stronger in the substrate. Pollen analysis confirmed the adaptability of *T. maritima* plants to the conditions of the lower littoral by a high percentage of normal and, consequently, fertile pollen, which ensures sexual reproduction of the species. *T. maritima* can be considered as a Fe hyperaccumulator as the plant accumulates very high levels of Fe (22–34 g kg⁻¹), especially in the lower and middle littoral zones, both in underground and aboveground organs. The ability of *T. maritima* plants to actively deposit metals was revealed on the basis of the coefficient of biological absorption of metals and makes it possible to suggest potential possibility of using the species in phytoremediation technologies on coastal territories.

Key words: anatomy of vegetative organs, *Triglochin maritima*, clone morphology, pollen grain, heavy metal, coefficient of biological absorption, hyperaccumulator

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Introduction

Considerable attention nowadays is paid to the Arctic region (Minin 2014). Great prospects for economic development in the Arctic raise active discussion in the scientific community and stimulate multidisciplinary research, including studies of the vulnerability of different types of ecosystems and their components. The study of coastal ecosystems is necessary due to offshore hydrocarbon activity in the Arctic marine area (Dmitrievsky *et al.* 2015). Along the White Sea coast, tides create very dynamic and unstable environment so that littoral biota, including phototrophic organisms, has to adapt to it. The numbers of dominant vascular plants on the coasts of northern seas are much less compared to southern seas. The biology and ecology

of the halophyte *Triglochin maritima* L. has been studied (Davy and Bishop 1991, Buzgo *et al.* 2006, Bobrov 2018, Buffington *et al.* 2020, Edge *et al.* 2020). On the coast of the White Sea, cenopopulations of this species were studied on silty and sandy-pebble substrates in the diurnal dynamics of flooding (Sergienko *et al.* 2017). However, in general, the ecological and biological features of the species ensuring the successful survival and reproduction under dynamic conditions of the littoral zone are much wider and are still poorly understood. The purpose of this work was to evaluate ecological and biological characteristics of *T. maritima* on the White Sea coast in the littoral biotopes with different degree of flooding.

Material and Methods

T. maritima is a circumboreal temperate arctic species (Tsvelev 2000), often dominating in plant communities of coastal and marsh ecosystems. The biological feature of the species is the formation of a clonal biomorph, which ensures high tolerance to unstable environmental conditions. *T. maritima* is a herbaceous perennial with a long and branched rhizome, sometimes forming a rhizome ring protruding above the substrate. On the rhizome, ramets (shoots of vegetative origin) with fleshy basal narrow-linear leaves, 2–5 mm wide, develop annually. A mass is also formed from the sheaths of last year dead leaves. Peduncles are up to 45–50 cm. The study was carried out on the Pomor (western) coast of the White Sea, in the vicinity of the village Rastnavolok of the Belomorsk region (Republic of Karelia; 64°22'81"N, 35°93'14"E) (Fig. 1). A model transect (MT) 500 m long and 5 m wide was established from the water edge (lower littoral) to the bedrock coast (supralittoral) during the period of complete low tide. This part of the coast is the mouth of a small stream, widened

towards the sea. The estuarine zone, 180 m wide, reached a small rocky ridge covered with sandy-silty sediments. The central part of the transect was a slightly silted depression overgrown with fragmentary clumps of coastal plants. Water salinity did not exceed 17‰. The transect was divided into three zones with different types of substrate and floristic composition. The 1st zone located in the lower littoral, at the water edge and protected by a stone ridge, was inhabited by four plant species: *T. maritima*, *Tripolium pannonicum* (Jacq.) Dobrocz., *Plantago maritima* L. and *Glaux maritima* L. (cover up to 1%), with a predominance of *T. maritima* (10%) and *P. maritima* (10%). In the 2nd zone (the middle littoral), *T. maritima* also dominated in the communities with *Ruppia maritima* L. and *Carex mackenziei* V. Krecz. In the 3rd zone (the upper littoral, near the bedrock coast), *T. maritima* was a codominant in communities with *Bolboschoenus maritimus* (L.) Palla and *T. pannonicum*.

The study was carried out on three test plots (TP). TP1 (the 1st zone) was located at the water edge on the lower littoral; 300 m in length; substrate – clay:sand / 60:40%. TP2 (2nd zone) was located in the central part of the transect in the middle

littoral; 20 m in length; substrate – clay:sand:pebbles / 10:10:80). TP3 (3rd zone) was located near the bedrock in the upper littoral; 35 m in length; substrate – clay:sand:pebbles / 20:20:60).



Fig. 1. Map of the study area.

Morphological and anatomical analysis

The clones from three zones of the transect were separated into ramets. The number of clones in a ramets and fresh weight of the aboveground and underground parts of the clones were determined. Morphological analysis was performed on virginal (adult vegetative) shoots ($n = 10$). The shoot height, number and length of leaves, and length of adventitious roots were measured. To determine the anatomical parameters of vegetative organs they were fixed in 70% ethanol. Leaf sheaths of shoots of the current year (from the 1st, 2nd and 3rd zones), rhizomes (from the 1st and 2nd zones), and adventitious roots (from the 1st, 2nd and 3rd zones)

($n = 30$) were analyzed. Anatomical structures were measured on cross sections by a MIKMED–6 light microscope (LOMO, Russia). The assessment of the morphometric parameters of sheath mesostructure was carried out according to the method of Mokronosov and Borzenkova (1978). The volume of cells and intercellular spaces in tissues of vegetative organs was determined using the ellipsoid formula, as the ratio L/d is less than 2.5:

$$V = 4/3\pi * L/2 * (d/2)^2, \quad \text{Eqn. 1}$$

where L is the cell length, d is the cell width or diameter (Borzenkova and Khramtsova 2006).

Pollen analysis

Anthers were collected from 10 plants (one flower per plant) in each zone (n=600). Pollen viability was assessed using an acetocarmine test. For microscopic analysis, anthers were removed from fixed flowers and broken mechanically in a drop of acetocarmine on a glass slide (Pausheva

1980). The relative share of normally developed and malformed pollen grains was determined using a light microscope Axio Scope A1 (Carl Zeiss, Germany) at a 400 magnification. The descriptions of pollen grains given in the literature (Pires and Medeanic 2006) served as a reference.

Chemical analysis

In the middle part of each SP, 3 soil samples and samples of 5 plants were collected to determine the content of heavy

metals in soil and plant samples (from adventitious roots and aboveground organs).

Measurements of heavy metals

The concentration of Fe, Cu, Zn, Pb, Mn and Ni was estimated using the atomic absorption spectrophotometer AA-7000 with a flame atomizer, Shimadzu 7000 (Japan). The samples (0.2 g) were first dissolved in a mixture of concentrated acids (HNO₃, HCl, in the ratio 3:1) in the microwave digestion system (Speedwave four, Berghof, Germany). The heavy metal concentrations were measured at the Center of Shared Equipment Use «Analytical laboratory» of Forest Research Institute of the Karelian Research Centre of RAS (ISO

11466:1995, NBN EN 13657:2002, ISO 11407:1998, ISO 20280:2007). All measurements were done in triplicate. The coefficient of biological absorption (CBA) of Fe, Cu, Zn, Pb, Mn and Ni by a whole plant was calculated as a ratio of the metal content in the plant (in adventitious roots and aboveground organs) to the metal content in the soil and sea water (Polynov 1956, Batalov *et al.* 1991). The higher the value of CBA, the more intensively the element is absorbed by the plant (Polynov 1956).

Measurements of salinity and the content of chemical elements in soil and water

Field seawater salinity was determined using a refractometer RHS-10ATC (Russia). The degree of soil salinity was estimated by the mass fraction (%) of dry (dense) organic extract residue, the content of matter was determined by the method according to I.V. Tyurin (Vorobeva 2006). Total nitrogen was determined using ulti-

mate CHNS analyzer (PerkinElmer's 2400 Series II CHNS/O, USA). The phosphorus content was determined by the ammonium-molybdate method using spectrophotometer (OKB Spektr SF-2000, Russia). Labile potassium was determined by flame atomic absorption spectrophotometer (Shimadzu AA 7000, Japan) (Tan 2005).

Statistical analysis of the data obtained was carried out using Microsoft Excel, Statgraphics for Windows. The significance

of the differences in the parameters was assessed by the Student's *t*-test at P=95%.

Results

Morphological and anatomical analysis

According to the phytocoenotic biomorph, *T. maritima* belongs to the implicit polycentric type, characterized by the fact that adult plants have several closely located growth centres, which were difficult

to distinguish. The phytomass is distributed over the area occupied by an individual relatively evenly. The general view of the clones within the transect is shown in Fig. 2.



Fig. 2. *Triglochin maritima* on the model transect (foto by A.V. Sonina).

The aboveground part of the clone is represented by a set of closely located rosette shoots with two-row leaves with fleshy widened sheaths. The underground part of the clone consists of a strong rhizome with numerous adventitious roots and dead leaf sheaths of the last year (*see* Fig. 3).

The clone growth and biomass accumulation occur due to the branching of short rhizome (in a “net” mode) with a dense “brush” of firmly and closely seated sheaths of dead leaves, a large number of

adventitious roots and annually formed ramets. In each zone, the biomass of the clone underground part (rhizome with adventitious roots and sheaths of dead leaves) exceeded the biomass of the aboveground part by 1.5–2 times (Table 1). The highest total clone biomass was recorded in the 3rd zone while the lowest biomass was fixed in the 1st zone at the water edge. The same order was observed for the number of ramets in the clone. Their number increased from the water edge to the upper littoral zone.



Fig. 3. Part of the clone with a rhizome, adventitious roots, sheaths of last year dead leaves and aerial shoots of the current year (foto by A. V. Sonina).

Parameters	Zone		
	1	2	3
Number of ramets in clone, pcs.	24	75	116
Fresh weight of the clone aboveground part, g.	64.5	179.4	257.2
Fresh weight of the clone underground part, g.	92.3	355.0	340.0

Table 1. General characteristics of the *Triglochin maritima* clones.

Virginile shoots increased along the transect from 28–35 cm in the 1st zone to 38–40 cm in the 3rd zone. The shoot height in the 1st zone significantly differed from those in the 2nd and 3rd zones (Fig. 4). The number of leaves on the shoots was significantly higher in the 2nd zone than in the 1st and 3rd zones, where the same number of leaves was recorded. The leaf length was the smallest in the 1st zone. There were no significant differences in the length of adventitious roots in different zones, al-

though there was a tendency to its increase towards the 1st zone (Fig. 4).

In general, *T. maritima* clones growing in the lower littoral zone (the 1st zone) showed the lowest biomass, smaller number and morphological parameters of ramets (with the exception of adventitious roots length), which may indicate adaptation of plants to specific growth conditions. These plants need to be better anchored being in the zone of the greatest wave impact.

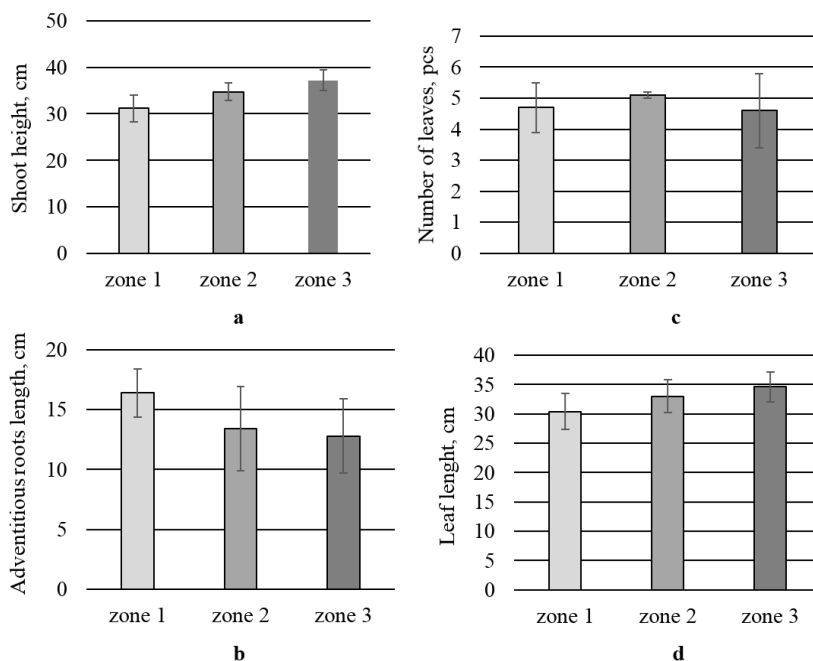


Fig. 4. Morphology of plants from different littoral zones: **a** – shoot height, **b** – adventitious roots length, **c** – number of leaves, **d** – leaf length.

The current year leaf sheaths were thicker in the 1st zone 1 (Table 2). Towards the upper littoral (the 3rd zone) the values of leaf sheaths thickness decrease. The leaf sheaths were covered with cuticle, the thickness of which increased along the transect towards the upper littoral. The cell size (length and width) of the upper and lower epidermis decreased from the 1st to the 3rd zone as the thickness of the sheaths do. In the upper epidermis, cell size was significantly different in three zones. The main part of the leaf sheaths was formed by aerenchyma, the cell volume of which increased from the 1st zone to the 3rd one by 1.3 times. The volume of intercellular spaces of aerenchyma also increased by almost 2.3 times. At the same time, a decrease in the vein diameter from the 1st zone to the 3rd one was recorded (Table 2).

The values of anatomical parameters of the rhizomes of *T. maritima* in the tidal

zone decreased from the 1st zone up to the 3rd one (Table 3). The primary cortex formed the largest part of the rhizome with intercellular spaces. The rhizomes of *T. maritima* had well-developed mechanical tissue represented by sclereids. Two or three layers of sclereids were apparent in the primary cortex under the epidermis and separate cell groups were in the central cylinder of the rhizome. The volume of sclereids in the primary cortex was 2 times greater than in the central cylinder. The most significant decrease (by 1.5 times) in the values along the transect was found in the thickness of the sclereid layer and in the volume of the storage parenchyma cells in the primary cortex.

For adventitious roots, length and width of epibleme or rhizodermal cells (the covering tissue) cells in plants from the 1st zone were 1.5 times greater than in plants from the 3rd zone (Fig. 5).

Parameters		Zone		
		1	2	3
Leaf sheaths thickness, μm		1 503.0 \pm 7.4*	1 400.6 \pm 9.2*	1 300.0 \pm 8.1*
Cuticle thickness, μm		6.7 \pm 0.2*	8.1 \pm 0.3*	12.7 \pm 0.1*
Upper epidermis	Cell length, μm	44.6 \pm 1.0*	39.0 \pm 1.0*	37.0 \pm 0.7*
	Cell width, μm	31.2 \pm 1.0*	28.6 \pm 0.7*	26.5 \pm 0.8*
Lower epidermis	Cell length, μm	37.4 \pm 1.1*	34.4 \pm 0.8	33.5 \pm 0.4
	Cell width, μm	24.1 \pm 0.6*	22.3 \pm 0.6	22.1 \pm 0.4
Volume of aerenchyma cells, thousand μm^3		162.5 \pm 15.8*	189.5 \pm 15.6	215.2 \pm 12.4*
Volume of aerenchyma intercellular spaces, thousand μm^3		3 118.3 \pm 201.4*	3 887.2 \pm 160.7*	7 032.8 \pm 265.5*
Vein diameter, μm		96.3 \pm 1.3*	85.6 \pm 3.0*	76.6 \pm 2.0*

Table 2. Anatomical parameters of leaf sheaths of *Triglochin maritima*.

Note: * differences in the parameters of plants from different zones of the transect are significant ($p < 0.05$).

Parameters		Zone	
		1	2
Epidermis	Cell length, μm	26.1 \pm 0.5*	23.1 \pm 0.6
	Cell width, μm	18.1 \pm 0.5*	16.0 \pm 0.5
Primary cortex thickness, μm		1 368.0 \pm 19.3*	1 236.5 \pm 20.7
Thickness of sclereid layer in primary cortex, μm		113.5 \pm 3.4*	70.7 \pm 2.0
Cell volume, thousand μm^3	storage parenchyma in the primary cortex	9.7 \pm 0.3*	6.0 \pm 0.4
	sclereids in the primary cortex	6.3 \pm 0.5*	4.8 \pm 0.3
	sclereids in the central cylinder	3.2 \pm 0.3*	2.4 \pm 0.3
Volume of intercellular spaces in primary cortex, thousand μm^3		51.7 \pm 3.0*	40.6 \pm 3.0

Table 3. Parameters of the anatomical structure of rhizomes of *Triglochin maritima*.

Note: * differences in the parameters of plants from different zones of the transect are significant ($p < 0.05$).

Exoderm cell sizes differed significantly among plants from three different zones. The mesoderm formed the main part of the root. Its cells were larger than other cortex cells. The size of the mesoderm cells was 2 times larger than the exoderm cells and 2.5–3 times larger than the endoderm cells. In the 1st and 2nd zone, there were no sig-

nificant differences in the length and width of mesoderm cells, but they were 1.5 times smaller in the 3rd zone. Starch grains were stored in this tissue. Intercellular spaces volume reached, $2\,480 \pm 318$ thousand μm^3 (1st zone), $1\,880 \pm 214$ thousand μm^3 (2nd zone), and $1\,400 \pm 158$ thousand μm^3 (3rd zone). The thickness of the mesoderm

decreased from $540 \pm 5 \mu\text{m}$ (the 1st zone) to $514 \pm 4 \mu\text{m}$ (the 2nd zone) and ended with $469 \pm 8 \mu\text{m}$ (the 3rd zone). Endoderm cells were the smallest among the cells of root tissues. In the 1st zone, the length and width of endoderm cells significantly differ from the sizes of cells in the 2nd and 3rd zones, where no significant differences were found.

The thickness of leaf sheaths, size of the cells of the upper and lower epidermis, diameter of veins, anatomical parameters of rhizomes and adventitious roots decreased, while the thickness of the cuticle and the volume of aerenchyma cells and intercellular spaces in leaf sheaths increased along the transect from the lower to upper littoral.

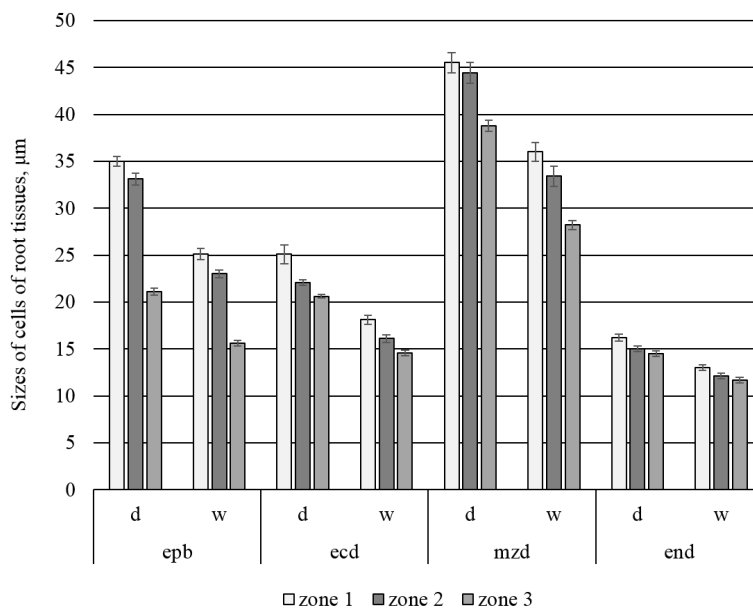


Fig. 5. Sizes of cells of root tissues of *Triglochin maritima*.

Note: epb – epibleme, ecd – exodermis, mzd – mesoderm, end – endoderm, d – cell length, w – cell width.

Palynological analysis

Palynological analysis showed that from 62 to 93% of *T. maritima* pollen grains corresponded to the norm described in the literature (Pires and Medeanis 2006, Halbritter 2016): they have a rounded or slightly elongated shape, a distinct reticular-columnar structure of the exine, stained dark pink with acetocarmine. The cytoplasm of the vegetative cells was uniformly structured and stained, nuclei were visible; no aperture; zone of exine thinning for the emergence of a pollen tube was

not visible. The CV values for normally formed pollen differed between the transect zones more than twice, but varied within 7% (Table 4).

The most common observed defect in the pollen structure was lumpy, unevenly stained cytoplasm of the vegetative cell (1.5–10.0%; CV 23–33%). The second most common developmental defect was empty pollen grains (0.2–1.7%; CV 75–100%). Such pollen grains do not have cytoplasm and generative cells, and their

membranes are almost unstained. Specific developmental defects of pollen were recorded for plants growing in the 2nd and 3rd zones. Pollen grains underwent destruction at the tetrad stage. They were without content and showed no response when stained with carmine (6.8–27.3%; CV 12–76%). This type of defects in development was observed almost four times more often in plants from the 3rd zone than in the other

ones. The quality of pollen from the plants of the 3rd zone was weak. Normally developed pollen grains reached minimum relative share, while cytoplasmic structural defects and destructed tetrads reached maximum share. This was probably due to the fact that this part of the tidal zone was exposed to air (*i.e.* not flooded) during the longest periods.

Pollen grain morphology		norm	empty	lumpy cytoplasm	gigant	dwarf	tetrads
Zone 1	%	91.9±2.3	1.7±1.7	5.7±1.3	0.4±0.4	0.3±0.2	0
	CV	3	100	23	100	67	0
Zone 2	%	78.9±5.3	1.6±1.2	1.5±0.5	1.0±0.7	10.2±2.5	6.8±5.2
	CV	7	75	33	70	24	76
Zone 3	%	62.6±4.2	0.2±0.2	10.0±2.9	0.1±0.2	0	27.3±3.5
	CV	7	100	29	200	0	13

Table 4. Analysis of the morphological structure of *T. maritima* pollen grains.

Notes: norm – pollen grains of normal morphological structure; empty – pollen grains without content; lumpy cytoplasm – pollen grains with unevenly stained cytoplasm shrinking away from the cell wall; giant – pollen grains, the size of which exceed the norm by 1.5 or more times; dwarf – pollen grains, the size of which is 1.5 or more times less than normal; tetrads – undivided pollen grains without content.

Content of elements in sea water and littoral soils

Sea water in the area where *T. maritima* grows was contaminated with Ni (14.8 maximum permissible concentration – MPC) and Pb (2.4 MPC); the values for nitrates were close to MPC (0.9 MPC). The content of Fe, Mn and Zn in water exceeded the background by factors of 4, 5.5 and 2.8, correspondingly. The Cu content in sea water was low, not exceeding background values (Table 5).

The littoral soils were not contaminated

with heavy metals. The contents of Cu, Zn, Pb and Ni did not exceed the values of the background content in the bottom sediments. Fe content reached 14 000 mg kg⁻¹ and Mn – 71 mg kg⁻¹. The content of macronutrients (N, P, K and C) in the littoral soils was also low compared to gray forest soils (Table 5). The content of metals in soils increased from the 1st to the 3rd zone, on average by 1.5–2.5 times (Table 5).

The content of heavy metals in T. maritima plants

Fe content in *T. maritima* plants (22–34 g kg⁻¹) was significantly higher than the known critical level for Fe in plants. In *T. maritima* plants Fe was dominating accumulated metal. The content of other

metals was much lower. Mn ranged 173–219 mg kg⁻¹, Cu: 22–36 mg kg⁻¹, Zn: 36–43 mg kg⁻¹, Pb: 16–24 mg kg⁻¹ and Ni: 13–18 mg kg⁻¹. These values did not exceed the MPC values in plants.

Element	Soil										
	C, %	N, %	P, %	K (mg kg ⁻¹)	Fe (mg kg ⁻¹)	Mn (mg kg ⁻¹)	Cu (mg kg ⁻¹)	Zn (mg kg ⁻¹)	Pb (mg kg ⁻¹)	Ni (mg kg ⁻¹)	
Zone 1	0.58±0.28*	0.06±0.01*	0.04±0.001	145.20±30.29*	6145.93±982.63*	41.32±6.20*	9.01±0.23*	9.96±0.80*	1.48±0.48*	6.36±0.12*	
Zone 2	2.07±1.04	0.24±0.16*	0.05±0.03	348.87±181.33*	18113.84±3552	87.07±20.12	12.83±5.26	21.24±5.21	7.70±2.14	10.19±2.87	
Zone 3	3.27±0.25	0.29±0.15*	0.04±0.001	235.25±25.63*	17115.09±4524	83.94±14.88	13.27±0.65	20.68±3.98	5.67±1.31	10.27±1.77	
Min	0.30	0.05	0.04	114.90	5163.30	35.12	8.78	9.16	1.00	6.23	
Max	4.52	0.46	0.07	454.98	25374.5	117.61	16.71	26.65	9.95	13.11	
M	1.98	0.20	0.05	243.11	13791.62	70.78	11.71	17.29	4.95	8.94	
Background ^{1,2}	45.70 ¹	2.17 ¹	0.10 ¹	14191 ¹	17505 ¹	282 ¹	18 ²	62 ²	15 ²	30 ²	
APC ³	-	-	-	-	46500	1500	35 ³	150 ³	30 ³	30 ³	
Sea water											
Element	NO ₃ ⁻	Cl ⁻	mineralization,	Fe	Mn	Zn	Ni	Cu	Pb		
	mg l ⁻¹	mg l ⁻¹	g l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹		
Background ⁴	43.68	1.76	7.8	0.04	0.011	0.028	0.148	0.00001	0.024		
MPC ⁵	39	2.5	-	0.01	0.002	0.01	0.002	0.0003	0.00003		
				0.05	0.05	0.05	0.01	0.005	0.01		

Table 5. Content of elements in sea water and littoral soils.

Notes: M – mean value; min – minimum; max – maximum value; 1 – Background concentrations in mineral upper soil layers – average data for Karelia (Terebova et al. 2017); 2 – Background values of heavy metals in bottom sediments of the seas (Novikov 2017); 3 – APC – approximately permissible concentrations for uncontaminated bottom sediments according to SFT for Zn, Cu, Ni and Pb (Ilyin et al. 2015); 4 – Background values of analyzed parameters in the seawater ([1] - Order of the Ministry 2016); 5 – MPC – maximum permissible concentrations (MPC) in seawater of fishery facilities ([1] - Order of the Ministry 2016); * differences in the content of metals in the whole plant in different zones are significant (p < 0.05).

The total content of all investigated metals was highest in the 1st zone – 34 g kg⁻¹. In the 2nd and the 3rd zones the total content of all studied metals was 22–23 g kg⁻¹. (Table 6).

Element	Fe mg kg ⁻¹	Mn mg kg ⁻¹	Cu mg kg ⁻¹	Zn mg kg ⁻¹	Pb mg kg ⁻¹	Ni mg kg ⁻¹	TMC g kg ⁻¹
Zone 1							
M roots	29 077.96 ±55.25	103.25 ±21.24	23.88 ±4.52	26.68 ±2.89	22.32 ±2.85	9.57 ±1.58	29 ±1*
M aboveground organs	4 883.99 ±115.21	77.84 ±15.28	4.11 ±1.07	8.99 ±1.96	2.08 ±0.85	3.67 ±0.52	5 ±0.5
M plant, mg kg ⁻¹	33 961.94 ±7.56*	181.09 ±15.29*	27.99 ±3.25	35.68 ±2.89*	24.40 ±3.25*	13.24 ±3.36*	34 ±3*
CBA roots	4.73	2.50	2.65	2.67	15.11	1.47	
CBA aboveground organs	0.79	1.88	0.46	0.90	1.41	0.56	
CBA whole plant	5.53	4.38	3.11	3.57	16.53	2.04	
Zone 2							
M roots	18 538.98 ±201.63	142.54 ±15.65	17.36 ±3.58	33.94 ±2.45	15.12 ±1.52	14.98 ±2.87	19 ±2
M aboveground organs	3 955.82 ±325.00	76.58 ±8.96	4.43 ±1.00	9.56 ±1.69	1.70 ±0.78	3.42 ±1.20	4 ±0.2
M plant, mg kg ⁻¹	22 494.80 ±154.25	219.12 ±10.23*	21.79 ±4.85	43.50 ±5.85	16.82 ±3.87	18.40 ±1.85	23 ±2
CBA roots	1.02	1.64	1.35	1.60	1.96	1.45	
CBA aboveground organs	0.22	0.88	0.35	0.45	0.22	0.33	
CBA whole plant	1.24	2.52	1.70	2.05	2.18	1.78	
Zone 3							
M roots	20 580.64 ±252.23	147.19 ±25.63	31.34 ±5.85	33.62 ±2.96	17.51 ±2.54	14.53 ±3.69	20 ±3
M aboveground organs	1 526.83 ±25.87	26.37 ±9.00	4.99 ±0.52	7.23 ±1.24	1.17 ±0.23	1.54 ±0.05	2 ±0.9
M plant, mg kg ⁻¹	22 107.47 ±127.00	173.56 ±8.23	36.33 ±1.89*	40.85 ±5.12	18.69 ±4.21	16.07 ±5.78	22 ±3
CBA roots	1.20	1.75	2.36	1.62	3.09	1.39	
CBA aboveground organs	0.09	0.31	0.38	0.35	0.21	0.15	
CBA whole plant	1.29	2.07	2.74	1.97	3.29	1.54	
Critical level of element in plants ¹ , mg kg ⁻¹	>500	300-500	20-100	>100	20-300	10-100	

Table 6. The average values of the element contents (M) and the coefficient of biological absorption (CBA) of metals by adventitious roots, aboveground organs and whole plant of *Triglochin maritima* in different zones along the flooding gradient. *Notes:* TMC – Total metal content. *Critical level of element in plants, mg kg⁻¹ (Pendias 2010); *differences in the content of metals in the whole plant in different zones are significant ($p < 0.05$).

T. maritima plants accumulated metals by the whole plant (CBA>1). However, roots accumulated metals more intensely than aboveground organs (Table 6). Metal accumulation by the whole plant followed the order: Pb (7.33) > Mn (2.99) > Fe

(2.69) > Zn (2.53) > Cu (2.51) > Ni (1.79). The CBA for Pb was very high (Table 6). Plants from the 1st zone had the maximum CBA of metals, compared to the plants in the 2nd and 3rd zones (Table 6).

Discussion

T. maritima dominated vegetation cover of the littoral zone within the studied transect. It has an important role in stabilization of initial communities (Sergienko 2008). In the present study, a complex of biological and environmental parameters was analyzed, which allowed to identify some adaptive features of *T. maritima* to specific environmental conditions. It was found that *T. maritima* plants successfully grown within the entire transect, where conditions differed due to tidal dynamics. In the 1st zone, plants have adapted by decreasing vegetative aboveground biomass, number of ramets in a clone and increasing adventitious root length (Table 1). Such adaptations may provide them stronger anchoring than in other two zones. This corresponds with increased length and width of root cells. Consequently, thickness of roots of plants in the 1st zone was significantly greater than in plants in the 3rd zone. A similar change in tissue cell size was found in rhizomes. The mechanical tissue of sclerenchyma was well developed in rhizomes, which also aimed at the sustainable existence of *T. maritima* plants under unstable conditions. Intensive formation of mechanical tissues in the aboveground and underground vegetative organs of different types of halophytes was also reported in other works (Nagalevsky 2001). The presence of sclerenchyma in rhizomes contributes to the retention of *T. maritima* plants under conditions of tidal dynamics, especially in the 1st zone, where the greatest thickness of the sclereid layer in the primary cortex was determined.

In the aboveground organs at the water edge (in the 1st zone), thickening of leaf sheaths was revealed, while the cuticular layer was reduced. Similar data were obtained for leaves of *T. maritima* in the tidal zone of the White Sea (Morozova and Anisimova 2015). Thin cuticles were also observed in other halophytes (Nagalevsky 2001, Markovskaya and Gulyaeva 2020). This might be associated with the regulation of transpiration since the plants growing in the lower littoral do not save water in contrast to plants in the upper littoral (*i.e.* not flooded and exposed to air for longer periods). Volumes of aerenchyma cells and intercellular spaces also increase towards the upper littoral in leaves (Morozova and Anisimova 2015) and their sheaths, which indicates an increase in oxygen and carbon dioxide supply in plants from the 3rd zone with irregular water supply and high illumination.

Anatomical features of *T. maritima* vegetative organs are consistent with the data on the accumulation and distribution of metals in the tissues and organs of plants depending on the habitat state. In the lower littoral zone plant had more developed protective tissues (epiblema, exoderm, mesoderm, endoderm) in adventitious roots (Table 3, Fig. 5) and higher concentrations of accumulated metals (especially Fe in the roots) compared to the plants in the upper littoral zone (Table 6). According to their role in metal metabolism, root tissues can be divided into five groups: (1) absorbers responsible for the absorption of heavy metals from the environment (epiblema with

rhizodermal transfer cells); (2) tissues performing barrier function, which limit the radial transport of metals in the roots (endoderm); (3) metal accumulators (exoderm, mesoderm); (4) collectors that ensure the redistribution of ions along the perimeter of the central cylinder and their entry into conducting system (pericycle); (5) inter-organ transporters that participate in the long-distance transport of metals through the plant (xylem, phloem) (Seregin and Kozhevnikova 2008). Consequently, the more developed the primary root bark, the more metal ions can be absorbed and accumulated in plant roots. Due to the root accumulation of heavy metals, plant roots along with bacteria and fungi, are used in wastewater phytoremediation (Choubey and Godbole 2021). High adsorption capacity of roots of freshwater plants (*Eichhornia crassipes* (Mart.) Solms, *Tripa latifolia* L., *Sparganium minimum* Wallr. and *Menyanthes trifoliata* L.) to absorb copper, lead, uranium and mercury ions from aqueous solution was established (Zheng *et al.* 2016, Robichaud *et al.* 2021).

In general, the littoral soil in the study area was not contaminated, but increased concentrations of some elements were revealed in water, for example, Ni concentration was 0.148 mg l^{-1} , Pb – 0.024 mg l^{-1} (Table 5). Thus, water was contaminated with Ni (14.8 MPC), Pb (2.4 MPC) and nitrates (0.9 MPC). According Ilyin *et al.* (2015), the input of nutrients and pollutants in the White Sea occurs with the runoffs of large rivers (the Onega, Severnaya Dvina, Kem, Nizhniy Vyg, Verkhniy Vyg, Keret). The volume of wastewater discharged into surface water bodies of the White Sea basin in the year of 2019 amounted to 73.87 million m^3 (in 2018 – 70.13 million m^3), including 14.98 million m^3 of wastewater from the tailing dump of joint stock company Karelsky Okatysh. The main pollutants in the water of the Karelsky Okatysh tailing dump are Ni ($0.017\text{--}0.025 \text{ mg l}^{-1}$), Mn ($0.432\text{--}0.650 \text{ mg l}^{-1}$) and Zn ($0.05\text{--}0.075 \text{ mg l}^{-1}$), and in

the technogenic substrate of the plant is Fe ($39\ 505\text{--}45\ 120 \text{ mg kg}^{-1}$) (Terebova *et al.* 2017). Among pollutants discharged into the water bodies of the White Sea basin in 2019, the largest contribution by mass was made by sulphate lignin (3014.88 tons), K (1982.43 tons), nitrates (1446.41 tons), Mn (601.51 tons), Na (524.35 tons), Fe (30.51 tons), oil products (11.92 tons), and Ni (898.64 kg) ([2]-State report 2020).

In addition to the technogenic influx of heavy metals from river runoffs into the waters of the White Sea, geologists associate the high level of iron with natural factors. These are the features of the White Sea drainage basin such as the widespread swamps and the inflows of groundwater into rivers. For example, the iron content in waters of the mouth area of the Northern Dvina was $0.289\text{--}0.453 \text{ mg l}^{-1}$ (2015–2019). This is five times higher than the background concentration of Fe (0.066 mg l^{-1}) in the rivers of the world (Gordeev *et al.* 2021, Dzhamaalov *et al.* 2019).

T. maritima plants actively absorb heavy metals from the environment, as evidenced by the value of CBA>1 (Table 6). However, there are some differences between the zones along the transect. Thus, the content of analyzed elements in the soil from the 1st zone is less than from the 3rd zone (Table 5), while their content in plants is higher in the 1st zone. It might be that in the 1st zone *T. maritima* plants have no competitors for the absorption of mineral substances from the soil as in the 1st zone (a) vegetation cover is sparse and (b) *T. maritima* plants grow as separate medium-sized clones. In the upper littoral (in the 3rd zone), where the vegetation cover is sufficiently developed covering 100 % of surface area, the competition for mineral substances increases and *T. maritima* plants accumulate less mineral elements even at their higher content in the soil.

There are no data on the accumulation of elements in plants under conditions of lower, middle and upper littoral zones. It is known that the content of calcium, magne-

sium, potassium and sodium in the bottom sediments of the Kandalaksha Bay of the White Sea decreases from the lower littoral to the coast soils and the content of organic carbon, on the contrary, increases in the same direction (Sidorova et al. 2015). Our studies carried out within the littoral zone only have shown that the content of all elements (organic carbon, nitrogen, phosphorus and iron) decreases from the lower littoral (the 1st zone) to the upper littoral (the 3rd zone).

In all three zones among plant organs, adventitious roots accumulate more minerals (Table 6). It is consistent with the data of anatomical analysis, which indicate an increase in the size of root cells and all root tissues (Fig. 5), as well as an increase in the morphological parameters of shoots (Fig. 4), which indirectly reflects plant vigor. It is well known that the root system and its tissues are the first plant barrier against pollutants (Van Osten and Maggio 2015). Plant adaptation is aimed to immobilize contaminants in roots in order to protect reproductive organs and seeds from their toxic effects (Yadav 2010, Naila et al. 2019). It should be noted that *T. maritima* is a rhizome plant that accumulates metals in the underground organs throughout the life of the plant, while the above-ground part of the plants dies off every year and its mineral elements feed the littoral and coast soils.

Halophytes ordinarily have high tolerance to heavy metals compared with glycophytes (Manousaki and Kalogerakis 2011). The high resistance of halophytes to heavy metals is strongly connected to their salt tolerance characteristics (Wang et al. 2013). In general, plants respond to heavy metal toxicity via several molecular mechanisms. These include metal ions binding to cell wall, metals chelating within cytosol, ROS defense mechanisms (Bose et al 2014), and metal sequestration in vacuoles (Gargouri et al. 2013, Kushwaha et al. 2016). The cell wall is an important site for metal storage in plants as it provides a large number

of metal-binding sites (Krzyszowska 2011). The cell wall is rich in carboxyl groups and plays a key role in the immobilization of metal ions, which alleviates metal toxicity to plant cells (Terebova et al. 2020). The toxic effects of metal ions in cytosol can be eliminated by specific high affinity ligands, such as phytochelatins (PCs) (Zhang et al. 2010), soluble protein (Luo et al. 2011) and prolin (Wali et al. 2016, Liang et al. 2017). Therefore, the halophyte *Suaeda salsa* (L.) Pall. can grow in heavy metal-polluted areas along intertidal zones having high salinity. Since phytochelatins can effectively chelate heavy metals, it was hypothesized that *S. salsa* possessed a phytochelatin synthase (PCS) gene. The *Suaeda salsa* PCS transcript was more expressed in elongated and fibered roots and stems than in leaves. Lead and mercury exposure significantly enhanced the mRNA expression of *Suaeda salsa* PCS (Cong et al. 2016). In addition, *Sesuvium portulacastrum* (L.) L., a facultative halophyte, is known to induce the synthesis of PCs, specific metal(loid) binding ligands, in the presence of Pb (Zaier et al. 2010). Cd and Cu toxicity in the sea grass, *Zostera marina* L., was reported to be mitigated via the PC-dependent detoxification pathway. Interestingly, it was observed that a PC gene was upregulated under high concentrations of Cd and Cu and low concentration of Cu. This showed a HM-specific response of the PC gene in *Z. marina* (Greco et al. 2019).

According to the results of this study, *T. maritima* can be considered as a hyper-accumulator of Fe since the plant accumulates very high levels of Fe (22 – 34 g kg⁻¹) (Naila et al. 2019), especially in the 1st and 2nd zones, both in underground and above-ground organs (Table 6). Fe content in the *T. maritima* tissues was thousands times higher than the content of other elements and five times higher than Fe content in the halophyte habitat (CBA for Fe: 1.29 – 5.53).

We have previously shown that the plants *Plantago maritima* L. and *T. maritima* inhabiting the littoral zone of the White Sea near the village of Keret also accumulate Fe up to levels of 13–22 g kg⁻¹, respectively (Terebova *et al.* 2020). It is known that halophytes (*Salicornia europaea* L., *Suaeda maritima* (L.) Dumort, *Salsola soda* L. and *Halimione portulacoides* (L.) Aellen) from inland and maritime saline areas can accumulate up to 2.3 g kg⁻¹ Fe in the whole plant and 1.3 g kg⁻¹ in the roots (Milić *et al.* 2012). Heavy metals can bind to plant cell wall components (Pelloux *et al.* 2007, Richter *et al.* 2017). It is possible that the binding of Fe atoms by the cell wall of *T. maritima* roots and leaves can increase its rigidity, providing an increase in the plant organ strength under the conditions of the greatest dynamics of the sea.

According to the results of pollen analysis, indicating the level of plant well-being in specific habitat conditions, it can be concluded that in the 1st zone, in the lower littoral, *T. maritima* plants grow under more favourable conditions. In this zone plants have the least percentage of teratomorphic pollen (92% of normally formed pollen) with the lowest CV (2%). In the 3rd zone, the percentage of normal pollen has decreased to 63% (CV=7%). The higher amount of teratomorphic pol-

len than 11% is considered as an indicator of unfavourable environmental conditions. For the first time, specific types of developmental disorders (undivided tetrads with pollen grains without content) were found in pollen samples from the 2nd and 3rd transect zones. Their number in the 3rd zone reached 27.4%. Thus, it can be concluded that habitat conditions for *T. maritima* in the 2nd and 3rd zones were stressful, affecting negatively pollen grain development. The 3rd zone is characterized by the longest periods when plants are exposed to air, and in the 2nd zone plants are affected by the most aggressive effect of the tidal cycle.

The morphological structure of *T. maritima* pollen grains indicate plant adaptation to wind pollination, *i.e.* pollen grains are small and smooth, and the absence of a pore for the exit of the pollen tube makes them less vulnerable to the influence of the aquatic environment. *T. maritima* flowers are protogynous, therefore, for the sexual process the transfer of pollen from another flower or plant is necessary. It is possible that much larger amount of normally formed, and therefore potentially fertile, pollen in plants in the 1st zone facilitates the sexual reproduction of *T. maritima* under conditions of a short waterless period during low tide in this part of the littoral zone.

Conclusion

The study of the ecological and biological features of *T. maritima*, which ensure the successful distribution of the dominant species within ecotopes with different conditions in the littoral of the White Sea, is of great scientific interest.

An integrated approach, including measurements of a number of parameters, allows concluding that in the littoral zone along the flooding gradient from the water edge to the supralittoral, the plants of this species are quite well adapted to the dy-

namic conditions. Adaptation to wave and storm impact is manifested in a well-developed system of underground vegetative organs. In the lower littoral (in the 1st zone), underground part surpasses the aboveground vegetative organs in terms of the mass and the formation of mechanical tissues. This allows the plants to anchor stronger in the substrate. Pollen analysis confirmed the adaptability of *T. maritima* plants to the conditions of the lower littoral by a high percentage of normal and,

consequently, fertile pollen, which ensures sexual reproduction of the species.

The ability of *T. maritima* plants to accumulate metals, revealed on the basis of the coefficient of biological absorption of metals, makes it possible to suggest potential utilization of the species in phytoremediation technologies on coastal territories.

Despite the fact that *T. maritima* has recently attracted the attention of scientists,

for the restoration of transformed coastal territories, in particular, our study raises new questions in connection with the revealed ability of the species to hyperaccumulate Fe. The capacity of *T. maritima* to accumulate Fe and other metals should be addressed in follow-up studies. Another task is to evaluate adaptive characteristics that allow the species to grow under unstable biotope conditions.

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