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Some Aspects of the Relationship between Redox Metabolism and the Structure of Calciphytes

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Abstract. Calciphyte species form a systematically and structurally heterogeneous group of plants capable of tolerating highly stressful conditions. Various structural adaptations occur in calciphytes to protect them against excess light (leaf pubescence) and moisture loss (waxy coating). Their shoot structure determines the volume of primary plant production. The present work studied the relationship between the antioxidant status and structural features of some calciphyte species. Redox metabolism in plant leaves was assessed using parameters such as water content, photosynthetic pigments, soluble carbohydrates, water-soluble phenolic compounds, water-soluble and membrane-bound proteins, and lipid peroxidation (LPO) level. The data obtained showed that the contents of the components regulating redox metabolism correlate both with each other and with the structural parameters of plants. In particular, the content of photosynthetic pigments in multi-species communities is lower in taller plants than in low-growing ones. The content of phenolic compounds and the level of LPO in calciphyte leaves are associated with the level of development of wax covering. The plants forming clumps and vigorous shoots exhibit increased LPO activity.

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Особенности взаимосвязи редокс-метаболизма и структуры растений кальцефитов

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Аннотация. Растения кальцефитных флор образуют систематически и структурно неоднородную группу растений, способных переносить высокострессовые условия. Кальцефиты реализуют различные структурные адаптации, противодействуя избытку света (опушение), снижая потери влаги (восковой налет). Структура их побегов определяет объем первичной продукции растений. Цель настоящей работы – изучить взаимосвязи антиоксидантного статуса со структурными особенностями некоторых представителей кальцефитной флоры. Редокс-метаболизм оценивали по оводненности листьев, содержанию фотосинтетических пигментов, углеводов, фенольных соединений, водорастворимых и мембранно-связанных белков, интенсивности накопления продуктов перекисного окисления липидов (ПОЛ). Полученные данные показали, что количественное содержание компонентов, регулирующих редокс-метаболизм, демонстрирует наличие корреляционных связей как между отдельными группами этих веществ, так и со структурными показателями растений. В частности, в многовидовых сообществах у более высоких растений содержание фотосинтетических пигментов ниже, чем у низкорослых. Содержание фенольных соединений и уровень ПОЛ в листьях кальцефитов связаны с уровнем развития воскового налета. Растения, формирующие куртины и мощные побеги, характеризуются повышенной активностью ПОЛ.

Ключевые слова: кальцефиты, редокс-метаболизм, пигменты, фенольные соединения, углеводы.

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Introduction

Calciphyte species form a systematically and structurally heterogeneous group of plants capable of tolerating highly stressful conditions (Tyler, 2003; Malysheva, Malakhovsky, 2011). Calciphytes grow in specific habitats: soils exhibit a high initial pH value, rockiness, and a special moisture regime (Escudero et al., 2015). In addition to specific soil conditions, the plants are constantly exposed to winds, high air temperatures, and excessive insolation. Plants of chalk slopes and carbonate outcrops, as a rule, have a xeromorphic structure with their characteristic external features such as pubescence and smaller leaves, which often develop a silvery sheen (Kurovsky, 2009). They are represented by different life-forms: dwarf shrubs, semi-shrubs, root and rhizome perennials, etc. Low-growing, creeping plants predominate among calciphytes. The main part of photosynthetic apparatus can be represented by many small stem-covering leaves or well-developed root leaf rosettes, or openwork leaf rosettes (Lambers, Oliveira, 2019).

Thus, the conditions for the growth of calciphytes are highly stressful, and, therefore, different structural adaptations occur in the plants.

The physiological adaptations of plants are based on alterations in cellular processes resulting in changes of quantitative and qualitative composition of compounds closely related to the main metabolic pathways including redox metabolism. At the same time, redox regulation of cellular processes is considered as one of the fundamental mechanisms regulating cell functional activity (Martinovich, Cherenkevich, 2008). Under adverse environmental conditions, plants experience oxidative stress due to the formation of an increased amount of highly reactive oxygen species (ROS) (Gupta et al., 2018). Lipid

peroxidation (LPO) is one of the redox regulation factors of enzymatic systems (Hasanuzzaman et al., 2020).

Under abiotic stresses such as drought, salinity, heavy metals, waterlogging, extreme temperatures, oxygen deprivation, etc., the activity of free-radical processes is also regulated by non-enzymatic antioxidants. The low molecular weight organic antioxidants (such as ascorbate, glutathione, carotenoids, tocopherols, flavonoids, betaines, etc.) sometimes can be more effective as metabolism protectors from ROS than enzyme systems. Phenolic compounds are the most common among them (Hasanuzzaman et al., 2020). They are broad-range mediators of biotic relationships, plant metabolism regulators, and participants in responses to abiotic stresses (D'Amelia et al., 2018). Recently, sugars have been considered as direct antioxidants (Bolouri-Moghaddam et al., 2010). The amount, chemical structure, and mechanism of action of antioxidants can vary significantly across plant species, such as calciphytes (Hasanuzzaman et al., 2020).

The aim of this work was to study the relationship between the elements of antioxidant system and the structural features of some calciphile plant species.

Materials and methods

Plant material

The study was conducted on 13 species from 9 families: *Artemisia salsoloides* Willd., *Anthemis trozkiana* Claus (Asteraceae); *Pimpinella titanophila* Woronow, *Bupleurum falcatum* L. (Apiaceae); *Krascheninnikovia ceratoides* (L.) Gueldenst. (Chenopodiaceae); *Onosma volgensis* Dobrocz (Boraginaceae); *Gypsophila volgensis* Krasnova (Caryophyllaceae); *Astragalus zingeri*

Korsh., *Hedysarum grandiflorum* Pall. (Fabaceae); *Linum flavum* L., *L. uralense* Juz. (Linaceae); *Polygala sibirica* L. (Polygalaceae); *Reseda lutea* L. (Resedaceae). The plants were growing in the Shigonsky District of the Samara Region in two ecotopes: Ecotope 1–53°29' N, 49°00' E, and Ecotope 2–53°35' N, 48°51' E.

We took into account such structural parameters of the species as the height of plants (average values in cm), the vigor and the position of their shoots, the presence/absence of clumps and rosettes, and the comparative levels of leaf pubescence and wax coating (Ryabinina, Knyazev, 2009; Maevsky, 2014).

For biochemical analyzes, we used freshly cut leaves collected from 12–15 plants. Three independent biological samples, 0.2–2.0 g of wet weight, were prepared from the total mass and stored in liquid nitrogen until laboratory studies.

The water content of the tissues was calculated after determining the wet and air-dry weight and expressed as %.

Biochemical analyses

The lipid peroxidation rate in leaves of plants was determined by measuring the accumulation of malonyldialdehyde (MDA), determined using the color reaction with thiobarbituric acid at $\lambda = 532$ nm (Lukatkin, Golovanova, 1988).

The content of photosynthetic pigments was determined spectrophotometrically in an acetone extract (90 %) at $\lambda = 662$, 645, and 470 nm. The concentration of chlorophylls *a*, *b* and carotenoids was calculated using the method of H. K. Lichtenthaler (1987).

The water-soluble phenolic substances were extracted from air-dry plant material, their content was determined in aqueous extracts using the Folin-Chocalteu reagent according to the method (Swain, Hillis, 1959) in the drop modification proposed by the manufacturer of the Pancreac Quimica reagent, Spain. The

absorbance of the solutions was determined on a photocolorimeter («KFK-2», Russia) using a red light filter at $\lambda = 725$ –730 nm. Gallic acid was used to make a calibration graph.

The amounts of water-soluble proteins and membrane-bound proteins were determined by the O.N. Lowry method (Lowry et al., 1951) on a spectrophotometer (PromEcoLab PE-3000, Russia) at $\lambda = 750$ nm, using calibration curves with a standard solution of bovine serum albumin (Calbiochem, Germany) in distilled water and in a 0.05 % Triton solution X-100, respectively.

The content of soluble carbohydrates was determined in freeze-dried material. The weighed portion (0.3 g) was extracted by 70 % ethanol; the evaporated hydroalcoholic extract of the plant sample was dissolved in water and subjected to purification by solid-phase extraction method in cartridges with sorbents Disorb-60-S16T and Diasorb-60-Amine. After the purification, the solution was analyzed under the following conditions: column Kromasil 4.6 x 250 mm 100–5NH₂ was used, the rate of eluent flow was 0.94 mL min⁻¹, and a refractometer served as a detector. The retention time of control substances served as the criterion of peak identification. Quantitative analysis was performed by absolute calibration method using peak areas as a reference.

Statistical analysis

The results of biochemical analyzes were presented as the average of three biological and three analytical replicates. The data obtained were presented in the form of arithmetic means (M), and the scattering of values was presented as standard errors (\pm SE). Comparison of quantitative data was carried out using one-way analysis of variance (One-way ANOVA) ($p < 0.05$) followed by the Tukey's test to compare the means. Calculations were performed using the Statistica 6.0 for Windows and Past 3 software.

For an expert assessment, the species were assigned conditional scoring characteristics, which were entered into the data matrix and, together with biochemical indicators, were used to calculate the pair correlation coefficients in the Microsoft Excel (Zaitsev, 1984).

Results and discussion

The typical structural and morphological traits of the aboveground organs of the species studied in this work are presented in Table 1.

According to the literature data, plants differ in both habit and characteristics of leaves. Low (20–40 cm) and medium-sized (50–60 cm) plants predominate among the species studied here, but one species, the subshrub *K. ceratoides*, forms vigorous leafy shoots up to 1 m in height and more. Most of the plants have shoots rising above the surface of the soil substrate. In four species, the main apparatus of photosynthesis is well-developed near-root leaf rosettes, and two species have openwork leaf rosettes. The other species are characterized by a relatively weak development of the leaf surface; they form thin branched shoots. The species also differ significantly in the pubescence of leaves and stems and the thickness of the wax coating.

Redox metabolism in plant leaves was assessed using parameters such as water content, photosynthetic pigments, soluble carbohydrates, water-soluble phenolic compounds, water-soluble and membrane-bound proteins, and MDA level (Table 2). The content of MDA, one of the final products of lipid oxidation, varied within wide limits depending on the plant species (0.1–1.7 mmol g⁻¹ dry weight). Calciphytes grow in water-limited soil conditions, and, therefore, it is important for them to maintain water homeostasis. Our results showed that the water content of the leaves was 51.1–78.4 % of dry weight, which corresponds to the values of xerophytic plants (Table 2). The largest water deficit was found in

O. volgensis, *K. ceratoides* and *A. zingeri* plants. The water content in their leaves was 1.2 times lower than in most of the species studied.

The content of photosynthetic pigments in leaves is considered as an indicator of the physiological state of plants, which characterizes the efficiency of the photosynthetic apparatus. The concentration of chlorophylls varied from 2.4 to 6.3 mg g⁻¹ and carotenoids from 0.4 to 1.2 mg g⁻¹ of dry weight. Plants *L. flavum*, *P. sibirica*, and *R. lutea* had high pigment contents. The calciphytes studied in the present work were heliophytes. They exhibited a high chlorophylls *a/b* ratio. This parameter varied in the range of 2.4–4.1.

The carbohydrates synthesized by plants in the photosynthesis process are the initial material for plastic and energy metabolism. In addition, they are known to have antioxidant properties and the ability to maintain the water balance of cells (Zakhochiy et al., 2019). The total content of soluble carbohydrates in the dry mass of leaves varied from 14.9 to 78.0 mg g⁻¹ (Table 2). Most of the calciphyte species demonstrated the predominance of disaccharides. The lowest concentration of sugars was found in the leaves of *H. grandiflorum*, which was mainly due to the low content of disaccharides. These plant species are able to slow down or speed up metabolic processes depending on external conditions (Ilyina, 2019). One can assume that the low sugar content compared to other species is a consequence of these processes.

The evaluation of protein components showed that the amount of membrane-bound proteins ranged from 6.8 to 81.0 mg g⁻¹ and water-soluble ones – from 12.9 to 267.6 mg g⁻¹ dry weight. Moreover, the content of water-soluble proteins may be 1.2–8.0 times greater than the content of the membrane-bound ones. The largest amount of membrane-bound proteins was found in the leaves of *B. falcatum*,

Table 1. Life-forms and morphometric parameters of calciphytes

Species	Life-form	Shoot height, cm	Vigor of shoots	Position of shoots relative to the surface of the substrate	Formation of dense aerial shoots*	The presence of a root leaf outlet*	The degree of leaf pubescence**	The degree of the waxy coating of leaves**
<i>A. trotzkiana</i>	SS	Up to 25 cm	Medium	CP	+	+(openwork)	++	-
<i>A. salsoloides</i>	SS	Up to 50 cm	High	RP	+	-	-	++
<i>A. zingeri</i>	SS	Up to 50cm	Medium	CP	+	+	+++	-
<i>B. falcatum</i>	PP	Up to 60 cm	Low	RP	-	+(openwork)	-	+
<i>G. volgensis</i>	PP	Up to 90 cm	Low	RP	-	-	-	+
<i>H. grandiflorum</i>	PP	Up to 50 cm	Medium	RP	+	+	++	-
<i>K. ceratoides</i>	SS	1 m and more	High	RP	+	-	++	-
<i>L. flavum</i>	PP	Up to 40 cm	Medium	RP	+	-	-	+
<i>L. uralense</i>	PP	Up to 20 cm	Low	RP	+	+	-	+
<i>O. volgensis</i>	PP	Up to 50 cm	High	CP	+	-	+++	-
<i>P. titanophila</i>	SS	Up to 40 cm	Low	RP	-	+	++	-
<i>P. sibirica</i>	PP	Up to 20 cm	Low	RP	+	-	+	-
<i>R. lutea</i>	PP	Up to 60 cm	High	RP	-	-	-	+

Note: SS – semi-shrubs; PP – perennial plants; CP – creeping plants; RP – raised plants. Expert characteristics criteria for some morphological features of plants: *absence (-) or presence (+); **absence (-); minimal (+), medium (++), maximal (+++) levels.

Table 2. Physiological and biochemical parameters of calciphyte leaves

Species	MDA, mmol g ⁻¹ dry weigh	Water content, %	Total chlorophylls	Carotenoids	Chlorophyll a/b	mg g ⁻¹ dry weight				Phenolic compound
						Monosaccharides	Disaccharides	Water-soluble proteins	Membrane-bound proteins	
Ecotope 1										
<i>A. salsoloides</i>	1.7±0.5a	64.8±1.4bc	2.8±0.2d	0.6±0.1c	2.5	40.4±2.1a	19.3±0.5c	267.6±11.3a	37.5±3.4c	132.5±7.0a
<i>A. trotzkiana</i>	0.2±0.1b	70.1±2.3b	2.4±0.3d	0.4±0.0d	2.4	32.5±2.6b	40.2±2.5a	84.9±4.5e	14.7±2.0e	25.9±2.3e
<i>P. titanophila</i>	0.4±0.1b	64.8±2.0b	3.5±0.4c	0.7±0.0c	2.9	29.7±1.3b	23.1±2.0b	144.6±12.5c	22.7±1.9d	60.0±3.0b
<i>K. ceratoides</i>	0.2±0.1b	57.7±1.0d	3.8±0.1c	0.7±0.0c	3.8	7.6±1.7d	11.6±1.5e	153.7±12.4c	42.1±1.4c	48.4±2.1c
<i>O. volgensis</i>	0.3±0.1b	51.1±1.1e	3.8±0.2c	0.6±0.1c	2.8	14.0±1.3c	24.6±1.3b	69.5±1.9f	10.2±2.0f	37.3±3.0d
<i>G. volgensis</i>	0.1±0.0c	67.5±2.7b	2.7±0.1d	0.5±0.1cd	3.2	1.2±0.1f	25.0±1.4b	80.3±1.8e	15.1±1.0e	26.4±1.0e
<i>L. uralense</i>	0.3±0.1b	66.0±1.6b	3.5±0.3c	0.6±0.1c	2.9	–	–	12.9±1.2h	6.8±1.0g	–
Ecotope 2										
<i>A. zingeri</i>	0.4±0.1b	57.6±2.0d	4.4±0.3b	0.9±0.1b	3.0	4.8±0.3d	15.6±1.0d	122.9±12.0d	17.7±1.1e	47.6±2.2c
<i>B. falcatum</i>	0.4±0.1b	62.6±3.0bc	4.6±0.3b	0.9±0.1b	4.1	–	–	184.0±15.6b	81.0±3.0a	51.9±2.5c
<i>H. grandiflorum</i>	0.5±0.2b	62.0±2.1c	4.9±0.3b	0.9±0.1b	3.1	5.0±1.0d	9.9±0.9e	120.0±11.0d	15.0±1.5e	26.5±2.5e
<i>G. volgensis</i>	0.1±0.0c	67.5±3.5b	2.7±0.2d	0.6±0.1c	2.9	3.4±0.3e	21.7±1.6b	112.3±9.0d	24.3±2.0d	57.0±3.6b
<i>L. flavum</i>	0.4±0.1b	78.2±4.0a	6.3±0.4a	0.9±0.2ab	2.9	32.1±2.0b	45.9±3.0a	81.2±2.5e	57.8±3.0b	27.5±2.1e
<i>K. ceratoides</i>	0.5±0.2b	53.1±2.0e	2.6±0.3d	0.6±0.1c	3.3	–	–	136.9±13.8cd	56.9±3.6b	17.5±2.0f
<i>P. sibirica</i>	0.1±0.0c	62.4±2.4c	5.4±0.5b	1.2±0.1a	2.9	–	–	44.1±1.2g	34.3±6.0c	27.4±2.6e
<i>R. lutea</i>	0.4±0.2b	78.4±3.0a	5.1±0.3b	0.8±0.1bc	2.9	38.5±2.1a	26.6±2.3b	115.7±10.4d	17.6±2.3e	54.9±2.4b

Note: data are mean ± SE (n = 9). Different letters indicate significant differences at the level of $p < 0.05$.

and water-soluble proteins were the highest in *A. salsoloides*. It is well-known that individual components of water-soluble proteins are responsible for protection against oxidative stress (Orlova et al., 2007).

Plant polyphenols have pronounced antioxidant and antiradical properties. Due to the antioxidant effect, phenolic compounds with the combined action of the antioxidant system are able to «quench» free radicals, stabilize and protect cell membranes from damage, prevent the autolysis of lysosomes, mitochondria, etc. (Martinovich, Cherenkevich, 2008; Gupta et al., 2018; Zagoskina, Nazarenko, 2016). The content of phenolic compounds, as well as proteins and carbohydrates, which are also involved in the redox metabolism, varied widely across the plant species (17.5–132.5 mg g⁻¹ dry weight). In two species used as an example – *K. ceratoides* and *G. volgensis* – the content of phenolic compounds depends not only on the species traits but also on the growing conditions. Thus, in the leaves of both species, sampled in different ecotopes, the content of phenolic compounds differed by more than a factor of two.

The content analysis of primary and secondary metabolism components, including those involved in the regulation of redox metabolism, shows that their amounts vary significantly in different calciphyte species.

We used the correlation analysis method to identify the possible relationship between some structural traits and physiological and biochemical parameters. To this purpose, the primary expert assessment of structural features was fulfilled. The plants were assigned quantitative estimates: heights (average values in cm), the relative degree of development of aerial shoots (from 1 to 10 points), the presence or absence of clumps (0–1 points), the presence of outlets (absence – openwork rosettes – well-developed rosettes, from 1 to 3 points), the presence and degree of

development of pubescence (from 0 to 3 points), the presence and degree of development of wax coating (from 0 to 2 points), the position of the shoots (creeping over the substrate or rising above it (1 and 2 points). Table 3 presents the results of the analysis of relationships between the metabolic parameters and structural traits of the calciphytes studied. Both positive and negative correlations were found.

A high positive pair correlation was found between photosynthetic pigment contents – chlorophyll *a*/chlorophyll *b*, chlorophyll *a*/carotenoids, chlorophyll *b*/carotenoids ($r = 0.91$; 0.86 ; 0.78 , respectively). Similarly, a high positive correlation was found between the MDA level/the content of water-soluble proteins, the MDA level/the content of phenolic compounds ($r = 0.77$ and 0.79 , respectively). That means that under stressful conditions, all antioxidant components are activated, contributing to the development of adaptive plant responses. The accumulation of water-soluble phenolic compounds in leaves of calciphytes correlated with the level of development of wax coating on the vegetative parts of the shoots ($r = 0.67$), and an average positive level of correlation between the development of wax coating and MDA level ($r = 0.52$) was also revealed.

It is well-known that under water deficient conditions, wax coating on the surface of plant leaves not only contributes to the regulation of the water balance, but also, unlike pubescence, better reflects sunlight, thereby protecting the assimilation organs of plants from ultraviolet radiation and burns (Lambers, Oliveira, 2019).

The plant height expressed in conditional points negatively correlated with the content of photosynthetic pigments (r values from -0.36 to -0.59), which is quite consistent with the level of light exposure of plants with different shoot heights in multispecies communities – the maximal for the highest and more limited for the

Table 3. Paired correlation coefficients of biochemical and structural parameters of calciphytes

Parameters	Dry mass	Monosaccharides	Disaccharides	Phenolic compounds	Chlorophyll a	Chlorophyll b	Carotenoids	Water-soluble proteins	Membrane-bound proteins	MDA
Dry mass	1.00									
Monosaccharides	-0.55*	1.00								
Disaccharides	-0.64**	0.54*	1.00							
Phenolic compounds	-0.08	0.44	-0.28	1.00						
Chlorophyll a	-0.25	0.14	0.11	-0.20	1.00					
Chlorophyll b	-0.36	0.37	0.25	-0.07	0.91***	1.00				
Carotenoids	-0.03	-0.06	-0.23	-0.13	0.86***	0.78***	1.00			
Water-soluble proteins	0.12	0.35	-0.44	0.82***	-0.15	-0.20	-0.07	1.00		
Membrane-bound proteins	0.03	0.31	0.28	0.05	0.33	0.09	0.33	0.46	1.00	
MDA	0.01	0.53*	0.15	0.79***	-0.11	0.05	-0.09	0.77***	0.23	1.00
Plant height	0.14	-0.54*	-0.32	-0.12	-0.40	-0.59*	-0.36	0.34	0.31	-0.11
Vigor of shoots	0.32	0.26	-0.23	0.19	-0.24	-0.13	-0.35	0.12	-0.25	0.40
Clumps	0.32	0.12	-0.36	0.13	-0.18	-0.09	-0.30	0.11	-0.36	0.36
Rosettes	-0.09	-0.45	-0.11	-0.22	0.14	0.08	0.16	0.03	-0.10	-0.15
Leaf pubescence	0.57*	-0.25	-0.24	-0.27	-0.01	0.04	0.03	-0.12	-0.39	-0.15
Waxy coating of leaves	-0.38	0.26	0.09	0.67**	-0.08	-0.03	-0.07	0.36	0.28	0.52*
Shoot position	-0.52*	0.31	0.17	0.05	-0.06	-0.11	-0.05	0.13	0.31	0.07

Note: The average level of correlation ($|0.3 < r < 0.6|$) is indicated by bold font and light gray color; high ($|r > 0.6|$) – by bold font and dark gray; *The reliability of the correlation coefficient at a confidence level of 0.95 for a sample size of 15 pairs of values (species) corresponds to the values of the correlation coefficient of 0.51 and higher; **At a confidence level of 0.99 – the correlation coefficient is 0.63 and higher; ***At a confidence level of 0.999 – the correlation coefficient of 0.75 and higher.

undersized. At the level of an average positive relationship, an increase in lipid peroxidation was observed in plants that had more vigorous shoots and formed clumps of shoots ($r = 0.40$ and 0.36 , respectively), which is logically associated with the successful development of species that form a significant amount of phytomass of densely leaved shoots in ecologically harsh habitats.

Multiple connections of medium strength, both positive and negative, were found for a number of monosaccharides as a group of primary metabolites. The level of their accumulation was associated with the activity of metabolic processes (water soluble proteins) and tissue antioxidant status (MDA). There was a tendency towards a decrease in the number of monosaccharides in

plants with an increase in their height ($r = -0.54$) or the formation of basal rosettes ($r = -0.45$).

Conclusion

The data obtained showed that the quantitative level of the elements of the redox system correlates both with each other and with the structural parameters of calciphytes. In particular, the content of photosynthetic pigments in multi-species communities in taller plants is lower than in low-growing ones. The content of phenolic compounds and the level of MDA in calciphyte leaves is associated with the level of development of wax covering. In ecologically harsh habitats, plants forming clumps and vigorous shoots are characterized by increased LPO activity.

References

- Bolouri-Moghaddam M.R., Le Roy K., Xiang L., Rolland F., Van den Ende W. (2010) Sugar signalling and antioxidant network connections in plant cells. *FEBS Journal*, 277(9): 2022–2037
- D'Amelia V., Aversano R., Chiaiese P., Carputo D. (2018) The antioxidant properties of plant flavonoids: their exploitation by molecular plant breeding. *Phytochemistry Reviews*, 17(3): 611–625
- Escudero A., Palacio S., Maestre F. T., Luzuriaga A. L. (2015) Plant life on gypsum: a review of its multiple facets. *Biological Reviews*, 90(1): 1–18
- Gupta D.K., Palma J.M., Corpas F.J. (2018) *Antioxidants and antioxidant enzymes in higher plants*. Springer International Publishing AG, 300 p.
- Hasanuzzaman M., Bhuyan M.H.M.B., Zulfiqar F., Raza A., Mohsin S.M., Al Mahmud J., Fujita M., 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
- Ilyina V.N. (2019) Ontogenetic structure and types of cenopopulation of *Hedysarum grandiflorum* Pall. in the middle Volga basin. *Proceedings of the National Academy of Sciences of Belarus. Biological Series* [Izvestiya Natsional'noi akademii nauk Belarusi. Seriya biologicheskikh nauk], 64(3): 302–310 (in Russian)
- Kurovskiy A.V. (2009) Ecological-physiological aspects of calcium requirement of herbs. *Tomsk State University Journal* [Vestnik Tomskogo gosudarstvennogo universiteta], 329: 237–240 (in Russian)
- Lambers H., Oliveira R.S. (2019) *Plant physiological ecology*. Springer Nature Switzerland AG, 755 p.
- Lichtenthaler H.K. (1987) Chlorophylls and carotenoids: pigment of photosynthetic biomembranes. *Methods in Enzymology*, 148: 350–382
- Lowry O.H., Rosebrough N.J., Farr A.L., Randall R.J. (1951) Protein measurement with the Folin phenol reagent. *Journal of Biological Chemistry*, 193(1): 265–275

Lukatkin A. S., Golovanova V. S. (1988) Intensity of lipid peroxidation in chilled leaves of thermophilic plants. *Plant Physiology* [Fiziologiya rastenij], 35(4): 773–780 (in Russian)

Maevsky P. F. (2014) *Flora of the middle zone of the European part of Russia*. Moscow, KMK, 635 p. (in Russian)

Malysheva G. S., Malakhovsky P. D. (2011) Vegetation of chalk outcrops in the Khvalynsky National Park. *Povolzhskiy Journal of Ecology* [Povolzhskij ekologicheskij zhurnal], 2: 223–230 (in Russian)

Martinovich G. G., Cherenkevich S. N. (2008) Redox homeostasis of cells. *Uspekhi Fiziologicheskikh Nauk*, 39(3): 29–44 (in Russian)

Orlova N. V., Kusakina M. G., Suchkova N. V. (2007) Dependence of contain of water-soluble protein in organs halophytes from soil salinity. *Bulletin of Perm University. Biology* [Vestnik Permskogo universiteta. Seriya: biologiya], 5: 31–34 (in Russian)

Ryabinina Z. N., Knyazev M. S. (2009) *Keys to vascular plants of the Orenburg region*. Moscow, KMK, 758 p. (in Russian)

Swain T., Hillis W. E. (1959) The phenolic constituents of *Prunus domestica*. I. – The quantitative analysis of phenolic constituents. *Journal of the Science of Food and Agriculture*, 10(1): 63–68

Tyler G. (2003) Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behavior – contribution to a debate. *Folia Geobotanica*, 38(4): 419–428

Zagoskina N. V., Nazarenko L. V. (2016) Active oxygen species and antioxidant system of plants. *Bulletin of the Moscow City Pedagogical University. Series: Natural Sciences* [Vestnik Moskovskogo gorodskogo pedagogicheskogo universiteta. Seriya: estestvennye nauki], 2: 9–23 (in Russian)

Zaitsev G. N. (1984) *Mathematical statistics in experimental botany*. Moscow, Nauka, 424 p. (in Russian)

Zakhozhiy I. G., Maslova S. P., Tabalenkova G. N., Dymova O. V. (2019) Productivity, physiological and biochemical properties of *Menyanthes trifoliata* (Menyanthaceae) in the middle taiga subzone of the Komi Republic. *Plant Resources* [Rastitelnye resursy], 55(2): 246–258 (in Russian)