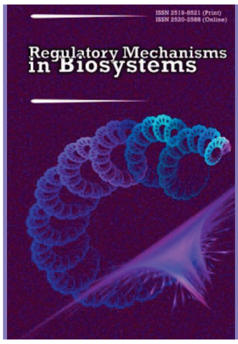

Regulatory Mechanisms in Biosystems

ISSN 2519-8521 (Print)
ISSN 2520-2588 (Online)
Regul. Mech. Biosyst.,
2021, 12(4), 710–717
doi: 10.15421/022198

Oxidative stress in moss *Bryum caespiticium* (Bryaceae) under the influence of high temperature and light intensity in a technogenically transformed environment

O. L. Baik*, N. Y. Kyyak*, O. M. Humeniuk**, V. V. Humeniuk**

**Institute of Ecology of the Carpathians of National Academy of Sciences of Ukraine, Lviv, Ukraine*
***Danylo Halytskyy Lviv National Medical University, Lviv, Ukraine*

Article info

Received 15.10.2021
Received in revised form 08.11.2021
Accepted 09.11.2021

Institute of Ecology
of the Carpathians
of NAS of Ukraine,
Kozelnytcka st., 4,
Lviv, 79026, Ukraine.
Tel.: +38-032-270-74-30.
E-mail:
baik.oksana@gmail.com

Danylo Halytskyy Lviv
National Medical
University, Pekarska st.,
69, Lviv, 79010, Ukraine.
Tel.: +38-032-239-37-05.
E-mail:
olhahumenyuk@ukr.net

Baik, O. L., Kyyak, N. Y., Humeniuk, O. M., & Humeniuk, V. V. (2021). Oxidative stress in moss Bryum caespiticium (Bryaceae) under the influence of high temperature and light intensity in a technogenically transformed environment. Regulatory Mechanisms in Biosystems, 12(4), 710–717. doi:10.15421/022198

Mosses are pioneer plants in post-technogenic areas. Therefore, the question of adaptive reactions of mosses from these habitats represents a scientific interest. The research is devoted to the study of adaptive changes in the metabolism of the dominant moss species *Bryum caespiticium* Hedw., collected in the devastated territories of the Novoyavorivsk State Mining and Chemical Enterprise (SMCE) "Sirka (Sulfur)" exposed to hyperthermia and insolation, which cause oxidative stress in plants. The influence of these stressors on the activity and thermal stability of antioxidant enzymes, hydrogen peroxide content, anion radical generation and accumulation of prooxidant components in moss shoots was studied. The activity and thermal stability of peroxidase and superoxide dismutase (SOD) were analysed for*B. caespiticium* moss from different locations of northern exposure at the sulfur mining dump No 1 in summer and autumn. We established the dependence of the activity of antioxidant enzymes of moss on the intensity of light and temperature on the experimental plots of the dump No 1. In summer, the highest activity and thermal stability rates of peroxidase and SOD were observed. Under the conditions of the experiment in shoots of *B. caespiticium* from the northern peak of the dump under the influence of 2 hours temperature action (+ 42 °C) the most significant increase in peroxidase activity was found by 1.78 times and SOD by 1.89 times, as well as increase in its thermal stability by 1.35–1.42 times, respectively. The increase in peroxidase and SOD activity, as well as the increase in their thermal stability caused by hyperthermia were negated by pre-processing with a protein biosynthesis inhibitor cyclohexamide, which may indicate the participation of the protein-synthesizing system in this process. The effect of increasing the thermal stability of enzymes can be considered as a mechanism of adaptation of the protein-synthesizing system to the action of high temperatures. Increase in the activity and thermal stability of antioxidant enzymes is caused primarily by changes in the expression of stress protein genes, which control the synthesis of specific adaptogens and protectors. The obtained results indicate that the extreme conditions of the anthropogenically transformed environment contribute to the development of forms with the highest potential abilities. The mechanism of action of high temperatures is associated with the development of oxidative stress, which is manifested in the intensification of lipid peroxidation and the generation of superoxide anion radical. It was found that temperature stress and high insolation caused an increased generation of superoxide anion radical as the main inducers of protective reactions in the samples of *B. caespiticium* from the experimental transect of the sulfur mining heap. It is known that the synthesis of H_2O_2 occurs under stress and is a signal to start a number of molecular, biochemical and physiological processes of cells, including adaptation of plants to extreme temperatures. It is shown that high temperatures initiate the generation of hydrogen peroxide. Increased reactive oxygen species (ROS) formation, including H_2O_2, under the action of extreme temperatures, can cause the activation of signaling systems. Therefore, the increase in the content of H_2O_2 as a signaling mediator is a component of the antioxidant protection system. It is determined that adaptive restructuring of the metabolism of the moss *B. caespiticium* is associated with the accumulation of signaling prooxidant components (diene and triene conjugates and dienketones). The increase in primary lipid peroxidation products, detected by us, under the action of hyperthermia may indicate the intensification of free radical oxidation under adverse climatic conditions in the area of the sulfur production dump, which leads to the intensification of lipid peroxidation processes. The accumulation of radical and molecular lipid peroxidation products are signals for the activation of protective systems, activators of gene expression and processes that lead to increased resistance of plants.

Keywords: peroxidase; superoxide dismutase; thermal stability; superoxide anion radical; hydrogen peroxide; conjugated dienes; dienketones; conjugated triens; moss.

Introduction

The effect of various abiotic factors, such as drought, salinity, temperature stress (especially in the summer months), increased insolation, strong winds, can lead to activation of protective and adaptive reactions of plants (Karpets & Kolupaev, 2009; Khorkavtsiv at al., 2009; Dey & De, 2012; Alvarez & Sanchez-Blanco, 2014). Plant adaptation is controlled by a complex molecular genetic system, which induces a certain stress-response mechanism, which maintains the homeostasis of the plant organism and protects against the destruction of the molecular and structural organization of cells (Seel et al., 1992; Guan & Scandalios, 2000; Pyatygin, 2008; Gill & Tuteja, 2010). The main adaptive changes in plants occur at the morphological and, first of all, at the biochemical levels (Lobachevska et al., 2005; Smirnoff, 2005; Kolupaev & Oboznyi, 2012). Plant resistance to abiotic stressors is associated with gene expression, involved in signaling or regulatory systems, in starting the synthesis of stress proteins and metabolites (Yurina & Odintsova, 2007; Rampitsch & Srinivasan, 2011; Kolupaev & Oboznyi, 2013; Kimura et al., 2017).

Temperature is one of the most important environmental factors, controlling the ontogenesis of plant organisms (Choudhury et al., 2017; Kyyak & Bunio, 2017; Zhang et al., 2017; Grishutkin et al., 2020; Boychuk, 2021). Currently, the main focus is on the study of biochemical and molecular genetic aspects of plant resistance to stress temperatures (Wahid & Close, 2007; Schmitt et al., 2014; Noctor et al., 2016). During the adaptation of plants to high temperatures, the thermal stability of cells increases, which is to a great extent associated with changes in the thermal stability of proteins and enzymes (Khan et al., 2015; Sidana et al., 2015; Khan et al., 2017). There are suggestions that induced protein synthesis participates in the formation of thermoresistance (Karpets & Kolupaev, 2009; Khan et al., 2015; Karpets, 2019).

Influence of temperature on the plant organism is one of the powerful abiotic environmental factors (Wadavkar et al., 2017; Zhang et al., 2017). Studies of plant resistance to adverse temperatures, which is the result of physiological and biochemical transformations, are relevant today (Kyyak et al., 2017; Song et al., 2020; Wani et al., 2021). Nonspecific protective systems, in particular the antioxidant system, play a significant role in the resistance of plants to the action of stress factors (Oboznyi et al., 2012; Karpets et al., 2016; Kyyak & Baik, 2016). The antioxidant complex, consisting of enzymes and low molecular weight antioxidants, belongs to the stress-protective systems involved in the formation of plant resistance, including against hyperthermia (Helena & Carvalho, 2008; Fan et al., 2009; Kolupaev & Karpets, 2009, 2010).

The protective role of antioxidants in the development of stress tolerance to hyperthermia and insolation, in particular in mosses, has been insufficiently researched. Therefore, the aim of the research was to study changes in the activity of enzymatic antioxidants, analysis of superoxide anion radical generation, hydrogen peroxide content and accumulation of diene conjugates, dienketones and triene conjugates as indicators of oxidative stress in moss *Bryum caespiticium* Hedw. under the influence of high temperature and light intensity in the technogenically transformed environment.

Material and methods

The object of investigations was the moss *Bryum caespiticium* Hedw., collected on the research areas (base, northern slope, crest and northern top) of the sulfur mining dump of the Novoyavorivsk State Mining and Chemical Enterprise "Sirka (Sulfur)" (Lviv region). The research was done during 2018–2020 in summer and autumn. Inveatigations were conducted in summer at the temperatures t = 35.0–38.0 ºC and light intensity – 110 thousand lux and in autumn at the temperature t = 14–16 ºC, insolation ≈ 80 thousand lux. The light intensity at the experimental areas was measured with a luxometer U-116.

To determine the peroxidase activity, a portion of the plant material was homogenized in 0.1 M acetate buffer (pH 5.4) in the ratio 1:1, extracted for 30 min at room temperature and centrifuged for 15 min, at 4000 g. The supernatant was used as an enzyme drug. To determine the activity of peroxidase 2 mL of the enzyme drug was mixed with 0.5% solution of benzidine and 0.1 M acetate buffer (pH 5.4). The qualitative reaction was started by adding a 3.0% solution of hydrogen peroxide. After 5 min, the samples were photometered at a wavelength of 412 nm on a spectrophotometer Specord 210 Plus. The enzyme activity was determined in relative units per 1 g of crude mass (Ermakov et al., 1987).

To determine the activity of superoxide dismutase, the plant material was extracted for 30 min in 0.15 M phosphate buffer (pH 7.8). Supernatant obtained after centrifugation (10 min, 5000 g) was added to the incubation medium containing: 0.33 mM ethylenediamine-N,N,N',N'-tetraacetic acid disodium salt (EDTA), 0.4 mM nitrosine tetrazolium, 0.01 mM phenazine metasulfate and 0.8 mM nicotinamide adenine dinucleotide phosphate (NADPH). The optical density of the solution was measured spectrophotometrically at a wavelength of 540 nm. SOD activity was expressed in conventional units per mg of protein per minute (Chevari et al., 1991).

To determine the thermal stability of peroxidase and SOD, gametophores of mosses were kept for two hours at a temperature of +42 ºC in a thermostat. Thermal stability was calculated as the ratio of the value of the residual activity of the enzyme after heating the samples in the thermostat to its value at room temperature (t = +20 ºC). Part of the plant material during one day was incubated in a solution of cyclohexamide, inhibitor of protein biosynthesis. Cyclohexamide at a concentration 20 μM almost completely evened out the increase of the activity of enzymes of the studied moss under the action of sublethal temperature.

To determine the hydrogen peroxide, the plant content material was homogenized and extracted into 50 mm phosphate buffer pH 7.0. The homogenate was centrifuged for 15 min at 13000 g and +5 ºC. The peroxide content was determined spectrophotometrically (Di Toppi et al., 1999). To determine the content of hydrogen peroxide to 1 mL of supernatant was added 3 mL of 0.1% $Ti(SO_4)_2$. The colour intensity was determined at a wavelength of 410 nm. The calibration curve was built for H_2O_2. The hydrogen peroxide content was calculated in mg per 1 g of dry matter.

Superoxide anion radical generation was determined by the reduction of nitroblue tetrazolium. To verify the specificity of the generation of superoxide anion radical in special experiments in the samples, SOD was added (50 units/mL). SOD inhibited the generation of superoxide anion radical by at least 90% (Kolupaev & Oboznyi, 2013). The optical density of the incubation solution was determined on a spectrophotometer Specord 210 Plus at a wavelength of 530 nm.

To determine the amount of diene conjugates and dienketones, a portion of the plant material was homogenized in 0.1 M potassium phosphate buffer (pH 7.0), a mixture of heptane-isopropanol added (1:1) and extracted for 20 minutes. The content of diene conjugates, dienketones and triene conjugates was determined spectrophotometrically in the heptane layer at wavelengths of 233, 278 and 275 nm, respectively, according to the method of Kurganova et al. (1997).

The results were statistically analyzed, determining the mean value, median, standard deviation (SD), and the first and the third quartiles for each characteristic in all the variants of the experiment. The selections were compared using single-factor dispersion analysis (ANOVA) with Bonferroni correction, considering differences between the selections reliable at the level of $P < 0.05$, 0.01, and 0.001. All calculations and developments of diagrams were made in Statistica 8.0 software (StatSoft, USA, 2012).

Results

One of the central enzymes in the study of adaptation mechanisms are isoforms of peroxidases, which belong to the extremely labile and multifunctional "stress" enzymes (Onele et al., 2018). We determined the dependence of peroxidase activity from light intensity and temperature of *B. caespiticium* from different locations of the northern exposure of the sulfur mining dump No. 1. Peroxidase activity of *B. caespiticium* is especially distinguished in summertime at high temperatures and light intensity at the northern top (peak) and northern slope of the dump, compared with the base. Indicators of peroxidase activity in *B. caespiticium* moss shoots were the highest at the northern exposure (peak and slope) of the dump and was 20.9 ± 0.2 and 24.7 ± 0.2 (relative units/g of dry weight) respectively, i.e. 1.21–1.43 times higher than at the base of the dump (Fig. 1). In autumn, when the temperature and insolation levels decreased, the activity of moss peroxidase from all localities decreased slightly, although the highest values of enzyme activity in the samples from the peak of the dump were maintained. Experimental studies have shown an increase in peroxidase activity by approximately 1.82 times in all samples of *B. caespiticium*. Thus, the highest peroxidase activity under the action of hyperthermia was observed in the samples of *B. caespiticium* from the northern peak and the northern slope: 37.3 ± 0.2 and 44.7 ± 0.2 relative units/g of dry weight, respectively (Fig. 1).

During the adaptation of plants to hyperthermia there is a change not only in activity but also in the kinetic characteristics of many enzymes, including peroxidase. Differences in the thermal stability of *B. caespiticium* moss shoots peroxidase from the experimental localities of the dump under the influence of hyperthermia were revealed. The strongest was the thermal stability of peroxidase under the action of hyperthermia in the experiment in samples of *B. caespiticium* from the slope (0.81 ± 0.05 relative units) and the peak of the dump (0.78 ± 0.03 relative units), where the highest intensity of environmental factors is noted (Fig. 2).

The increase in peroxidase activity, as well as the increase in its thermal stability under experimental conditions, were eliminated by pre-conditioning with protein biosynthesis inhibitor cyclohexamide. Obviously, the increase in the thermal stability of peroxidase is associated with increased synthesis of its more thermostable molecular forms, which was leveled by cyclohexamide. Such results may indicate the participation of the protein-synthesizing system in increasing the thermal stability caused by hyperthermia.

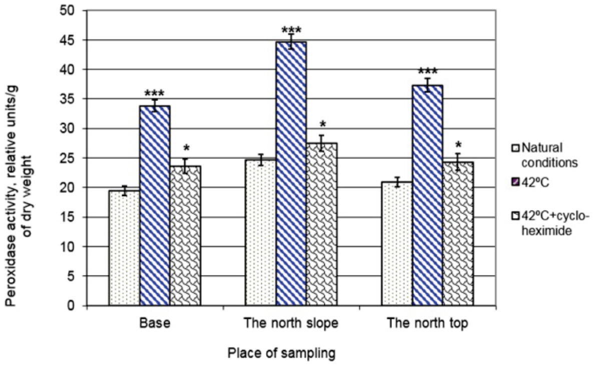

Fig. 1. Peroxidase activity (relative units/g of dry weight) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the sulfur mining dump No. 1 (base, slope and top): x ± SD, n = 4; * – difference between experimental sample and control is statistically reliable at $P < 0.05$; *** – at $P < 0.001$

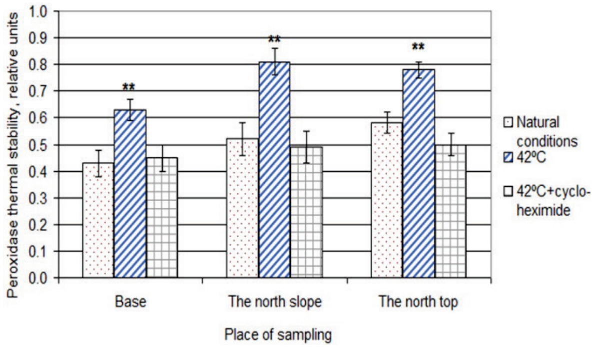

Fig. 2. Peroxidase thermal stability (relative units) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the sulfur mining dump No. 1 (base, slope, top): x ± SD, n = 4; ** – difference between experimental sample and control is statistically reliable at $P < 0.01$

Superoxide dismutase is considered not only as an antioxidant enzyme, but also as a component of signaling systems. Signals generated by reactive oxygen species (ROS) lead to increased gene expression and activation of stress-protective systems. Literature sources indicate that an induced protein synthesis may be involved in the formation of thermal stability of plants. It is believed that hyperthermia causes increased synthesis of more thermostable forms of the enzyme. The question of the effect of high temperatures on the activity and thermal stability of SOD of mosses remains unexplored.

The activity and thermal stability of SOD in moss *B. caespiticium* shoots were analyzed from different areas of the dump of sulfur deposit in summer and autumn. It was found that the activity of SOD of moss significantly depends on light intensity and temperature. The activity of SOD in the summer at high temperature and light intensity is especially distinguished. Thus, the activity of SOD in *B. caespiticium* during this period on the northern top and the base of the dump was 9.1 ± 0.3 and 9.8 ± 0.3 relative units/min•mg/protein, respectively. In autumn, when the temperature and insolation levels decreased, the activity of SOD of moss from all localities slightly decreased. Under the conditions of the experiment, an increase in the activity of SOD in samples of *B. caespiticium* by 1.61–1.89 times was determined. The most significant increase in SOD activity was found in moss from the northern top of the dump 17.1 ± 0.5 relative units/min•mg/protein (Fig. 3).

The thermal stability of SOD was highest in samples of moss from the northern slope and the northern peak of the dump at high temperature and insolation levels, especially in summer. Under the experimental conditions, the thermal stability under the action of hyperthermia in samples of *B. caespiticium* moss shoots from these habitats increased and was 0.76 ± 0.05 relative units and 0.88 ± 0.04 relative units respectively (Fig. 4).

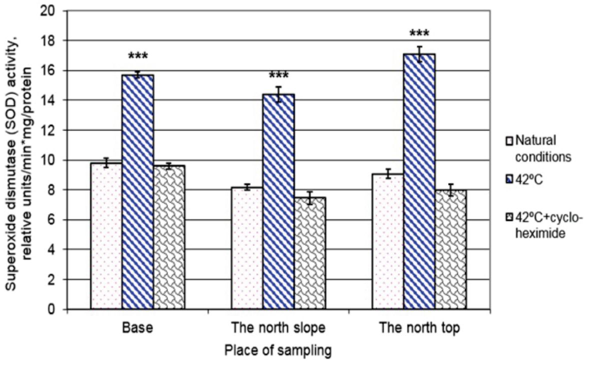

Fig. 3. Superoxide dismutase activity (SOD, relative units/min•mg/protein) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the sulfur mining dump No. 1 (base, slope, top): x ± SD, n = 4; *** – difference between experimental sample and control is statistically reliable at $P < 0.001$

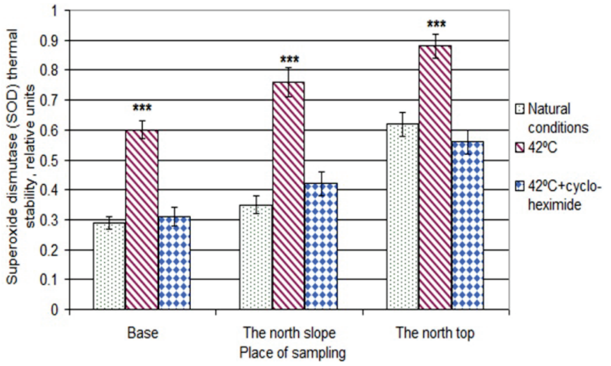

Fig. 4. Superoxide dismutase thermal stability (relative units) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the sulfur mining dump No. 1 (base, slope, top): x ± SD, n = 4; *** – difference between experimental sample and control is statistically reliable at $P < 0.001$

The effect of increased activity and thermal stability of SOD, caused by hyperthermia, was levelled by processing of gametophores of the studied moss samples with an inhibitor of protein biosynthesis cyclohexamide. The obtained results indicate the possibility of hyperthermia-induced biosynthesis of thermostable forms of SOD. Experimental studies have shown that heating of moss samples led to increased enzyme activity, which generates superoxide anions, in particular peroxidase with its subsequent conversion to H_2O_2 by increasing the activity of SOD.

It is shown that the highest generation of superoxide anion radicals in samples of *B. caespiticium* moss shoots, collected in the summer from the northern peak of the dump, was 38.2%, from the crest – 25.1%, 15.3% – from the northern slope, and the lowest was from the base of the dump – 10.2% (Fig. 5a). In autumn, indexes of superoxide anion radical generation decreased. Thus, in plants from the northern peak of the dump, they were up to 20.3%, and from the base 5.1%, which is obviously connected with the optimal temperature conditions and the decreasing of light intensity in this season (Fig. 5b). The effect of short-term temperature stress in the experiment led to a slight increase in the generation of superoxide anion radical in samples collected in summer – by 5.1–10.2% and its increase in samples of *B. caespiticium* collected in autumn – by 10.2–20.3% (at the base and northern slope ~ 10.2%, on the crest and the northern peak ~ 20.3%, Fig. 5).

Therefore, it was found that hyperthermia caused increased generation of superoxide anion radicals in samples of *B. caespiticium* from experimental transects of the sulfur deposit dump. The highest indicators of the prooxidant unit (amount of superoxide anion radicals) were found in samples from the northern peak of the dump at the highest temperatures and insolation. According to the results of research, under the influence of hyperthermia and high light intensity, the activation of redox processes took place. The accumulation of prooxidant components had a signal adaptive value in the restructuring of moss metabolism to changes in living conditions.

Hydrogen peroxide plays a central role in the response of plants to biotic and abiotic stresses. It is established that the highest content of hydrogen peroxide in summer was in samples of *B. caespiticium* moss shoots from the northern peak (1.29 ± 0.09 µM/g of dry weight), slightly lower in the samples from the crest (1.19 ± 0.05 µM/g of dry weight). The lowest content of this metabolite was in the samples from the base of the dump (0.74 ± 0.05 µM/g of dry weight), where the temperature was optimal. Under the conditions of the experiment there was observed an increase in H_2O_2 content in all experimental samples. It is shown that high temperatures initiate the generation of hydrogen peroxide. Hyperthermia in the experiment caused an increase of H_2O_2 content in all experimental samples 1.21–1.52 times (Fig. 6). Increased ROS formation, including H_2O_2, under the action of extreme temperatures, may be the cause of activation of signaling systems, which leads to adaptive changes in gene expression.

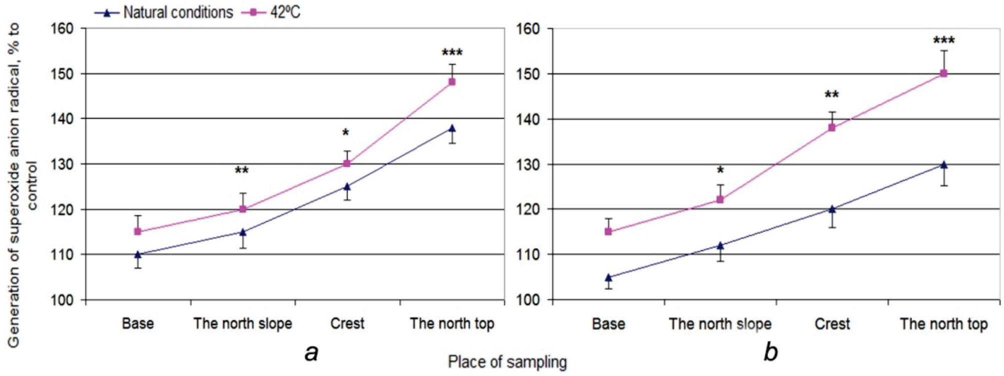

Fig. 5. Generation of superoxide anion radical (% to control) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the dump No. 1 (base, the north slope, crest, the north top): *a* – in summer, *b* – in autumn (x ± SD; n = 4); * – difference between experimental sample and control is statistically reliable at $P < 0.05$; ** – $P < 0.01$; *** – at $P < 0.001$

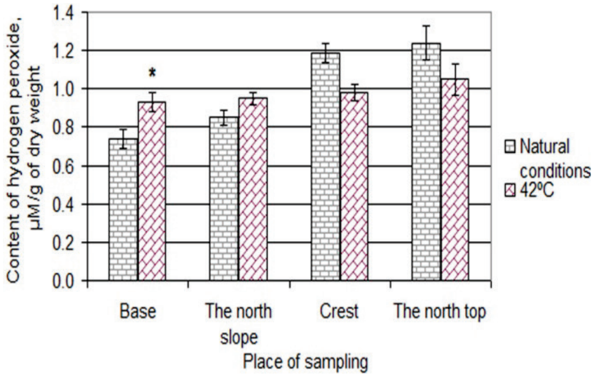

Fig. 6. Hydrogen peroxide content (µM/g of dry weight) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the dump No. 1 (base, the north slope, crest, the north top) (x ± SD; n = 4); * – difference between experimental sample and control is statistically reliable at $P < 0.05$

The obtained results of the research showing the increase in the H_2O_2 content under the action of hyperthermia are in good correlation with the obtained data, which testify about an increase in the activity of basic antioxidant enzymes – SOD and peroxidase. Based on the research, it can be concluded that the increase in H_2O_2 content as a signaling mediator is a manifestation of a single system of antioxidant protection.

Under stressful conditions, the activation of redox processes was accompanied by the accumulation of prooxidant components (diene conjugates, dienketones), which had a signal and adaptive value in the restructuring of plant metabolism to adverse environmental factors. The influence of high temperatures and light intensity on the content of diene conjugates and dienketones in *B. caespiticium* moss samples from the territory of the dump of the sulfur deposit was studied. According to our research, these indicators significantly depended on the ecological conditions of both the place of plant growth and the season of material collection. It is shown that the highest values of diene conjugates and dienketones content in samples from the northern peak of the dump in summer were respectively 23.3 ± 0.2 and 19.1 ± 0.2 units of absorption/mg of dry weigh, and lowest – at the dump base, where the temperature (up to +25 ºC) and intensity of light (up to 90 thousand lux) are relatively smaller – 9.2 ± 0.6 and 8.8 ± 0.2 units of absorbtion/mg of dry weight (Fig. 7, 8a).

In autumn, when the temperature and insolation regimes decreased, the content of diene conjugates and dienketones decreased by approximately 1.21–1.42 times (Fig. 7, 8b). Thus, the content of diene conjugates and dienketones in the *B. caespiticium* moss shoot samples from the top of the dump was accordingly 18.3 ± 0.8 and 16.5 ± 0.9 units of absorption/mg of dry weight, and from the base – 7.4 ± 0.3 and 6.1 ± 0.2 units of absorption/mg of dry weight. Under the conditions of the experiment, a short-term temperature stress led to a slight (in 1.23 times) increase in the content of diene conjugates and dienketones in the samples, collected in the summer, and more significant (in 1.22–1.51 times) in autumn. Thus, under the action of hyperthermia in the experiment, the content of diene conjugates in samples of moss collected in the summer from the northern peak, increased to 25.4 ± 0.6 units of absorption/mg of dry weigh, at the base up to 11.2 ± 0.3 units of absorption/mg of dry weight, and dienketones content to 26.3 ± 0.5 units of absorption/mg of dry weight and 10.1 ± 0.5 units of absorption/mg of dry weight, accordingly (Fig. 7, 8a).

Indicators of diene conjugates content in the experiment in moss samples collected in the autumn, increased to 21.5 ± 0.6 units of absorption/mg of dry weight (northern top) and to 8.9 ± 0.2 units of absorption/mg of dry weight (base), and dienketones – to 24.2 ± 0.4 units of absorption/mg of dry weight (northern top) and to 7.5 ± 0.3 units of absorption/mg of dry weight (base, Fig. 7, 8b). Therefore, the increase in the primary products of lipid peroxidation of diene conjugates' content and dienketones under the action of hyperthermia, found by us, may indicate the intensification of free radical oxidation under adverse climatic conditions in the territory of the sulfur mining dump, which leads to the strengthening of lipid peroxidation processes.

The increase in the diene conjugates' content and dienketones in conditions of hyperthermia and high light intensity was accompanied by the accumulation of triene conjugates. The highest indicators of triene conjugates in *B. caespiticium* moss shoots was determined in summer on the northern peak and on the crest of the dump – 28.1 ± 0.3 and 25.2 ± 0.2 units of absorption/mg of dry weight, accordingly, the smallest were in the base – 14.5 ± 0.3 units of absorption/mg of dry weight (Fig. 9).

In the conditions of the experiment under the action of short-term hyperthermia in the summer period, the triene conjugates' content increased approximately by 1.23 times in all samples from the experimental transect of the dump (Fig. 9a). In autumn, in all samples of *B. caespiticium* moss shoots the triene conjugates content decreased approximately by 2.00 times (Fig. 9b). Thus, the triene conjugates content in the moss samples from the northern peak decreased to 14.1 ± 0.2 units of absorption/mg of dry weight, and from the base – up to 6.9 ± 0.3 units of absorption/mg of dry weight. Under conditions of experimental hyperthermia, the triene conjugates content increased by 1.42–1.71 times in all samples of *B. caespiticium* moss shoots. Thus, the highest triene conjugates' content was in the samples from the northern peak 19.2 ± 0.2 units of absorption/mg of dry weight, and the lowest – in samples from the base 11.5 ± 0.2 units of absorption/mg of dry weight.

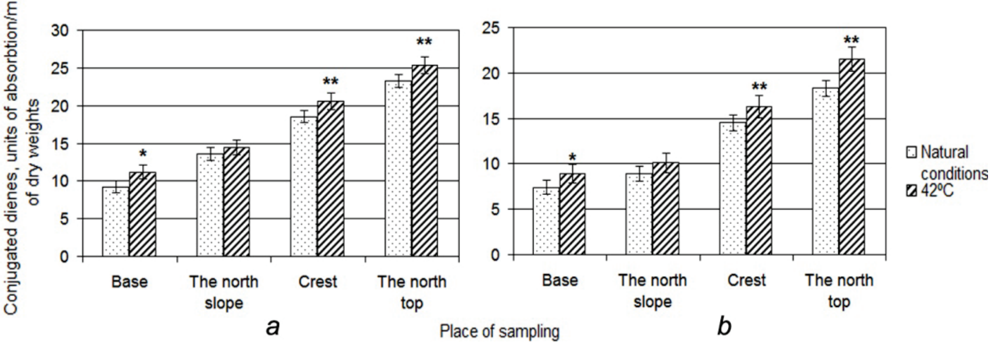

Fig. 7. Diene conjugates content (units of absorption/mg of dry weight) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the dump No. 1 (base, north slope, crest, the north top): *a* – in summer, *b* – in autumn; x ± SD, n = 4; * – difference between experimental sample and control is statistically reliable at P < 0.05, ** – P < 0.01

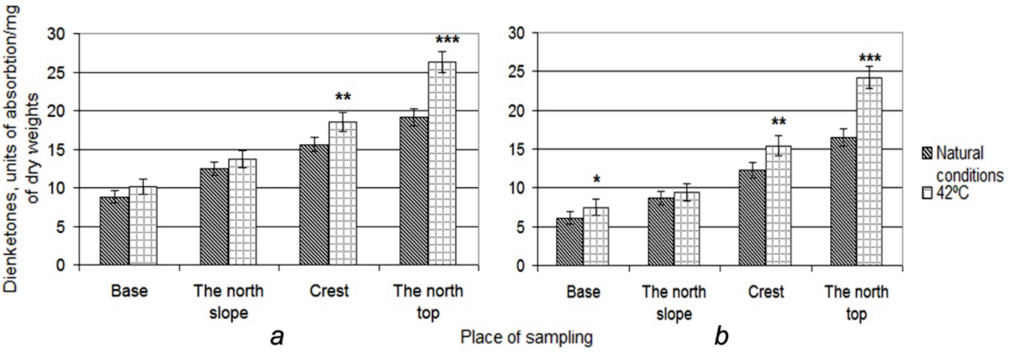

Fig. 8. The content of dienketones (units of absorption/mg of dry weight) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the dump No. 1 (base, the north slope, crest, the north top): *a* – in summer, *b* – in autumn; x ± SD, n = 4; * – difference between experimental sample and control is statistically reliable at P < 0.05, ** – P < 0.01, *** – P < 0.001

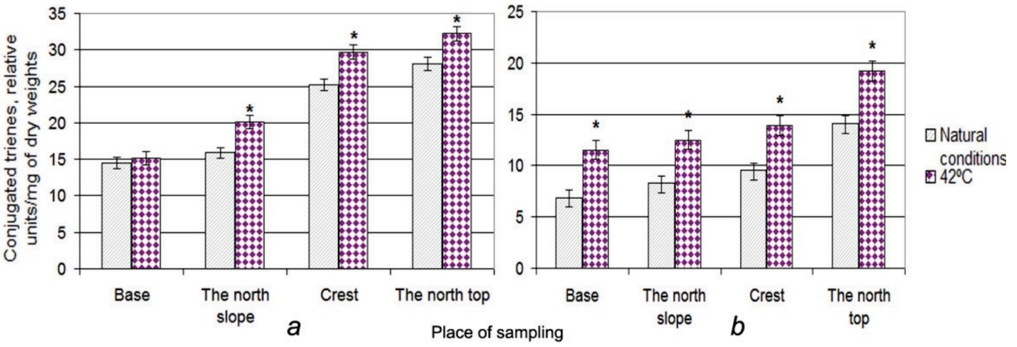

Fig. 9. Triene conjugates content (units of absorption/mg of dry weight) in shoots of the moss *Bryum caespiticium* from different locations of the northern exposure of the dump No. 1 (base, the north slope, crest, the north top): *a* – in summer, *b* – in autumn; x ± SD, n = 4; * – difference between experimental sample and control is statistically reliable at P < 0.05

Thus, hyperthermia and insolation cause the increase in the primary lipid peroxidation products' content. The development of oxidative stress is manifested in the intensification of lipid peroxidation. The accumulation of radical and molecular products of lipid peroxidation can be a signal for the activation of protective systems, enhancing the expression of genes and processes that lead to increased plant resistance.

Discussion

Temperature regime is one of the determining factors of the environment that affects plant life. Hyperthermia destabilizes metabolic processes. It is believed that reactions to stress influences provide a short-term plant protection, and further contribute to the formation of mechanisms of specialized adaptation (Kosakivska et al., 2014, 2015, 2017). Lipid peroxidation is important for the renewal of biological membranes, rotation of their protein and lipid components, regulation of physical and chemical properties of membranes and subcellular structures (Ayala et al., 2014; Choudhury et al., 2017; Wani et al., 2021). Enhancement of lipid peroxidation processes is a universal mechanism by which the most important homeostatic physicochemical parameters of the cell are controlled, which play a significant role in the survival of organisms under the influence of extreme factors of various origins, including hyperthermia (Richards et al., 2015; Sofo et al., 2015; Ren et al., 2021).

The mechanism of action of high temperatures is associated with the development of oxidative stress, which is manifested in the intensification of lipid peroxidation and the generation of superoxide anion radical (Nakamura, 2000; Scarpeci et al., 2008; Shevyakova et al., 2009). It is known that during the adaptation of plants to hyperthermia there is a change not only in activity but also in the kinetic characteristics of many enzymes, including peroxidase (Aleksandrov, 1985; Lyutova & Kamentseva, 2001; Obozny et al., 2010). Hyperthermia leads to significant changes in cell metabolism, accompanied by an increase in the formation of reactive oxygen species in them and, as a consequence, damage to cellular structures (Kosakivska et al., 2016; Moyo et al., 2017). It is known that stress factors, including high temperature, induce an antioxidant system (AOS) (Neill et al., 2002c; Oboznyi et al., 2012; Kusvuran et al., 2016; Noctor et al., 2016).

We found the dependence of the activity of antioxidant enzymes of moss on the intensity of light and temperature on the experimental plots of the dump No. 1. In the summer period, the highest activity and thermal stability of peroxidase and SOD were observed. At the conditions of the experiment in *B. caespiticium* moss shoots from the northern peak of the dump under the influence of 2-hour temperature +42 ºC the most significant increase in peroxidase activity by 1.78 and for SOD – by 1.89 times as well as its thermal stability by 1.35–1.42 times, respectively, was discovered. The increase in peroxidase and SOD activity, as well as the increase in their thermal stability, caused by hyperthermia, were offset by pre-conditioning with a protein biosynthesis inhibitor cyclohexamide, which may indicate the participation of the protein-synthesizing system in this process.

The determining stage of ROS formation is the generation of superoxide anion radical, which is the initial component of all chain reactions of the oxidative cascade (Miller et al., 2008; Pavlovskaya & Grinblat, 2010; Mittler et al., 2011; Schmitt et al., 2014). Superoxide is converted by superoxide dismutase into hydrogen peroxide, which is a component of signal transduction and triggers the peroxidation of biopolymers, oxidizes sulfhydryl groups of enzymes, carries out double-stranded breaks in DNA (Uchida et al., 2002; Smirnoff, 2005). Temperature stress, like other abiotic factors as well, leads to the increase in the level of ROS in cells, such as superoxide anion radical, H_2O_2 and hydroxyl radical (Karpets et al., 2015b; Ren et al., 2021; Wani et al., 2021). The leading role among ROS is played by hydrogen peroxide, because the reaction of systems of its formation to the influence of extreme factors is very important for adaptive processes in plants (Kolupaev, 2016; Thakur & Kapila, 2017; Smirnoff & Arnaud, 2019).

Experimental studies have shown that heating of moss samples led to increase of superoxide anion radical with its subsequent conversion to H_2O_2 by increasing the activity of SOD. It was found that the highest index of superoxide anion radical generation in *B. caespiticium* moss shoots samples, collected in the summer from the northern peak of the dump, was 38.2%, from the crest – 25.1%, 15.3% – from the northern slope, and the lowest at the base of the dump – 10.2%. It was found that temperature stress and high insolation caused an increased generation of H_2O_2 as the main inducer of protective reactions in the *B. caespiticium* samples from experimental plots of the sulfur deposit dump.

There are literature data (Kimura et al., 2014; Demidchik, 2015; Karpets et al., 2017) on the functions of SOD not only in the antioxidant protection of cells, but also in the transduction of the high temperature signal into the genome by converting the superoxidation radical to the H_2O_2 signaling molecule. SOD is an intracellular enzyme involved in superoxide anion radical dismutation reactions (Zyn, 2012; Kolupaev & Oboznyi, 2013; Khan et al., 2017). Signaling with a participation of ROS is necessary for the further formation of adaptive responses that increase the heat resistance of plants (Cavalcanti et al., 2004; Kolupaev & Oboznyi, 2012; Khorobrykh, 2019).

It is known that plants under stress increase the content of hydrogen peroxide (Kacperska, 2004; Alvarez & Sanchez-Blanco, 2014; Legostayeva & Volyanyk, 2017). Production of ROS, in particular H_2O_2, under the influence of abiotic stress initiates a cascade of reactions in plants, which helps them to avoid stress (Neill et al., 2002a; Neill et al., 2002b; Karpets et al., 2016; Kolupaev, 2016). Hydrogen peroxide is one of the ROS and being the most stable of them, it plays an important role as a signaling molecule in cellular metabolism (Sung et al., 2003; Kolupaev & Karpets, 2009; Wani et al., 2021). Under stress conditions, H_2O_2 concentration in plants increased sharply, activating protective systems (Prasad et al., 1994; Dat et al., 2000; Jiang & Zhang, 2002). It participates in the intercellular signal-mediated system of acquired stability. Synthesis of H_2O_2 occurs under stress conditions and is a signal to start a number of molecular, biochemical and physiological processes of cells, including the adaptation of plants to extreme temperatures (Proctor et al., 2007; Siddiqui et al., 2011; Demidchik, 2015; Karpets et al., 2015a). The antioxidant system is the main mechanism for eliminating toxic peroxides. It is shown that H_2O_2 can cause the expression of genes potentially involved not only in its degradation but also in its generation (Guan & Scandalios, 2000; Neill et al., 2002a; Karpets, 2019; Li et al., 2020). It is shown that high temperatures initiate the generation of hydrogen peroxide. Hyperthermia in the experiment caused an increase in H_2O_2 content in all samples by 1.21–1.52 times. Increased ROS formation, including H_2O_2, under the influence of extreme temperatures, can be a reason for the activation of signaling systems. Therefore, increasing the content of H_2O_2 as a signaling mediator is a component of the antioxidant protection system.

Literature data show that lipid peroxidation products are involved in the transmission of signals from primary messengers aimed at triggering a cascade of reactions, necessary for the adaptation and survival of organisms in extreme conditions (Dubinina, 2001; Apel & Hirt, 2004; Gupta & Igamberdiev, 2015; Hasanuzzaman et al., 2020). It is known that in biological membranes, mainly polyunsaturated fatty acids are oxidized, so the detection of diene and triene conjugates and dienketones can serve as a sensitive test of their oxidation (Durand et al., 2019). It is established that adaptive reconstructions of *B. caespiticium* moss metabolism are associated with the accumulation of signal prooxidant components (diene and triene conjugates and dienketones). Under the conditions of the experiment under the action of short-term hyperthermia, the content of diene conjugates and dienketones increased by 1.21–1.53 times, respectively, and the content of triene conjugates approximately 1.23 times in all samples from the experimental plots of the dump. Therefore, the increase in the primary products of lipid peroxidation, found by us, under the action of hyperthermia may indicate the intensification of free radical oxidation under unfavourable climatic conditions on the territory of the sulphur deposit dump, which leads to the intensification of processes of lipid peroxidation.

Conclusions

The effect of high temperature was accompanied by the appearance of more stable molecular forms of peroxidase and SOD. The effect of increase in the thermal stability of enzymes can be considered as a mechanism of adaptation of the protein-synthesizing system to the action of high temperatures. The increase in H_2O_2 content as a signaling mediator and increase in the activity and thermal stability of enzymes-antioxidants of moss are parts of a single system of antioxidant protection. It can be assumed that increased ROS formation, including H_2O_2 under the action of extreme temperatures, may be the cause of activation of signaling systems, which leads to adaptive changes in gene expression.

It was found that hyperthermia and insolation caused increased generation of superoxide anion radical in the samples of *B. caespiticium* from the experimental areas of the sulfur mining dump. The highest indexes of superoxide anion radical generation were found in samples from the northern peak of the dump, where the intensity of abiotic factors was the highest. The mechanism of action of high temperatures is associated with the development of oxidative stress, which is manifested in the intensification of lipid peroxidation and the generation of superoxide anion radical.

Under stressful conditions, the activation of redox processes was accompanied by the accumulation of prooxidant components (diene and triene conjugates and dienketones), which had a signal and adaptive value in the restructuring of plant metabolism to adverse environmental factors.

References

Aleksandrov, V. Y. (1985). Reaktivnost’ kletok i belki [Cell reactivity and proteins]. Nauka, Leningrad (in Russian).

Alvarez, S., & Sanchez-Blanco, M. J. (2014). Long-term effect of salinity on plant quality, water relations, photosynthetic parameters and ion distribution in *Callistemon citrinus*. Plant Biology, 16, 757–764.

Apel, K., & Hirt, H. (2004). Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. The Annual Review of Plant Biology, 55, 373–399.

Ayala, A., Muñoz, M. F., & Argüelles, S. (2014). Lipid peroxidation: Production, metabolism, and signaling mechanisms of malondialdehyde and 4-hydroxy-2-nonenal. Oxidative Medicine and Cellular Longevity, 360, 438.

Boychuk, M. A. (2021). Mosses (Bryophyta) of the Kostomuksha State Nature Reserve, Russia. Nature Conservation Research, 6(Suppl.1), 89–97.

Cavalcanti, F. R., Oliveira, J. T. A., Martins-Miranda, A. S., Viégas, R. A., & Silveira, J. A. G. (2004). Superoxide dismutase, catalase and peroxidase activities do not confer protection against oxidative damage in salt-stressed cowpea leaves. New Phytologist, 163, 563–571.

Chevari, S., Andyal, T., & Shtrenger, Y. (1991). Opredeleniye antioksidantnikh parametrov krovi i ikh diagnosticheskoye znacheniye v pozhilom vozdaste [Determination of antioxidant blood parameters and their diagnostic value in elderly patients]. Laboratornoe Delo, 18(2), 9–13 (in Russian).

Choudhury, F. K., Rivero, R. M., Blumwald, E., & Mittler, R. (2017). Reactive oxygen species, abiotic stress and stress combination. The Plant Journal, 90(5), 856–867.

Dat, J., Vandenabeele, S., Vranova, E., Van Montagu, M., Irize, D., & Van Breusegem, F. (2000). Dual action of the active oxygen species during plant stress responses. Cellular and Molecular Life Sciences, 57(5), 779–795.

Demidchik, V. (2015). Mechanisms of oxidative stress in plants: From classical chemistry to cell biology. Environmental and Experimental Botany, 109, 212–228.

Dey, A., & De, J. N. (2012). Antioxidative potential of Bryophytes: Stress tolerance and commercial perspectives: A review. Pharmacologia, 3(6), 151–159.

Di cyclohexamidelo, L., Lambardi, M., & Pazzagli, L. (1999). Response to cadmium in carrot *in vitro* plants and cell suspension cultures. Plant Science, 137, 119–129.

Dubinina, E. E. (2001). Rol' aktivnykh form kisloroda v kachestve signal'nykh molekul v metabolizme tkaney pri sostoyaniyakh okislitel'nogo stressa [The role of reactive oxygen species as signaling molecules in tissue metabolism under oxidative stress conditions]. Problems of Medicinal Chemistry, 47(6), 561–581 (in Russian).

Durand, E., Zhao, Y., Ruesgas-Ramón, M., Cruz Figueroa-Espinoza, M., Lamy, S., Coupland, J. N., Elias, R. J., & Villeneuve, P. (2019). Evaluation of antioxidant activity and interaction with radical species using the vesicle conjugated autoxidizable triene (VesiCAT). European Journal of Lipid Science and Technology, 121(5), 180–199.

Ermakov, A. I., Arasimovich, V. V., & Yarosh, N. P. (1987). Metody biokhimicheskogo issledovaniya rasteniy [Methods of biochemical research of plants]. Agropromizdat, Leningrad (in Russian).

Fan, X. W., Li, F. M., Song, L., Xiong, Y. C., An, L. Z., Jia, Y., & Fang, X. W. (2009). Defense strategy of old and modern spring wheat varieties during soil drying. Physiologia Plantarum, 136, 310–323.

Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiology and Biochemistry, 48, 909–930.

Grishutkin, O. G., Boychuk, M. A., Grishutkina, G. A., & Rukavishnikova, V. V. (2020). Check-list and ecology of *Sphagnum* mosses (Sphagnaceae) in the Republic of Mordovia (Russia). Nature Conservation Research, 5(3), 114–133.

Guan, L. M., & Scandalios, J. G. (2000). Hydrogen-peroxide-mediated catalase gene expression in response to wounding. Free Radical Biology and Medicine, 28(8), 1182–1190.

Gupta, K. J., & Igamberdiev, A. U. (2015). Compartmentalization of reactive oxygen species and nitric oxide production in plant cells: An overview. In: Gupta, K. J., & Igamberdiev, A. U. (Eds.). Reactive oxygen and nitrogen species signaling and communication in plants, signaling and communication in plants. Springer, Heidelberg, New York, Dordrecht, London. Pp. 1–14.

Hasanuzzaman, M., Borhannuddin Bhuyan, M. H. M., Zulfiqar, F., Raza, A., Mohsin, M. S., Mahmud, J. A., 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, 681.

Helena, M., & Carvalho, C. (2008). Drought stress and reactive oxygen species. Production, scavenging and signaling. Plant Signaling and Behavior, 3, 156–165.

Jiang, M., & Zhang, J. (2002). Water stress-induced abscisic acid accumulation triggers the increased generation of reactive oxygen species and up-regulates the activities of antioxidant enzymes in maize leaves. The Journal of Experimental Botany, 53, 2401–2410.

Kacperska, A. (2004). Sensor types in signal transduction pathways in plant cells responding to abiotic stressors: Do they depend on stress intensity? Physiologia Plantarum, 122(2), 159−168.

Karpets, Y. V. (2019). Donors of nitric oxide and their application for increase in plants resistance to action of abiotic stressors. The Bulletin of Kharkiv National Agrarian University, Series Biology, 48, 28–51.

Karpets, Y. V., & Kolupaev, Y. E. (2009). Otvet rastenyya na hypertermyyu: Molekulyarno-kletochnye protsessy [Plant response to hyperthermia: Molecular and cellular processes]. The Bulletin of Kharkiv National Agrarian University, Biological Series, 1, 19–39 (in Russian).

Karpets, Y. V., Kolupaev, Y. E., & Vayner, A. A. (2015a). Functional interaction between nitric oxide and hydrogen peroxide during formation of wheat seedling induced heat resistance. Russian Journal of Plant Physiology, 62(1), 65–70.

Karpets, Y. V., Kolupaev, Y. E., Grigorenko, D. O., & Firsova, K. M. (2016). Reaktsiya rasteniy yachmenya razlichnykh genotipov na pochvennuyu zasukhu i deystviye donora oksida azota [Response of barley plants of various genotypes to soil drought and influence of nitric oxide donor]. The Bulletin of Kharkiv National Agrarian University, Series Biology, 38, 94–105 (in Russian).

Karpets, Y. V., Kolupaev, Y. E., Yastreb, T. O., & Lugova, G. A. (2017). Activity of antioxidant enzymes in leaves of barley plants of various genotypes under influence of soil drought and sodium nitroprusside. Plant Physiology and Genetics, 49(1), 71–81.

Karpets, Y. V., Kolupaev, Y. E., Yastreb, T. O., & Oboznyi, A. I. (2015b). Effects of NO-status modification, heat hardening, and hydrogen peroxide on the activity of antioxidant enzymes in wheat seedlings. Russian Journal of Plant Physiology, 62(3), 292–298.

Khan, M. N., Mobin, M., & Abbas, Z. K. (2015). Nitric oxide and high temperature stress: A physiological perspective. In: Khan, M. N. (Ed.). Nitric oxide action in abiotic stress responses in plants. Springer, Heidelberg, New York, Dordrecht, London, 7, 77–94.

Khan, T. A., Fariduddin, Q., & Yusuf, M. (2017). Low-temperature stress: Is phytohormones application a remedy? Environmental Science and Pollution Research, 24(27), 21574–21590.

Khorkavtsiv, Y. D., Ripetskyj, R. T., & Baik, O. L. (2009). Phenotypic and epigenetic adaptation of the moss clone to mercury. Cytology and Genetics, 43(5), 311–315.

Khorobrykh, A. (2019). Hydrogen peroxide and superoxide anion radical photoproduction in PSII preparations at various modifications of the water-oxidizing complex. Plants, 8(9), 329.

Kimura, M., Umemoto, Y., & Kawano, T. (2014). Hydrogen peroxide-independent generation of superoxide by plant peroxidase: Hypotheses and supportive data employing ferrous ion as a model stimulus. Frontiers in Plant Science, 5, 285.

Kimura, S., Waszczak, C., Hunter, K., & Wrzaczek, M. (2017). Bound by fate: The role of reactive oxygen species in receptor-like kinase signaling. Plant Cell, 29, 638–654.

Kolupaev, Y. E. (2016). Antioksidanty rastitelnoy kletki, ikh rol v AFK-signalinge i ustoychivosti rasteniy [Plant cell antioxidants and their role in ROS signaling and plant resistance]. Uspekhi Sovremennoy Biologii, 136(2), 181–198 (in Russian).

Kolupaev, Y. E., & Karpets, Y. V. (2009). Aktivnyye formy kisloroda pri adaptatsii rasteniy k stressovym temperaturam [Reactive oxygen species during plant adaptation to stress temperatures]. Fiziologiya i Biokhimiya Kulturnykh Rasteniy, 41(2), 95–108 (in Russian).

Kolupaev, Y. E., & Karpets, Y. V. (2010). Formirovaniye adaptativnykh reaktsiy rasteniy na deystviye abioticheskikh stressorov [Formation of adaptive responses of plants to the action of abiotic stressors]. Osnova, Kiev (in Russian).

Kolupaev, Y. E., & Obozny, A. I. (2013). Aktyvni formy kysnyu i antyoksydantna systema pry perekhresniy adaptatsiyi roslyn do diyi abiotychnykh stresoriv [Reactive forms of oxygen and antioxidant system in cross-adaptation of plants to the action of abiotic stressors]. The Bulletin of Kharkiv National Agrarian University, Series Biology, 30, 18–31 (in Ukrainian).

Kolupaev, Y. E., & Oboznyi, A. I. (2012). Uchastiye aktivnykh form kisloroda v indutsirovanii askorbatperoksidazy i gvayakolperoksidazy pri teplovom zakalivanii prorostkov pshenitsy [Participation of reactive oxygen species in the induction of ascorbate peroxidase and guaiacol peroxidase during heat hardening of wheat seedlings]. The Ukrainian Biochemical Journal, 84(6), 131–138 (in Russian).

Kosakivska, I. B., Yarotska, K. M., Voytenko, L. V., & Babenko, L. M. (2016). Effect of hyperthermia on cytokinin and pigments content of *Glycine max* (L.) Merr. varieties differed in thermotolerance. Plant Physiology and Genetics, 48(1), 56–64.

Kosakivska, I. V., Voytenko, L. V., & Likhnyovskiy, R. V. (2015). Effect of temperature on *Triticum aestivum* L. seedlings growth and phytohormone balance. The Journal of Stress Physiology and Biochemistry, 11(4), 91–99.

Kosakivska, I. V., Voytenko, L. V., & Yarotska, K. M. (2017). Effect of hyperthermia on accumulation and localization of abscisic acid in varieties of *Glycine max* (L.) Merr. differing in resistance to abiotic stressors. The Bulletin of Kharkiv National Agrarian University, Series Biology, 42, 62–71.

Kosakivska, I. V., Voytenko, L. V., Likhnyovskiy, R. V., & Ustinova, A. Y. (2014). Effect of temperature on accumulation of abscisic acid and indole-3-acetic acid in *Triticum aestecum* L. seedling. Genetics and Plant Physiology, 4, 201–208.

Kurganova, L. N., Veselov, A. P., & Goncharova, T. A. (1997). Perekisnoye okisleniye lipidov i antioksidantnaya sistema zashchity v khloroplastakh gorokha pri teplovom shoke [Lipid peroxidation and antioxidant defense system in pea chloroplasts under heat shock]. Plant Physiology, 44(5), 725–730 (in Russian).

Kusvuran, S., Kiran, S., & Ellialtioglu, S. (2016). Antioxidant enzyme activities and abiotic stress tolerance relationship in vegetable crops. In: Shanker, A., & Shanker, C. (Eds.). Abiotic and biotic stress in plants – Recent advances and future perspectives. IntechOpen, London.

Kyyak, N. Y., & Baik, O. L. (2016). Role of the bryophyte cover in accumulation of organic carbon and biogenic elements in technogenic substrate on the territory of sulfur deposit. Biologichni Studii, 10(3), 48–55.

Kyyak, N. Y., Baik, O. L., & Kit, N. A. (2017). Morfo-fiziolohichna adaptatsiia briofitiv do ekolohichnykh faktoriv na devastovanykh terytoriiakh vydobutku sirky

[Morpho-physiological adaptation of bryophytes to environmental factors on the devastated territories of sulphur extraction]. ScienceRise: Biological Science, 5(8), 33–38 (in Ukrainian).

Kyyak, N., & Bunio, L. (2017). Mekhanizmy prystosuvannia briofitiv do sol'ovogo stresu na terytoriji khvostoskhovyshha Stebnytckogo girnycho-khimichnogo pidpryjemstva "Polimineral" [Mechanisms of adaptation of bryophytes to salt stress on the territory of tailing of Stebnyk Mining and Chemical Enterprise "Polimineral"]. Visnyk of the Lviv University, Series Biology, 76, 87–96 (in Ukrainian).

Legostayeva, T. V., & Volyanyk, K. O. (2017). Dynamika aktyvnosti peroksydazy u lystkakh *Ailanthus altissima* za aerotekhnohennoho zabrudnennia [Dynamics of peroxidase activity in *Ailanthus altissima* leaves under aerotechnogenic pollution]. Issues of Steppe Forestry and Forest Land Reclamation, 46, 81–86 (in Ukrainian).

Li, P., Cai, Q., Wang, H., Li, S., Cheng, J., Li, H., Yu, Q., & Wu, S. (2020). Hydrogen peroxide homeostasis provides beneficial micro-environment for SHR-mediated periclinal division in *Arabidopsis* root. New Phytologist, 228(6), 1926–1938.

Lobachevska, O., Kyjak, N., Khorkavtsiv, O., Dovgalyuk, A., Kit, N., Klyuchivska, O., Stoika, R., Ripetsky, R., & Cove, D. (2005). Influence of metabolic stress on the inheritance of cell determination in the moss, *Pottia intermedia*. Cell Biology International, 29(3), 181–186.

Lyutova, M. I., & Kamentseva, I. E. (2001). Termoindutsirovannoye uvelicheniye ustoychivosti nitratreduktazy iz list'jev pshenitsy k inaktivirujushchim vozdeystvijam [Thermal-induced increase in the resistance of nitrate reductase from wheat leaves to inactivating influences]. Plant Physiology, 48(1), 100–105 (in Russian).

Miller, G., Shulaev, V., & Mittler, R. (2008). Reactive oxygen signaling and abiotic stress. Physiologia Plantarum, 133(3), 481–492.

Mittler, R., Vanderauwera, S., Suzuki, N., Miller, G., Tognetti, V. B., Vandepoele, K., Gollery, M., Shulaev, V., & Breusegem, F. V. (2011). ROS signaling: The new wave? Trends in Plant Science, 16, 300–309.

Moyo, C. E., Beckett, R. P., Trifonova, T. V., & Minibayeva, F. V. (2017). Extracellular redox cyclingand hydroxyl radical production occurs widely in lichenized Ascomycetes. Fungal Biology, 121, 582–588.

Nakamura, A., Ohori, Y., & Watanabe, K. (2000). Peroxidative formation of lipid hydroperoxides in etiolated leaves. Pesticide Biochemistry and Physiology, 66, 206–212.

Neill, S. J., Desikan, R., Clarke, A., Hurst, R. D., & Hancock, J. T. (2002b). Hydrogen peroxide and nitric oxide as signalling molecules in plants. Journal of Experimental Botany, 53(372), 1237–1247.

Neill, S. J., Gould, K. S., & Kilmartin, P. A. (2002c). Antioxidant activities on red versus green leaves in *Elatostema rugosum*. Plant, Cell and Environment, 25, 539–547.

Neill, S., Desikan, R., & Hancock, J. (2002a). Hydrogen peroxide signaling. Current Opinion in Plant Biology, 5, 388–395.

Noctor, G., Mhamdi, A., & Foyer, C. H. (2016). Oxidative stress and antioxidative systems: Recipes for successful data collection and interpretation. Plant, Cell and Environment, 39, 1140–1160.

Oboznyi, A. I., Kolupaev, E. Y., & Shvidenko, N. V. (2012). Dinamika aktivnosti antioksidantnykh fermentov pri kross-adaptatsii prorostkov pshenitsy k gipertermii i osmoticheskomu shoku [Dynamics of the activity of antioxidant enzymes during cross-adaptation of wheat seedlings to hyperthermia and osmotic shock]. The Bulletin of Kharkiv National Agrarian University, Series Biology, 26, 71–84 (in Russian).

Oboznyi, A. I., Yastreb, T. O., Kolupaev, Y. E., Popov, V. N., & Krivoruchko, R. V. (2010). Vliyaniye kratkovremennogo nagreva na aktivnost' i termostabil'nost' rastvorimoy peroksidazy korney pshenitsy raznykh ekotipov [Influence of short-term heating on the activity and thermal stability of soluble peroxidase of wheat roots of different ecotypes]. The Bulletin of Kharkiv National Agrarian University, Series Biology, 20, 61–68 (in Russian).

Onele, A. O., Chasov, A., Viktorova, L., Beckettc, R. P., Trifonova, T., & Minibayeva, F. (2018). Biochemical characterization of peroxidases from the moss *Dicranum scoparium*. South African Journal of Botany, 119, 132–141.

Pavlovskaya, N. E., & Grinblat, A. I. (2010). Aktivnyye formy kisloroda i apoptoz u pshenitsy i gorokha [Active forms of oxygen and apoptosis in wheat and pea]. Sel'skokhozyaistvennaya Biologiya, 1, 51–55 (in Russian).

Prasad, T. K., Anderson, M. D., & Stewart, C. R. (1994). Acclimation, hydrogen peroxide, and abscisic acid protect mitochondria against irreversible chilling injury in maize seedlings. Plant Physiology, 105, 619–627.

Proctor, M. C., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., & Mishler, B. D. (2007). Desiccation-tolerance in bryophytes: A review. Bryologist, 110, 595–621.

Pyatygin, S. S. (2008). Stress u rasteniy: Fiziologicheskiy podkhod [Stress in plants: A physiological approach]. Zhurnal Obshchei Biologii, 69(4), 294–298 (in Russian).

Rampitsch, C., & Srinivasan, M. (2011). The application of proteomics to plant biology: A review. Canadian Journal of Botany, 84(6), 883–892.

Ren, X., Wang, M., Wang, Y., & Huang, A. (2021). Superoxide anion generation response to wound in *Arabidopsis* hypocotyl cutting. Plant Signaling and Behavior, 16(2), 27–58.

Richards, S., Wilkins, K., Swarbreck, S., Anderson, A., Habib, N., Smith, A., McAinsh, M., & Davies, J. (2015). The hydroxyl radical in plants: From seed to seed. Journal of Experimental Botany, 66(1), 37–46.

Scarpeci, T. E., Zanor, M. I., Carrillo, N., Mueller-Roeber, B., & Valle, E. M. (2008). Generation of superoxide anion in chloroplasts of *Arabidopsis thaliana* during active photosynthesis: A focus on rapidly induced genes. Plant Molecular Biology, 66(4), 361–378.

Schmitt, F. J., Renger, G., Friedrich, T., Kreslavski, V. D., Zharmukhamedov, S. K., Los, D. A., Kuznetsov, V. V., & Allakhverdiev, S. I. (2014). Reactive oxygen species: Re-evaluation of generation, monitoring and role in stress-signaling in phototrophic organisms. Biochimica et Biophysica Acta – Bioenergetics, 1837(6), 835–848.

Seel, W. E., Hedry, G. A. F., & Lee, J. A. (1992). Effects of desiccation on some activated oxygen processing enzymes and antioxidants in mosses. Journal of Experimental Botany, 43, 1031–1037.

Shevyakova, N. I., Bakulina, Y. A., & Kuznetsov, V. V. (2009). Antioksidantnaya rol' prolina u galofita khrustal'noy travki pri deystvii zasoleniya i parakvata, indutsiruyushchikh okislitel'nyy stress [Antioxidant role of proline in halophyte of crystal grass under the action of salinity and paraquat, inducing oxidative stress]. Plant Physiology, 56, 736–742 (in Russian).

Sidana, S., Bose, J., Shabala, L., & Shabala, S. (2015). Nitric oxide in drought stress signalling and tolerance in plants. In: Khan, M. N. (Ed.). Nitric oxide action in abiotic stress responses in plants. Springer, Heidelberg, New York, Dordrecht, London. Pp. 95–114.

Siddiqui, M. H., Al-Whaibi, M. H., & Basalah, M. O. (2011). Role of nitric oxide in tolerance of plants to abiotic stress. Protoplasma, 248, 447–455.

Smirnoff, N. (2005). Ascorbate, tocopherol and carotenoids: Metabolism, pathway engineering and functions. In: Smirnoff, N. (Ed.). Antioxidants and reactive oxygen species in plants. Blackwell Publishing Ltd., Oxford. Pp. 53–86.

Smirnoff, N., & Arnaud, D. (2019). Hydrogen peroxide metabolism and functions in plants. New Phytologist, 221, 1197–1214.

Sofo, A., Scopa, A., Nuzzaci, M., & Vitti, A. (2015). Ascorbate peroxidase and catalase activities and their genetic regulation in plants subjected to drought and salinity stresses. International Journal of Molecular Sciences, 16, 13561–13578.

Song, J., Wu, W., & Hu, B. (2020). Light and temperature receptors and their convergence in plants. Biologia Plantarum, 64, 159–166.

Sung, D.-Y., Kaplan, F., Lee, K.-J., & Guy, C. L. (2003). Acquired tolerance to temperature extremes. Trends in Plant Science, 8(4), 179–187.

Thakur, S., & Kapila, S. (2017). Seasonal changes in antioxidant enzymes, polyphenoloxidase enzyme, flavonoids and phenolic content inthree leafy liverworts. Lindbergia, 40(5), 39–44.

Uchida, A., Jagendorf, A. T., Hibino, T., Takabe, T., & Takabe, T. (2002). Effects of hydrogen peroxide and nitric oxide on both salt and heat stress tolerance in rice. Plant Sciences, 163, 515–523.

Wadavkar, D. S., Murumkar, C. V., Deokule, S. S., & Chavan, S. J. (2017). Secondary metabolite and enzyme activity on some moss species from Western Ghats, Maharashtra, India. Bioscience Discovery, 8(4), 716–719.

Wahid, A., & Close, T. J. (2007). Expression of degidrins under heat stress and their relationship with water relations of sugarcane leaves. Biologia Plantarum, 51, 104–109.

Wani, K. I., Naeem, M., Castroverde, C. D. M., Kalaji, H. M., Albaqami, M., & Aftab, T. (2021). Molecular mechanisms of nitric oxide (NO) signaling and reactive oxygen species (ROS) homeostasis during abiotic stresses in plants. International Journal of Molecular Sciences, 22(17), 56–96.

Yurina, N. P., & Odintsova, M. S. (2007). Signal'nyye sistemy rasteniy. Plastidnyje signaly i ikh rol' v ekspressii yadernykh genov [Plant signaling systems. Plastid signals and their role in the expression of nuclear genes]. Plant Physiology, 54(4), 485–498 (in Russian).

Zhang, X., Zhao, Y., & Wang, S. (2017). Responses of antioxidant defense system of epilithic mosses to drought stress in karst rock desertified areas. The Acta Geochimica, 36(2), 205–212.

Zyn, A. (2012). Prooksudantno-antuoksudantnuj homeostas i membrannuj transport u zuvuh organizmah [Prooxidant and antioxidant homeostasis and membrane transport in living organisms]. Visnyk of Lviv University, Series Biology, 60, 21–39 (in Ukrainian).