

Activity of catalase and superoxidedismutase in leaves of halophyte plants under the tidal dynamics of the White Sea

Elena N. Terebova¹, Maria A. Pavlova¹, Natalia V. Oreshnikova²

¹*Petrozavodsk State University, Department of Botany and Plant Physiology, Lenin st. 33, Petrozavodsk 185910, Russian Federation*

²*Lomonosov Moscow State University, GSP-1, Leninskie Gory, Moscow 119991, Russian Federation*

Abstract

Activity of catalase (CAT) and superoxide dismutase (SOD) enzymes in the leaves of halophyte plants *Triglochin maritima* L., *Plantago maritima* L., *Tripolium vulgare* Bess. ex Nees and *Zostera marina* L. was investigated in a 2-year field experiment carried out in the community of the middle littoral marsh on the Pomor (western) coast of the White Sea (Belomorsk region, Russia). The community *Tripolium vulgare*–*Bolboschoenus maritimus*–*Triglochin maritima*–*Plantago maritima*, was investigated during the tidal cycle. The plants grew under conditions of seawater pollution with high concentration of nitrates (43.68 mg l⁻¹), iron (0.15 mg l⁻¹), nickel (0.15 mg l⁻¹) and lead (0.024 mg l⁻¹). The total projective cover of species in the plant community reached 50% for *T. vulgare*, and 20% for other dominant species. A direct positive correlation was found between the activity of CAT and SOD in halophyte leaves ($r = 0.51–0.68$). This research revealed the species specificity of the enzyme activity level in *Z. marina*. The activity of CAT and SOD in its leaves was significantly lower (0.16 ± 0.06 $\mu\text{mol H}_2\text{O}_2/\mu\text{g}$ of protein; 2.61 ± 0.08 c.u./mg of protein, respectively), than in other species. The maximum values of CAT activity were found in *T. vulgare* and *T. maritima* ($0.23–0.26$ $\mu\text{mol H}_2\text{O}_2/\mu\text{g}$ of protein), and SOD in *T. vulgare* 4.65 ± 1.12 c.u./mg of protein. The activity of CAT in plant leaves varied over a wide range (1.14–11.83 c.u./mg of protein) and did not depend on the tidal dynamics of the sea. In halophyte leaves, the regulation of plant redox metabolism under hypoxic conditions during flooding is supported by an increase in SOD activity, on average 1.98–2.95 at low tide and 4.12 ± 6.73 c.u./mg of protein at high tide.

Key words: plant communities, salt marshes, tidal cycle, halophytes, catalase, superoxide dismutase, the White Sea

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*Corresponding author: E. Terebova <eterebova@gmail.com>

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Introduction

Enzymes take part in the regulation of metabolic processes as biological activators of chemical reactions, and changing their activity, thereby ensuring that the metabolism of organisms corresponds to changing environmental conditions. The enzymes catalase (CAT, EC 1.11.1.6) and superoxide dismutase (SOD, EC 1.15.1.1) belong to the antioxidant system of organisms (AOS). The AOS protects cells from the negative effects of reactive oxygen species (ROS), which cause oxidative damage stress (Knox *et al.* 1985). SOD and CAT are some of the most important enzymes of antiradical defense, and are found in all aerobic organisms (Brioukhanov and Netrusov 2004, Zheng *et al.* 2023). According to evolutionary studies, they appeared in organisms earlier than other enzymes of the AOS (Inupakutika *et al.* 2016). SOD catalyzes the conversion of superoxide anion radical ($O_2^{\bullet -}$), which has a very high oxidizing ability, into hydrogen peroxide (H_2O_2) and molecular oxygen (O_2). This universal dismutation reaction is considered the first line of defense against oxidative stress in eukaryotic cells (Alscher *et al.* 2002). SOD activity regulates the balance between superoxide radicals and hydrogen peroxide, which play the role of second messengers in many processes (Mittler 2017). CATs decompose hydrogen peroxide to water and molecular oxygen. $O_2^{\bullet -}$ and H_2O_2 are products of aerobic cell metabolism, formed as a result of a number of enzymatic and non-enzymatic reactions in the cell wall, mitochondria, chloroplasts, peroxisomes and glyoxisomes (Bose *et al.* 2014, Anjium *et al.* 2016).

Halophytes live in the littoral zone of the White Sea with a perpetual variation in plant habitat conditions: oxygen content, insolation, temperature, wave dynamics, salinity level and elemental composition of seawater and soils. Vascular plants are adapted to high salinity of soil and water. Twice a day at high tide, plants are gradu-

ally completely covered with sea water for about eight hours, and drained at low tide, successfully ensuring their growth and development due to ecological and physiological adaptations (Rozentsvet *et al.* 2017) in such unstable conditions of existence (Markovskaya *et al.* 2020, Sonina *et al.* 2021).

It is considered that halophytes have several physiological and biochemical mechanisms of cross-adaptation to the combined effects of salts and heavy metals (Wang *et al.* 2013), which is why halophytes are more resistant to the latter compared to glycophytes (Manousaki and Kalogerakis 2011). In response to the influx of heavy metals into the cell, the specialized mechanisms of resistance to this stressor are activated: 1) the immobilization of metal ions in the cell wall (Pelloux *et al.* 2007, Krzeslowska 2011); 2) inhibition of ion transport through the plasmalemma (Hall 2002, Liu *et al.* 2003), as well as the active release of ions from the cell into the environment, *e.g.* through the salt glands (Hall 2002, Manousaki *et al.* 2013, Toderich *et al.* 2001); and 3) formation of a complex with phytochelatins followed by transport to the vacuole for storage (Rascio and Navari-Izzo 2011). Non-specialized systems (ROS formation, activation of antioxidant systems, accumulation of low molecular weight protective compounds, activation of stress proteins, *etc.*) are also activated at the same time. At the organism level, the mechanisms that determine the resistance of plants to heavy metals include the delayed absorption of heavy metals by the roots (Hall 2002) and the ability of plants to regulate transport of ions to various organs (Clemens *et al.* 2002). The ability of halophytes to accumulate heavy metals can be used for phytoremediation of contaminated coastal territories (Manousaki and Kalogerakis 2011, Lokhande 2011). In review, Van Oosten and Maggio (2015) summarized informa-

tion on 26 species from 18 genera of halophytes, which are considered as perspective plants for phytoremediation. It is known that halophyte plants growing in sea water can accumulate the following metals: Cu, Zn, Cd, Pb, Mn, Fe, Hg, Co, Cr, As, Ni and non-metal ions of Na. Accumulator plants (18 out of 26) can concentrate from 3 to 8 metals simultaneously. Species such as *Suaeda maritima* (L.) Dumort., *Sporobolus montevidensis* (Arechav.) P. M. Peterson & Saarela, *Sporobolus alterniflorus* (Loisel.) P. M. Peterson & Saarela have the ability to hyperaccumulate heavy metals. Thirteen species can accumulate zinc, nine to ten species accumulate copper, cadmium, and lead; the remaining species accumulate one to three elements. The authors suggest the following species for phytoremediation: *Atriplex lentiformis* (Torr.) S.Wats. (Na), *Sesuvium portulacastrum* (L.) L. (Cd, Na, Pb), *Suaeda maritima* (As, Cd, Cu, Fe, Mn, Na, Pb, Zn) (Köhl 1997, Zaier et al. 2010, Rabhi et al. 2010, Alatorre et al. 2013). However, these species do not grow on the White Sea coast.

In halophytes of the littoral of the White Sea, following anatomical features of the leaf were noted: the presence of succulent leaves in *Triglochin maritima* L. and *Plantago maritima* L., aerenchyma with large intercellular spaces is formed in the center of the leaf blade of *T. maritima*, and the water-storing leaf parenchyma is well developed in the leaf of *P. maritima* (Gulyaeva et al. 2016). It was revealed that at maximum high and low tides, stomata open and the intensity of primary photosynthesis assessed by chlorophyll *a* fluorescence parameters in the leaf of *P. maritima* increases, compared to partial flooding of plants with sea water (Markovskaya and Gulyaeva 2020). In the plants of

T. maritima and *P. maritima*, a high ion exchange capacity of the leaf cell wall (2710–3700) and root (1160–2350 mmol/g of cell wall dry weight) was shown (Terebova et al. 2020). Plants growing in the littoral zone of the White Sea actively accumulate heavy metals from their environment and we identified; coefficients of biological absorption of metals greater than 1: (Pb (7.3) > Mn (3.0) > Fe (2.7) > Zn (2.5) > Cu (2.5) > Ni (1.9). At the same time, the absolute content of Fe in halophyte plants was very high and reached 23–36 g kg⁻¹, over ten times higher than the critical level of metal in plants (Terebova et al. 2023). Regarding the activity of AOS enzymes in halophytes, it is known that it can vary in different directions depending on the level of salinity (Bose et al. 2014, Kumar et al. 2021) and pollution (Rahman et al. 2021). The activity of CAT and SOD enzymes in plants tends to change differently depending on the level and time of exposure. That is, the change in the activity of antioxidant enzymes is multidirectional and depends on the species specificity and growth conditions of plants. However, halophytes are recognized to have relatively higher levels of SOD and CAT activity than glycophytes (Pirasteh-Anosheh et al. 2023). There are no data for plants on the Karelian coast of the White Sea under POC conditions. In our study, we focused on the activity of CAT and SOD in the leaves of halophyte plants under the influence of tidal dynamics of the White Sea. This study is an attempt to identify the correlation between the activities of CAT and SOD in the leaves of halophytes, as well as the dependence of the totality of enzyme activity on both stages of ebb and flow, and on their combined effects.

Material and Methods

Study area

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) (Fig. 1) in July 2021 (1st year of the experiment) and 2022 (2nd year of the experiment). A large part of the Pomor coast belongs to the fiard-skerry type, but the coastal area changes significantly south of Belomorsk. There is a transition to a swampy lowland, above which rare hills with gentle slopes (“varaki”) made of crystalline rocks rise near the shore. The coast is either flattened rocky surfaces smoothed by a glacier, gradually disappearing under the water's edge, or piles of blocks and boulders, usually framed on the sea side by clayey or sandy tidal drainages (Kaplin *et al.* 1991). A model (typical) transect was selected in the littoral zone in the village of Rastnavolok (64.578025, 34.905520). Model transect, with a total length of 170 m, was laid on a gently sloping silty-sandy shore with the presence of boulder and pebble accumulations in the middle part of the littoral zone. About 5–7% were large boulders, medium stones – 20%, pebbles – 60%, and the rest was sand.

Stagnant sea water is found in shallow depressions up to 2 cm. The salinity of seawater is 21 ‰. Based on the nature of the vegetation and the characteristics of the substrate on the transect, three zones are identified from the main shore to the edge line: 1st zone (lower sublittoral, low marshes) – begins at a distance of 130 m from the main shore, 2nd zone (middle littoral, middle marshes) – begins at a distance of 70 m from the main shore, and the 3rd zone (upper littoral, upper marshes, supralittoral) – 7 m wide. The total species richness of the studied plant communities is 13 species. In the lower littoral zone, coastal overgrowth begins with the forma-

tion of aster communities, which were identified within their natural contours. *Tripolium vulgare* Bess ex Nees dominates with significant abundance on sandy loam littoral soil, with a total projective cover (TPC) 50%, forming communities with *Triglochin maritima* L., TPC 10–20%, and *Bolboschoenus maritimus* (L.) Palla, TPC 20%. In the middle littoral zone, *T. vulgare* also forms *Bolboschoenus maritimus* - *Tripolium vulgare* community with a *B. maritimus* TCP of 20%, *Zostera marina* L. grows with a TCP of 10%, and *T. maritima* is found sporadically (TCP 2%). The supralittoral zone is inhabited by *Plantago maritima* L. with TCP 10%, *Honckenya diffusa* (Hornem.) Á. Löve), *Agrostis stolonifera* L., *Leymus arenarius* (L.) Hochst., *B. maritimus*, *Sonchus arvensis* L., *Vicia cracca* L., *Achillea millefolium* L., *Trifolium repens* L., *Juncus gerardii* Loisel. *subsp. atrofusca* (Rupr.) Printz). In the ecotone zone, *P. maritima* grows on sand. The highest TCP on the model transect was established for *Tripolium vulgare*, *Bolboschoenus maritimus*, *Triglochin maritima*, *Plantago maritima*. Thus, on the model transect the plant community can be described as *Tripolium vulgare*–*Bolboschoenus maritimus*–*Triglochin maritima*–*Plantago maritima*.

We investigated four species typical for the Pomor coast: *Triglochin maritima* L., *Plantago maritima* L., *Tripolium vulgare* Bess. ex Nees and *Zostera marina* L. (see Fig. 2). Species names are taken from the database «World Plants» (Hassler 2024).

Triglochin maritima belongs to the family *Juncaginaceae*, a euhalophyte, a Eurasian boreal species; herbaceous polycarpic; underground-stolon weakly rosette plant, forming small turfs with a thick rhizome, which is an overgrowing pioneer of silty marsh drains. Leaves of the seagrass are basal, fleshy, narrow-linear, grooved,

with parallel veins, and covered with a layer of cuticle. Mesophyll has a centric structure. In the center of the leaf blade, aerenchyma with large intercellular spaces is formed.

Plantago maritima is a member of the plantain family (*Plantaginaceae*), a euhalophyte, a Eurasian hypoarctic species; herbaceous polycarpic; perennial with a monopodial rhizome and a branched and particulate caudex. It prefers dry areas protected from wave erosion. The leaves of the sea plantain are collected in a basal rosette, fleshy, narrow-lanceolate, entire or sparsely toothed along the edge, covered with a layer of cuticle. The leaf mesophyll is isopalisade, poorly differentiated into palisade and spongy mesophyll. The water-storing parenchyma of the leaf is well developed (Gulyaeva et al. 2016). Palisade mesophyll cells are located in two layers on the upper and lower sides of the leaf. The rest of the leaf consists of water-storing parenchyma (60%).

Tripolium vulgare belongs to the *Asteraceae* family, euhalophyte, Eurasian

boreal species. The plant prefers muddy drainage at the mouths of all rivers and is a pioneer in their overgrowing. It is a biennial herbaceous plant with a branched stem, hollow only in the upper part. The leaves are broadly lanceolate, entire, and adjacent to the stem. The leaf mesophyll is differentiated into palisade and spongy mesophyll. Aster has a well-developed short rhizome.

Zostera marina is a representative of the eelgrass family (*Zosteraceae*), a secondary aquatic plant, an obligate herbaceous hydrophyte, completely immersed in seawater (not influenced by tides). In northern latitudes, it lives in shallow waters or at a depth of 1–4 m (rarely 10 m or more), mainly on a soft sandy or muddy bottom in the calm waters of bays. The rhizome is long, creeping. The leaf has a well-developed spongy mesophyll with aerenchyma (Sergienko et al. 2015).

Studied plants had no external signs of the toxic effects of metals (chlorosis, necrosis, spots).

Plant collection and handling

Plant samples (three leaves from five normally developed plants of each species) were taken from 6.00 to 15.00 in the middle littoral zone at full high tide (high water) and full low tide (low water) and fixed immediately with liquid nitrogen at Dewar flask. They were transported to the laboratory and stored in a refrigerator

(Termo Fisher Scientific Forma 8600 813 CV) at -80°C . Samples of water and soil from the experimental plants neighbourhood were collected and transferred to a laboratory as well. Measurements of salinity of water and soil were carried out with a refractometer (RHS-10ATC, China).

Determination of enzyme activity

Leaf tissues were ground with liquid nitrogen and homogenized at 4°C in a buffer of the following composition: 50 mM Hepes (pH 7.5), 1 mM EDTA, 1 mM EGTA, 3 mM DTT, 5 mM MgCl_2 , 0.5 mM PMSF. After a 20-minute extraction, the homogenate was centrifuged at 10,000 g for 20 minutes (Centrifuge 5804 R, Eppen-

dorf, Germany). Next, dialysis was performed at 4°C for 18–20 h against homogenization buffer diluted 10 times. Enzyme activity in the enzymatic preparations obtained after dialysis was determined spectrophotometrically (SF 2001, "OKB Spectr", Russia).



Fig. 1. Study area (Google Maps)



Fig. 2A. *Triglochin maritima* L.
(Photo by E. Terebova)



Fig. 2B. *Tripolium vulgare* Bess. ex Nees
(Photo by E. Terebova)



Fig. 2C. *Zostera marina* L.
(Photo <https://klau.club>)



Fig. 2D. *Plantago maritima* L.
(Photo by E. Terebova)

CAT activity was assessed by the enzymatic decomposition of hydrogen peroxide. The incubation medium contained 67 mM K, Na-phosphate buffer (pH 7.8) and 10.3 mM hydrogen peroxide, the amount of supernatant was 50–200 μ l, depending on the activity of the enzyme. A linear dependence of CAT activity on reaction time was observed within 30 min.; an incubation time of 20 min. was chosen for the reaction. To determine catalase activity, the decrease in optical density at 240 nm was measured, and the hydrogen peroxide content was calculated using a previously constructed calibration graph in the range of 1.5–20.6 mM hydrogen peroxide. CAT activity was expressed as μ mol of reduced hydrogen peroxide per 1 μ g of protein in 20 min. (μ mol H₂O₂ / μ g protein) (Ershova et al. 2022).

Measurements of the heavy metals content in a water and soil

The metal concentration in the soil and sea water was estimated using the atomic absorption method (the atomic absorption spectrophotometer AA-7000 with a flame atomizer, Shimadzu 7000, Japan). 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 Prod-

ucts, Germany). All the tests of heavy metal content were performed using the certified equipment of the Shared Use Centre Analytical laboratory of Forest Research Institute of the Karelian Research Centre of the RAS (ISO 11466:1995, NBN EN 13657:2002, ISO 11407:1998, ISO 20280:2007). All measurements were done in triplicate.

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

the differences in the parameters was assessed by the Student's t-test; one-way analysis of variance at $p < 0.05$.

Results

Seawater in the study area was contaminated with Fe (3.0 maximum permissible concentration MPC); Ni (14.8 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 4.0, 5.5 and 2.8, correspondingly. The Cu content in seawater was low, not exceeding background

values (Table 1). 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 14000 mg kg⁻¹ and Mn – 71 mg kg⁻¹. The content of macronutrients (N, P, K and C) in the littoral soils was found lower than in gray forest soils (Table 1).

Soil										
Element	C	N	P	K	Fe	Mn	Cu	Zn	Pb	Ni
	%	%	%	mg kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹	mg kg ⁻¹
M	1.98±0.08	0.20±0.01	0.05±0.01	243.11±12.87	13 791.62±500.56	70.78±14.10	11.71±5.14	17.29±3.95	4.95±1.21	8.94±2.81
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	25 374.50	117.61	16.71	26.65	9.95	13.11
Background ^{1,2}	45.70 ¹	2.17 ¹	0.10 ¹	14191 ¹	17 505 ¹	282 ¹	18 ²	62 ²	15 ²	30 ²
APC ³	-	-	-	-	46 500	1 500	35 ³	150 ³	30 ³	30 ³
Sea water										
Element	NO ₃ ⁻	Cl ⁻	Fe	Mn	Zn	Ni	Cu	Pb		
	mg l ⁻¹	mg l ⁻¹	mg l ⁻¹	mg 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	0.15	0.011	0.028	0.148	0.00001	0.024	0.00001	0.024
MPC ⁵	-	2.50	0.01	0.002	0.010	0.002	0.0003	0.00003	0.00003	0.00003
	39	-	0.05	0.050	0.050	0.010	0.005	0.010	0.005	0.010

Table 1. Content of elements in seawater 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 (Order of the Ministry 2016⁽¹⁾); 5 – MPC – maximum permissible concentrations (MPC) in seawater of fishery facilities (Order of the Ministry 2016⁽¹⁾);

Catalase activity

CAT activity in plant leaves varied in the range from 0.01 to 0.67 (67-fold difference) $\mu\text{mol H}_2\text{O}_2/\mu\text{g protein}$. A significant decrease in enzyme activity during high tide in the 1st year of the study, and an increase in its activity in the 2nd year of the study was found in *P. maritima*. In *T. maritima*, enzyme activity remained at the same stable level at high and low tides during both years of the study. Individual

intraspecific variability in the activity of CAT was quite high: the maximum in *T. vulgare* was CV 0.67–0.80 (Table 2). The average values of enzyme activity were minimal in *Z.marina* and *P.maritima* 0.14–0.16 $\mu\text{mol H}_2\text{O}_2/\mu\text{g protein}$; higher in other species *T. vulgare* and *T. maritima* 0.23–0.26 $\mu\text{mol H}_2\text{O}_2/\mu\text{g}$ of protein (Table 4).

Plant species	Year of experiment	$\mu\text{mol H}_2\text{O}_2/\mu\text{g protein}$		t-test
		low tide	high tide	
<i>Tripolium vulgare</i>	1 year	0.26±0.11 ^a	0.48±0.01 ^a	0.105
	2 year	0.07±0.01 ^b	0.10±0.01 ^b	0.053
	M	0.17±0.05 ^c	0.29±0.09 ^c	0.266
	CV	0.67	0.80	
<i>Triglochin maritima</i>	1 year	0.36±0.06 ^a	0.28±0.01 ^a	0.714
	2 year	0.19±0.01 ^b	0.21±0.01 ^a	0.815
	M	0.28±0.06 ^d	0.25±0.03 ^d	0.760
	CV	0.65	0.51	
<i>Plantago maritima</i>	1 year	0.21±0.02 ^a	0.15±0.01 ^a	0.039
	2 year	0.07±0.01 ^b	0.14±0.01 ^a	0.014
	M	0.14±1.16 ^c	0.15±0.01 ^c	0.930
	CV	0.55	0.12	
<i>Zostera marina</i>	1 year	0.23±0.01 ^a		
	2 year	0.08±0.01 ^b		
	M	0.16±0.04 ^c		
	CV	0.74		

Table 2. Activity of catalase (CAT) in leaves of halophyte plants.

Notes: Data presented with different letters (a, b) in the same column indicate a significant difference at $p \leq 0.05$ from different year of experiment for the same species to Fisher’s LSD test. Data presented with different letters (c, d, e) in the same column indicate a significant difference at $p \leq 0.05$ from different species to Fisher’s LSD test.

Superoxide dismutase activity

SOD activity in plant leaves ranged from 1.14 to 11.83 c.u. / mg of protein (10-fold difference). In all years of the study, SOD activity was significantly higher at high tide, compared to the enzyme activity at low tide. The only exception of SOD ac-

tivity in *P. maritima* was apparent in the second year of the experiment, when the activity did not change in response to the flood level (Table 3). Individual variability in SOD activity was greatest (CV 0.56–0.73) also in *T. vulgare*, as was the case

for the range of variation in CAT activity. The average minimum values of SOD activity were obtained for *Z.marina* and amounted to 2.61 c.u. / mg of protein. In *T. vulgare*, the average enzyme activity was maximum and amounted to 4.65 c.u. / mg of protein (Table 4).

One-way analysis of variance between the activities of CAT and SOD in the leaves of all halophyte plants (total sample) showed a positive significant correlation between these indicators (0.5–0.68) (Table 5, Fig. 3.).

Plant species	Year of experiment	c.u. / mg of protein		t-test
		low tide	high tide	
<i>Tripolium vulgare</i>	1 year	1.76±0.13 ^a	3.86±0.08 ^a	0.049
	2 year	3.36±0.11 ^b	9.61±1.46 ^b	0.018
	M	2.56±0.23 ^c	6.73±1.72 ^c	0.033
	CV	0.56	0.73	
<i>Triglochin maritima</i>	1 year	2.19±0.58 ^a	4.82±0.47 ^a	0.039
	2 year	1.76±0.24 ^a	3.43±0.52 ^a	0.041
	M	1.98±0.75 ^c	4.12±1.13 ^d	0.049
	CV	0.29	0.26	
<i>Plantago maritima</i>	1 year	3.36±0.11 ^a	6.95±0.68 ^a	0.015
	2 year	2.54±0.08 ^b	2.44±0.03 ^b	0.331
	M	2.95±0.20 ^c	4.70±0.91 ^d	0.026
	CV	0.18	0.53	
<i>Zostera marina</i>	1 year	3.90±0.56 ^a		
	2 year	1.32±0.01 ^b		
	M	2.61±0.85 ^c		
	CV	0.62		

Table 3. Activity of superoxide dismutase (SOD) in leaves of halophyte plants.

Notes: Data presented with different letters (a, b) in the same column indicate a significant difference at $p \leq 0.05$ from different year of experiment for the same species to Fisher’s LSD test. Data presented with different letters (c, d) in the same column indicate a significant difference at $p \leq 0.05$ from different species to Fisher’s LSD test.

Enzyme	Species			
	<i>Tripolium vulgare</i>	<i>Triglochin maritima</i>	<i>Plantago maritima</i>	<i>Zostera marina</i>
CAT μmol H ₂ O ₂ / μg protein	0.23±0.06 ^a	0.26±0.15 ^a	0.14±0.09 ^b	0.16±0.06 ^b
SOD c.u. / mg of protein	4.65±1.12 ^a	3.05±0.85 ^a	3.82±0.07 ^a	2.61±0.08 ^b

Table 4. Average activity of catalase and superoxide dismutase in leaves of halophyte plants.

Notes: Data presented with different letters in the same line indicate a significant difference at $p \leq 0.05$ from different halophyte plants to Fisher’s LSD test.

CAT/SOD	r	F	p	F critical
low tide	0.51	51.95	4.45E-09	4.05
high tide	0.68	39.91	9.67E-08	4.05
low and high tides	0.61	91.25	1.64E-15	3.94

Table 5. Results of variance analysis of the dependence of catalase and superoxide dismutase activities.

Discussion

A littoral-halophytic floristic complex represents a set of plant species, characterized by their habitats confined to coastal zones of seas, and primarily to soils saline with seawater (Sergienko 2008). Plant communities are formed under conditions of environmental pollution. In general, in the study area the littoral soil was not contaminated, but had increased concentrations of some elements in water. For example, Ni concentration was 0.148 mg l^{-1} , Pb reached 0.024 mg l^{-1} (Table 1). Thus, water was contaminated with Fe (3 MPC), 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 ($39505\text{--}45120 \text{ mg kg}^{-1}$) (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), Ni (898.64 kg) (State report 2020^[3]).

Apart to anthropogenic Fe contamination of the studied area, there is an increased Fe content in bottom sediments, due to the metallogenic factors of the region. Bottom sediments of the White Sea are characterized by the presence of a brown or black oxidized layer of millimeter thickness in the soils, enriched with oxyhydroxides of manganese and iron. This layer is underlain by dense gray silty-pelitic silts. Thus, the iron content Fe (III) in it can reach up to 7.5%, which is one and a half times higher than the average concentration of iron in the earth's crust (Rozanov and Volkov 2009). As a result, the release of iron from continental shelf sediments is a key source of both dissolved and particulate iron in marine areas (Lenstra et al. 2018). It is known that the content of dissolved iron in the silt water of the subsurface horizons of bottom sediments of the White Sea is $20 \text{ }\mu\text{M}$, which is a significant value (Rozanov and Volkov 2009).

In the study area, plants experience conditions of reduced aeration during flooding – hypoxia, the oxygen flow in sea water is $10\text{--}50 \text{ mM/m}^2 \text{ day}$ (Rozanov and Volkov 2009) and on average the oxygen content in sea water of the White Sea is $0.0007\text{--}0.001\%$ (Quality of sea 2021^[2]). Under such conditions, plants switch to anaerobic metabolism, the intensity of glycolysis increases (Shikov et al. 2021), the intensity

of photosynthesis changes (Hafeez *et al.* 2021), and the production of superoxide anion radical increases (Blokhina *et al.* 2003, Hasanuzzaman *et al.* 2012, Bose *et al.* 2014, 2017). These processes are associated with an increase in the activity of the SOD enzyme in plant leaves at high tide (Table 3). Through the dismutation reaction, SODs regulate the cellular concentration of superoxide radicals and hydrogen peroxide.

Previously, it was shown that the photosynthetic apparatus of halophyte plants changes its functioning during the tidal cycle of the sea (Markovskaya and Gulyaeva 2020). Fluctuating changes in the activity of the photosynthetic function can lead to an increase in the concentration of superoxide anion radical in the tissues of halophytes under high tide conditions and activation of SOD.

Hydrogen peroxide formed as a result of the dismutation reaction and the work of SOD has a lower oxidative potential compared to the superoxide radical and is neutralized by other enzymes (Hasanuzzaman *et al.* 2020), such as catalase, peroxidase (Zhao *et al.* 2016, Wang *et al.* 2018) (Fig. 3).

We did not detect any changes in CAT activity in halophyte leaves under the influence of the tidal cycle of the sea (Table 2). However, the total catalase activity in the leaves of the studied species varied in a 67-fold range, regardless of the TC. CAT differs from other AOS enzymes, since it does not require a reducing agent for the reaction to occur, has high specificity for hydrogen peroxide, and is localized predominantly in peroxisomes, glyoxysomes and mitochondria (Apel and Hirt 2004). The low affinity for hydrogen peroxide means that there is usually a linear relationship between CAT activity and peroxide concentrations, even when the concentrations are suprphysiological. CAT can maintain its activity for a long time. In addition, CAT is in a stable state, when the redox status of the cell changes

without requiring additional equivalents, and therefore is more resistant to stress compared to other components of AOS (Nikerova 2020). Hydrogen peroxide, like other ROS, is considered not only as a molecule that oxidizes and destroys compounds, but also as a regulatory signaling molecule (Allen and Balin 1989, Kreslavski *et al.* 2012). Hydrogen peroxide is involved in signal transduction as a second messenger for the action of HMs in the cell, which activates the expression of metallothionein genes (Chaturvedi *et al.* 2014, Babaei-Bondarti and Shahpiri 2020). Therefore, it is logical to expect that during the day the concentration of peroxide in tissues of halophytes constantly changes, and the enzyme catalase changes its activity in a wide range, regardless of the tidal dynamics of the sea.

A stable level of CAT activity is established in *T. maritima* at high and low tides, which is probably due to the use of internal oxygen reserves that accumulate in the aerenchyma of *T. maritima* developed in leaves and roots (Gulyaeva *et al.* 2016). Consequently, in tissues and organs, the intensity of the Krebs cycle is maintained at an optimal level; reoxygenation of tissues and organs, which can cause significant changes in the metabolism of halophytes at low tide, does not occur (Shikov *et al.* 2020).

The activity of CAT and SOD is usually studied in the tissues and organs of halophyte plants in a laboratory experiment when growing plants from seeds under the influence of different levels of salt stress. Depending on the level and time of exposure, enzyme activity can change in different directions. Thus, it was shown that CAT activity increased in the leaves of *Tripolium pannonicum* (Jacq.) Dobrocz under the influence of 800 mM NaCl solution (Ludwiczak *et al.* 2023); increase in CAT and SOD activity in the tissues of *Cakile maritima* Scop. with salt treatment of 400 NaCl (Ellouzi *et al.* 2011); decrease in CAT activity under the influence of 200–

1000mM NaCl in *Salicornia europaea* L. (Cardenas-Perez et al. 2022); decrease in CAT activity, but increase in SOD in *Sal-sola crassa* Bieb leaves treated with 250–1500 NaCl (Yildiztugay et al. 2014). Also, in the study of the halophytes *Arthrocnemum macrostachyum* (Moric.) Pirainen & G. Kadereit, *Sarcocornia fruticosa* (L.) A. J. Scott and *Salicornia europaea* L. it was established that SOD activity was increased at high salt levels (400–600 mM NaCl solution) (Ghanem et al. 2021). Modarresi et al. (2013) revealed that SOD activity increases in the root, while decreases in a shoot at 450- to 650-mM NaCl stress at *Aeluropus littoralis* (Gouan) Parl. Under natural habitat conditions, a decrease in CAT activity in the roots and stem of *Suaeda vermiculata* was shown in saline soils compared to non-saline soils (Al-Shamsi et al. 2020). All these data indicate that the enzymes CAT and SOD, depending on the operating conditions, regulate oxidation-reduction processes in the cells and organs of halophytes, changing their activity over a wide range.

We have established a direct positive correlation between the activity of CAT and SOD in the leaves of halophytes, both during high and low tides, and together during high and low tides in this general set of enzyme activities (Table 4, Fig. 4). This was expected, since all AOS enzymes are interconnected with each other due to the formation and utilization of ROS. The hydrogen peroxide formed as a result of the dismutation reaction during the activity of SOD is neutralized by CAT (Fig. 3).

Conclusion

The work investigated the activity of AOS enzymes in the leaves of halophyte plants in the coastal area of the White Sea. The plants lived in conditions where seawater was polluted with nitrates, iron, nickel and lead. The species formed a *Tripolium vulgare*–*Bolboschoenus maritimus*–

The species specificity of the level of enzyme activity in *Z. marina* was also established. The activity of CAT and SOD in its leaves is significantly lower than in other halophytes. The maximum values of enzyme activity were found in *T. vulgare* (Table 5). *Z. marina* is a hygrophyte, does not experience the tidal dynamics of the sea (more stable conditions), is constantly submerged in water, and lives in depressions in the middle littoral zone or in its lower parts. *T. vulgare* is a perennial plant, a species inhabiting all zones of coastal marshes from lower to upper parts. It is characterized by high plasticity of metabolic parameters, and high salt tolerance of seeds during germination (Markovskaya et al. 2024), and it's a hyperaccumulator of metals (Terebova and Pavlova 2021). Comparing the activity indicators of halophyte plant enzymes obtained by us with the data of other researchers is a very difficult task (Table 6).

Since units of measurement of enzyme activity are not always comparable, they can be presented in conventional units. Comparable levels of CAT and SOD activity in the leaf of *Betula pendula* under normal living conditions are known. CAT activity in birch leaves was 0.6–1.0 $\mu\text{mol} / \mu\text{g}$ protein – in the same range as in our species; SOD: 0.5–2.5 conventional units / mg protein – is lower than the values of enzyme activity in the halophyte species we studied. This again indicates a wide range of work of AOS enzymes and species specificity.

Triglochin maritima–*Plantago maritima* plant community with a TPC of 50% for *T. vulgare* and 20% for the remaining dominant species. The species specificity of the enzyme activity level in *Z. marina* has been established. The activity of CAT and SOD in its leaves was significantly

lower than that of other species. The maximum values of enzyme activity were found in *T. vulgare* and *T. maritima*. There is a direct positive correlation between the activity of CAT and SOD in the leaves of halophytes from the coastal area of the White Sea. The activity of the catalase en-

zyme in plant leaves varied over a wide range and did not depend on the tidal dynamics of the sea. Under hypoxic conditions during flooding in halophyte leaves, the regulation of plant redox metabolism was supported by an increase in SOD activity.

References

- ALATORRE, E. B., SHABALA, S., CHEN, Z. and POTTOSIN, I. I. (2013): Reduced tonoplast fast-activating and slow-activating channels activity is essential for conferring salinity tolerance in a facultative halophyte, quinoa. *Plant Physiology*, 162(2): 940-952. doi: 10.1104/pp.113.216572
- ALSCHER, R. G., ERTURK, N. and HEATH, L. S. (2002): Role of superoxide dismutases (SODs) in controlling oxidative stress in plants. *Journal of Experimental Botany*, 53: 1331-1341. doi: 10.1093/jexbot/53.372.1331
- ALLEN, R. G., BALIN, A. K. (1989): Oxidative influence on development and differentiation: An overview of a free radical theory of development. *Free Radical Biology & Medicine*, 6(6): 631-61. doi: 10.1016/0891-5849(89)90071-3
- AL-SHAMS, N., HUSSAIN, M. I. and EL-KEBLAWY, A. (2020): Physiological responses of the xerohalophyte *Suaeda vermiculata* to salinity in its hyper-arid environment. *Flora – Morphology Distribution Functional Ecology of Plants*, 273: 151705. doi: 10.1016/j.flora.2020.151705
- ANJUM, N.A., SHARMA, P., GILL, S.S., HASANUZZAMAN, M., KHAN, E.A., KACHHAP, K. and SOFO, A. (2016): Catalase and ascorbate peroxidase representative H₂O₂ detoxifying heme enzymes in plants. *Environmental Science and Pollution Research*, 23: 19002-19029. doi: 10.1007/s11356-016-7309-6
- APEL, K., HIRT, H. (2004): Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. *Annual Review of Plant Biology*, 55: 373-99. doi: 10.1146/annurev.arplant.55.031903.141701
- BABAEI-BONDARTI, Z., SHAHPURI, A. (2020): A metallothionein type 2 from *Avicennia marina* binds to iron and mediates hydrogen peroxide balance by activation of enzyme catalase. *Phytochemistry*, 176: 112396. doi: 10.1016/j.phytochem.2020.112396
- BLOKHINA, O., VIROLAINEN, E. and FAGERSTEDT, K. V. (2003): Antioxidants, oxidative damage and oxygen deprivation stress: A review. *Annals of Botany*, 91(2): 179-194. doi: 10.1093/aob/mcf118
- BOSE, J., RODRIGO-MORENO, A. and SHABALA, S. (2014): ROS homeostasis in halophytes in the context of salinity stress tolerance. *Journal of Experimental Botany*, 65(5): 1241-1257. doi: 10.1093/jxb/ert430
- BOSE, J., MUNNS, R., SHABALA, S., GILLIHAN, M., POGSON, B. and TYERMAN, S. D. (2017): Chloroplast function and ion regulation in plants growing on saline soils: Lessons from halophytes. *Journal of Experimental Botany*, 68(12): 3129-3143. doi: 10.1093/jxb/erx142
- BRADFORD, M. M. (1976): A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry*, 72: 248-254. doi: 10.1006/abio.1976.9999
- BRIOUKHANOV, A., NETRUSOV, A. (2004): Catalase and superoxide dismutase: Distribution, properties, and physiological role in cells of strict anaerobes. *Biochemistry (Moscow)*, 69(9): 949-962. doi: 10.1023/B:BIRY.0000043537.04115.d9
- CARDENAS-PEREZ, S., RAJABI DEHNAVI, A., LESZCZYNSKI, K., LUBINSKA-MIELINSKA, S., LUDWICZAK, A. and PIERNIK, A. (2022): *Salicornia europaea* L. functional traits indicate its optimum growth. *Plants*, 11(8): 1051. doi: 10.3390/plants11081051

- CHATURVEDI, A. K., PATEL, M. K., MISHRA, A., TIWARI, V. and JHA, B. (2014): The SbMT-2 gene from a halophyte confers abiotic stress tolerance and modulates ROS scavenging in transgenic tobacco. *PLoS One*, 9(10): e111379. doi: 10.1371/journal.pone.0111379
- CLEMENS, S., PALMGREN, M. G. and KRAMER, U. (2002): A long way ahead: Understanding and engineering plant metal accumulation. *Trends in Plant Science*, 7(7): 309-315. doi: 10.1016/s1360-1385(02)02295-1
- ELLOUZI, H., BEN HAMED, K., CELA, J., MUNNE-BOSCH, S. and ABDELLY, C. (2011): Early effects of salt stress on the physiological and oxidative status of *Cakile maritima* (halophyte) and *Arabidopsis thaliana* (glycophyte). *Physiologia Plantarum*, 142: 128-143. doi: 10.1111/j.1399-3054.2011.01450.x
- ERSHOVA, M. A., NIKEROVA, K. M. and GALIBINA, N. A. (2022): Some minor characteristics of spectrophotometric determination of antioxidant system and phenolic metabolism enzyme activity in wood plant tissues of *Pinus sylvestris* L. *Protein and Peptide Letters*, 29(8): 711-720. doi: 10.2174/0929866529666220414104747
- GHANEM, A.-M. F. M., MOHAMED, E., KAZEM, A. M. M. A. and EL-GHAMERY, A. A. (2021): Differential salt tolerance strategies in three halophytes from the same ecological habitat: Augmentation of antioxidant enzymes and compounds. *Plants*, 10(6): 1100. doi: 10.3390/plants10061100
- GULYAEVA, E. N., MOROZOVA, K. V., MARKOVSKAYA, E. F., NIKOLAEVA, N. N. and ZAPEVALOVA, D. S. (2016): Anatomical and morphological features of leaves of dominant species on the Barents Sea coast. *Proceedings of Petrozavodsk State University*, 2(155): 13-19. (In Russian).
- HAFEEZ, M. B., RAZA A., ZAHRA, N., SHAUKAT, K., AKRAM, M. Z., IQBAL, S. and BASRA., S. M. A. (2021): Gene regulation in halophytes in conferring salt tolerance. In: *Handbook of Bioremediation Physiological, Molecular and Biotechnological Interventions*, pp. 341–370.
- HALL, J. L. (2002): Cellular mechanisms for heavy metal detoxification and tolerance. *Journal of Experimental Botany*, 53: 1-11. doi: 10.1093/jexbot/53.366.1
- HASANUZZAMAN, M., HOSSAIN, M. A., DA SILVA, J. A. T. and FUJITA, M. (2012): Plant responses and tolerance to abiotic oxidative stress: antioxidant defenses is a key factor. In: B. Venkateswarlu, Arun K. Shanker, Chitra Shanker, M. Maheswari (eds.): *Crop stress and its management: Perspectives and strategies*. Springer, pp. 261–316. 10.1007/978-94-007-2220-0_8
- HASANUZZAMAN, M., BHUYAN, M. H. M., ZULFIGAR, F., RAZA, A., MOHSIN, S. M., MAHMUD, J. A., FUJITA, M. and FOTOPOULOS, V. (2020): Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*, 9(8): 681. doi: 10.3390/antiox9080681
- HASSLER, M. (1994–2024): World plants. Synonymic checklist and distribution of the world flora. Version 24.8; last update August 27th, 2024.
- ILYIN, G. V., USYGINA, I. S. and KASATKINA, N. E. (2015): Geocological state of seas in the environment in the Russian Arctic under the present technogenic stresses. *Bulletin of the Kola Science Center of the Russian Academy of Sciences*, 21: 82-93. (In Russian).
- INUPAKUTIKA, M. A., SENGUPTA, S., DEVIREDDY, A. R., AZAD, R. K. and MITTLER, R. (2016): The evolution of reactive oxygen species metabolism. *Journal of Experimental Botany*, 67: 5933-5943. doi: 10.1093/jxb/erw382
- KAPLIN, P. A., LEONTIEV, O. V., LUKYANOVA, S. A. and NIKIFOROV, L. G. (1991): Shores. «Izdatel'stvo Mysl'». 479 p. (In Russian).
- KNOX, J. P, DODGE, A. D. (1985): Singlet oxygen and plants. *Phytochemistry*, 24: 889-896. doi: 10.1016/S0031-9422(00)83147-7
- KÖHL, I. (1997) : The effect of NaCl on growth: Dry matter allocation and ion uptake in salt marsh and inland populations of *Armeria maritima*. *New Phytologist*, 135: 213-225. doi: 10.1046/j.1469-8137.1997.00639.x
- KRESLAVSKI, V. D., ALLAKHVERDIEV, S. L., LOS, D. A. and KUZNETSOV, V. V. (2012): Signaling role of reactive oxygen species in plants under stress. *Russian Journal of Plant Physiology*, 59(2): 141-154. doi: 10.1134/S1021443712020057

- KRZESLOWSKA, M. (2011): The cell wall in plant cell response to trace metals: polysaccharide remodeling and its role in defense strategy. *Acta Physiologiae Plantarum*, 33: 35-51. doi: 10.1007/s11738-010-0581-z
- KUMAR, A., MANN, A., KUMAR, A., KUMAR, N. and MEENA., B. L. (2021): Physiological response of diverse halophytes to high salinity through ionic accumulation and ROS scavenging. *International Journal of Phytoremediation*, 23(3): 1-11. doi: 10.1080/15226514.2021.1874289
- LENSTRA, W. K., EGGER, M., VAN HELMOND, N. A. G. M., KRITZBERG, E., CONLEY, D. J. and SLOMP, C. P. (2018): Large variations in iron input to an oligotrophic Baltic Sea estuary: Impact on sedimentary phosphorus burial. *Biogeosciences*, 15: 6979-6996. doi 10.5194/bg-15-6979-2018
- LIU, G., BAFICO, A., HARRIS, V. K. and AARONSON, S. A. (2003): A novel mechanism for Wnt activation of canonical signaling through the LRP6 receptor. *Molecular and Cellular Biology*, 23: 5825-5835. doi: 10.1128/MCB.23.16.5825-5835.2003
- LOKHANDE, V. H., SRIVASTAVA, S., PATADE, V. Y., DWIVEDI, S., TRIPATHI, R. D., NIKAM, T. D. and SUPRASANNA, P. (2011): Investigation of arsenic accumulation and tolerance in *Sesuvium portulacastrum* (L.). *Chemosphere*, 82: 529-534. doi: 10.1016/j.chemosphere.2010.10.059
- LUDWICZAK, A., CIARKOWSKA, A., RAJABI DEHNAVI, A., CARDENAS-PEREZ, S. and PIERNIK, A. (2023): Growth stage-, organ- and time-dependent salt tolerance of halophyte *Tripolium pannonicum* (Jacq.) Dobrocz. *Life*, 13(2): 462. doi: 10.3390/life13020462
- MANOUSAKI, E., KALOGERAKIS, N. (2011): Halophytes – An emerging trend in phytoremediation. *International Journal of Phytoremediation*, 13(10): 959-969. doi:10.1080/15226514.2010.532241
- MANOUSAKI, T., HULL, P. M., KUSHE, H., MACHADO-SCAFFINO, G., FRANCHINI, P., HAROD, C., ELMER, K. R. and MEYER, A. (2013): Parsing parallel evolution ecological divergence and differential gene expression in the adaptive radiations of thick-lipped midas cichlid fishes from Nicaragua. *Molecular Ecology*, 22: 650-669. doi: 10.1111/mec.12034
- MARKOVSKAYA, E. F., GULYAeva, E. N. (2020): Role of stomata in adaptation of *Plantago maritima* L. plants to tidal dynamics on the White Sea coast. *Russian Journal of Plant Physiology*, 67(1): 75-83. doi: 10.1134/S1021443719060086
- MARKOVSKAYA, E. F., TEREBOVA E. N. and PAVLOVA, M. A. (2024): The influence of salinity on the germination of halophyte seeds in the White Sea littoral: plasticity assessment. *Advances of Modern Natural Science*, 1: 80-86. (In Russian). doi: 10.17513/use.38211
- MITTLER, R. (2017): ROS are good. *Trends in Plant Science*, 22: 11-19. doi: 10.1016/j.tplants.2016.08.002
- MODARRESI, M., NEMATZADEH, G. and MORDIAN, F. (2013): Salinity response pattern and isolation of catalase gene from halophyte plant *Aeluropus litoralis*. *Photosynthetica*, 51: 621-629. doi: 10.1007/s11099-013-0060-z
- NIKEROVA, K. M. (2020): Activity of enzymes of the antioxidant system when changing xylogenesis scenarios in *Betula pendula* Roth and *Pinus sylvestris* L. *Dissertation for the degree of Candidate of Biological Sciences, specialty 03.01.05 – “Plant Physiology and Biochemistry”*, 201 p.
- NIKEROVA, K. M., GALIBINA, N. A., CHIRVA, O. V. and KLIMOVA (USPENSKAYA), A. V. (2021): Reactive oxygen species and components of the antioxidant system are participants in plant metabolism. Relationship with phenolic and carbohydrate metabolism. *Proceedings of the Karelian Scientific Center of the Russian Academy of Sciences*, 3: 5-20. (In Russian). doi: 10.17076/eb1312
- NOVIKOV, M. A. (2017): On the background values of heavy metal content in bottom sediments of the Barents Sea. *Bulletin of the Murmansk State Technical University*, 20(1/2): 280-288. (In Russian). doi: 10.21443/1560-9278-2017-20-1/2-280-288
- PELLOUX, J., RUSTERUCCI, C. and MELLEROWICZ, E. J. (2007): New insights into pectin methyl-esterase structure and function. *Trends in Plant Science*, 12: 267-277. doi: 10.1016/j.tplants.2007.04.001

- PIRASTEH-ANOSHEN, H., SAMADI, M., KAZEMEINI, S. A., OZTURK, M., LUDWICZAK, A. and PIERNIK, A. (2023): ROS homeostasis and antioxidants in the halophytic plants and seeds. *Plants*, 12(17): 3023. doi: 10.3390/plants12173023
- RABHI, M., FERCHICHI, S., JOUINI, J., HAMROUNI, M.H., KOYRO, H.-W., RANIERI, A., ABDELLY, C. and SMAOUI, A. (2010): Phytodesalination of a salt-affected soil with the halophyte *Sesuvium portulacastrum* L. to arrange in advance the requirements for the successful growth of a glycophytic crop. *Bioresource Technology*, 101: 6822-6828. doi: 10.1016/j.biortech.2010.03.097
- RAHMAN, M. M., MOSTOFA, M. G., KEYA, S. S., SIDDIQUI, M. N., ANSARY, M. M. U., DAS, A. K., RAHMAN, M. A. and TRAN, L.-S. P. (2021): Adaptive mechanisms of halophytes and their potential in improving salinity tolerance in plants. *International Journal of Molecular Sciences*, 22(19): 10733. doi: 10.3390/ijms221910733
- RASCIO, N., NAVARI-IZZO, F. (2011): Heavy metal hyperaccumulating plants: How and why do they do it? And what makes them so interesting? *Plant Science*, 180: 169-181. doi: 10.1016/j.plantsci.2010.08.016
- ROZANOV, A. G., VOLKOV, I. I., KOKRYATSKAYA, N. M. and YUDIN, M. V. (2006): Manganese and iron in the White Sea: Sedimentation and diagenesis. *Lithology and Mineral Resources*, 41(5): 483-501. doi:10.1134/S0024490206050087
- ROZENTSVET, O. A., NESTEROV, V. N. and BOGDANOVA, E. S. (2017): Structural, physiological, and biochemical aspects of salinity tolerance of halophytes. *Russian Journal of Plant Physiology*, 64(4): 464-477. doi: 10.1134/S1021443717040112
- SERGIENKO, L. A. (2008): Flora and vegetation of the Arctic coasts and adjacent territories. Publishing house of PertSU, Petrozavodsk, 225 p. (In Russian).
- SERGIENKO, L. A., STARODUBTSEVA, A. A., SMOLKOVA, O. V. and MARKOVSKAYA, E. F. (2015): The species of the genus *Zostera* L. in flora of White Sea' Eastern coasts. *Fundamental Research*, 2: 2606-2613. (In Russian).
- SHIKOV, A. E., CHIRKOVA, T. V. and EMEL'YANOV, V. V. (2021): Functions of reactive oxygen species in plant cells under normal conditions and during adaptation. *Ecological Genetics*, 19(4): 343-363. (In Russian). doi: 10.17816/ecogen75975
- SHIKOV, A. E., CHIRKOVA, T. V. and EMEL'YANOV, V. V. (2020): Post-anoxia in plants: reasons, consequences, and possible mechanisms. *Russian Journal of Plant Physiology*, 67(1): 45-59. doi: 10.1134/S1021443720010203
- SONINA, A. V., TEREBOVA, E. N., DYACHKOVA, T. YU., MOROZOVA, K. V. and ELKINA, N. A. (2021): 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. *Czech Polar Reports*, 11(2): 233-252. doi: 10.5817/CPR2021-2-16
- TEREBOVA, E. N., MARKOVSKAYA, E. F., ANDROSOVA, V. I. and GALIBINA, N. A. (2017): Potential for *Salix schwerinii* E. Wolf to uptake heavy metals in the contaminated territories of mining industry in the north-west Russia. *Siberian Journal of Forest Science*, 1: 74-86. doi: 10.15372/SJFS20170108
- TEREBOVA, E., MARKOVSKAYA, E., ANDROSOVA, V., PAVLOVA, M. and ORESHNIKOVA, N. (2020): Cell wall functional activity and metal accumulation of halophytic plant species *Plantago maritima* and *Triglochin maritima* on the White Sea littoral zone (NW Russia). *Czech Polar Reports*, 10(2): 169-188. doi: 10.5817/CPR2020-2-14
- TEREBOVA, E. N., PAVLOVA, M. A. (2021): The halophyte *Aster tripolium* L. is a hyperaccumulator of Fe, Ni, Pb on the littoral of the White Sea. *Advances of Modern Natural Science*, 11: 144-150. (In Russian). doi: 10.17513/use.37726
- TEREBOVA, E. N., PAVLOVA, M. A. and ORESHNIKOVA, N. V. (2023): Iron accumulation of halophytes in the littoral zone of the White Sea. *Biology Bulletin*, 50(4): 684-695. doi: 10.1134/S1062359023700243
- TODERICH, K. N., GOLDESTEIN, R. I., APARIN, V. B., IDZIKOWSKA, K. and RASHIDOVA, G. SH. (2001): Environmental state and analysis of phytogenetic resources of halophytic plants for rehabilitation and Livestock feeding in arid sandy deserts of Uzbekistan. In: S-W. Breckle,

- W. Weste, W. Wucherer (eds.): Sustainable Land use in deserts. Springer, BerlinHeidelberg, New York, pp. 154–165. doi: 10.1002/ldr.936
- VAN OSTEN, M. J., MAGGIO, A. (2015): Functional biology of halophytes in the phytoremediation of heavy metal contaminated soils. *Environmental and Experimental Botany*, 111: 135-146. doi: 10.1016/j.envexpbot.2014.11.010
- WANG, Y. J., ZHOU, L. M., ZHENG, X. M., QIAN, P. and WU, Y. H. (2013): Influence of *Spartina alterniflora* on the mobility of heavy metals in salt marsh sediments of the Yangtze River Estuary, China. *Environmental Science and Pollution Research*, 20(3): 1675-1685. doi: 10.1007/s11356-012-1082-y
- WANG, Y., BRANICKY, R., NOË, A. and HEKIMI, S. (2018): Superoxide dismutases: Dual roles in controlling ROS damage and regulating ROS signaling. *Journal of Cell Biology*, 6: 1915-1928. doi: 10.1083/jcb.201708007
- YILDIZTUGAY, E., OZFIDAN-KONAKCI, C. and KUCUKODUK, M. (2014): The role of antioxidant responses on the tolerance range of extreme halophyte *Salsola crassa* grown under toxic salt concentrations. *Ecotoxicology and Environmental Safety*, 110: 21-30. doi: 10.1016/j.ecoenv.2014.08.013
- ZAIER, H., MUDARRA, A., KUTSCHER, D., FERNANDES DE LA CAMPA, M. R., ABDELLEY, C. and SANZ-MEDEL, A. (2010): Induced lead binding phytochelatin in *Brassica juncea* and *Sesuvium portulacastrum* investigated by orthogonal chromatography inductively coupled plasma-mass spectrometry and matrix assisted laser desorption ionisation-time of flight mass spectrometry. *Analytica Chimica Acta*, 671: 48-54. doi: 10.1016/j.aca.2010.04.054
- ZHAO, H., YE, L., WANG, Y., ZHOU, X., YANG, J., WANG, J., CAO, K. and ZOU, Z. (2016): Melatonin increases the chilling tolerance of chloroplast in cucumber seedlings by regulating photosynthetic electron flux and the ascorbate-glutathione cycle. *Frontiers in Plant Science*, 7: 1814. doi: 10.3389/fpls.2016.01814
- ZHENG, M., LIU, Y., ZHANG, G., YANG, Z., XU, W. and CHEN, Q. (2023): The applications and mechanisms of superoxide dismutase in medicine, food, and cosmetics. *Antioxidants (Basel)*, 12(9): 1675. doi: 10.3390/antiox12091675

Web sources / Other sources

- [1] Order of Ministry of Agriculture of the Russian Federation of Decemder 13. 2016. №. 552. (2016). On the approval of water quality standards for water bodies of fishery value, including the standards of maximum permissible concentrations of harmful substances in the waters of water bodies of fishery value. (In Russian).
- [2] Quality of sea waters according to hydrochemical indicators. Handbook 2020. Publ. : «Nauka», 2021, 230 p. (In Russian).
- [3] State report on the state of the environment of the Republic of Karelia in 2019 (2020). In: A. N. Gromtsev (eds.), Petrozavodsk, 248 p. (In Russian).

Supplementary Materials

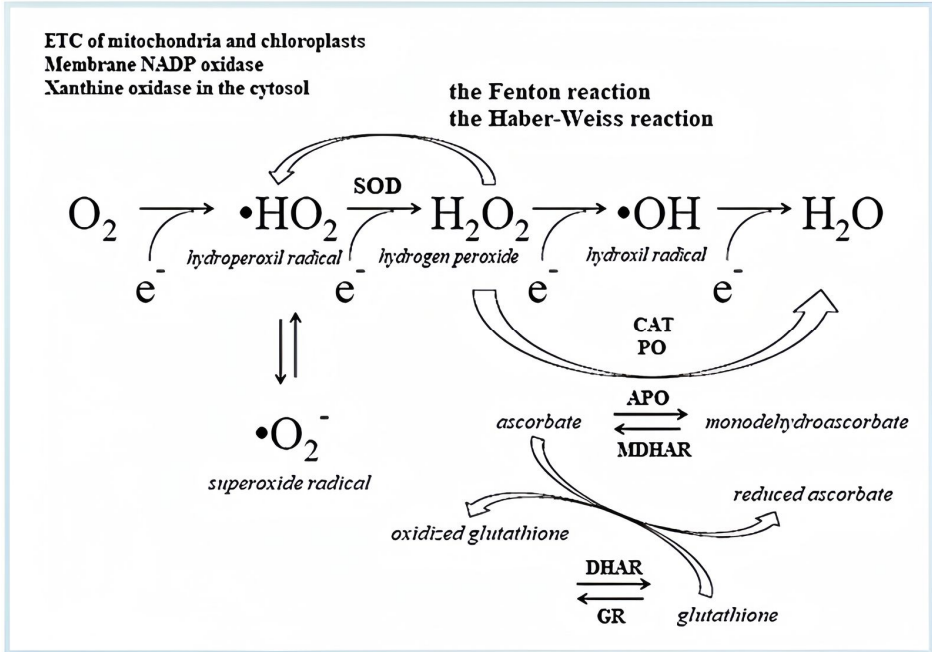


Fig. 3. The relationship between ROS, basic AO and AOS enzymes in the plant organism (Zhao et al. 2016, Wang et al. 2018, Nikerova et al. 2021). *Note:* PO – peroxidase; APO – ascorbate peroxidase; MDHAR – monodehydroascorbate reductase; DHAR – dehydroascorbate reductase; GR – glutathione reductase.

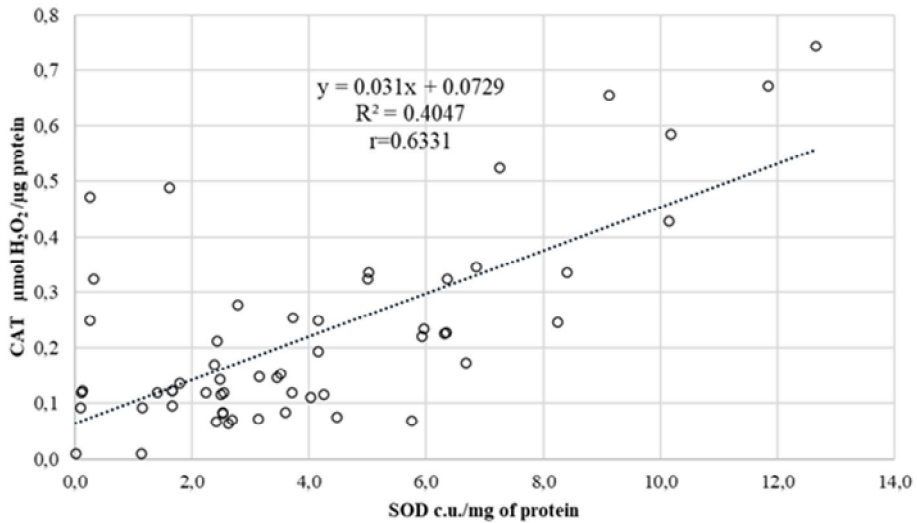


Fig. 4. Correlation between leaf activity of CAT and SOD of all halophytes at high and low tides (n=56).

Species	Conditions	Reference	Activity in leaves	
			CAT, μmol H ₂ O ₂ / μg protein	SOD, c.u. / mg of protein
<i>Salicornia europaea</i> L.	Pot experiment (control)	Cardenas-Perez et al. 2022	0.010 – 0.035	–
<i>Salsola crassa</i> Bieb		Yildiztugay et al. 2014	0.1 – 0.25	2.5 – 4.5
<i>Cakile maritima</i> Scop.		Ellouzi et al. 2011	0.005 – 0.015	20 – 150
<i>Betula pendula</i> Roth		Nikerova 2020	0.6 – 1.0	0.5 – 2.5

Table 6. Activity levels of catalase and superoxide dismutase enzymes in different plants under normal living conditions.