

BIOCHEMICAL MECHANISMS OF DROUGHT RESISTANCE IN SOFT WHEAT UNDER MODELING OF WATER DEFICIENCY AND EFFECTS OF SEED TREATMENT WITH METABOLICALLY ACTIVE SUBSTANCES

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ABSTRACT

Water deficiency is one of the major factors that limit crop production among those causing plant stress. Therefore, the study aimed to investigate the effect of metabolically active compounds on reducing the negative effects of drought and stimulating physiological and biochemical processes in the spring wheat variety Provintsialka. In the study, wheat seeds were soaked in solutions of substances: PEG-6000 (EG); PEG-6000 + vitamin E (PEG+E); PEG-6000 + ubiquinone-10 (PEG+Q); PEG-6000 + methionine (PEG+M); PEG-6000 + parahydroxybenzoic acid (PEG+P); PEG-6000 + MgSO₄ (PEG+Mg); PEG-6000 + vitamin E + ubiquinone-10 (PEG+EQ); PEG-6000 + vitamin E + methionine + parahydroxybenzoic acid (PEG+EMP); PEG-6000 + vitamin E + methionine + parahydroxybenzoic acid + MgSO₄ (PEG+EMPMg). The wheat seeds were then poured into a 12% PEG solution to simulate the water deficit and then germinated. The study determined the activities of ascorbate peroxidase and catalase, as well as the content of ascorbic acid and glutathione. It was found that the treatment of spring wheat seeds of the Provintsialka variety with metabolically active compounds and their combinations affected the activity of antioxidant protection enzymes in water-deficient conditions. Treatment of seeds with MgSO₄ solution most effectively reduces catalase activity compared to the indicators of seedlings whose seeds were in simulated drought conditions. The treatment of wheat seeds with vitamin E most effectively stimulated the activity of ascorbate peroxidase, increasing it by 65.5% compared to the control and by 2.4% relative to the PEG treated seedlings. A decrease in the activity of catalase correlates with an increase in the activity of ascorbate peroxidase and

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indicates the compensatory effect of the enzymes of the antioxidant system. The treatment of wheat seeds with ubiquinone-10 (PEG+Q) most effectively increased the ascorbate content in seedlings by 46.3% compared to seedlings whose seeds were in water deficit conditions. An increase in the ascorbate content in wheat seedlings was also noted when wheat seeds were treated with EMP (PEG+EMP) and EMPMg (PEG+EMPMg). The highest levels of glutathione in drought-stressed seedlings were observed in those treated with vitamin E and EMP (PEG+EMP), exceeding control levels by 31.4% and 30.7%, respectively, and PEG-treated seedlings by 59.9% and 59.2%. This confirms the promising use of metabolically active substances for plant adaptation under conditions of slow water flow.

Introduction

Wheat (*Triticum aestivum* L.) is one of the most important food crops, accounting for one third of the world's grain production. Every year, wheat grain production increases. In 2022, the world production of wheat was 808.4 M tons, of which 20.7 M tons were produced in Ukraine (FAO, 2024). The current trend of climate change toward a decrease in precipitation and increased temperatures affects the productivity of grain crops. The unfavorable environmental conditions resulting from global climate change present a critical challenge for farmers: increasing wheat productivity. One of the most acute environmental factors that negatively affect physiological and metabolic processes and, as a result, lead to a decrease in the amount of organic matter accumulated by plants in plants is the water deficit caused by drought. Drought, a consequence of climate change, is a spatial condition resulting from irregular rainfall or its absence, together with interactions between the atmosphere, water areas (oceans, seas, freshwater), and land area (Kaur et al., 2021). Water deficit is the most significant factor limiting crop production among plant stressors (Khomenko et al., 2017). It has been confirmed that abiotic stress associated with drought causes about 80% of all direct impacts on the socioeconomic life of people, especially in agricultural production (FAO, 2024).

The water deficit leads to a decrease in the water potential of the leaves and to the closure of the stomata, which ultimately reduces transpiration losses, increases the temperature of the leaves, and leads to violation of general metabolic functions, such as respiration, photosynthesis, absorption of nutrients, as well as the synthesis of amino acids and proteins (Nezhadahmadi et al., 2013). The inaccessibility of CO₂ due to the long-term closure of the stomata contributes to the accumulation of reduced compounds of the electron transport chain. The accumulation of these compounds reduces the availability of molecular oxygen and increases the production of reactive oxygen species (ROS). ROS are produced in plants mainly in response to abiotic stress conditions, acting as signaling molecules in important physiological pathways related to development and stress response (Dat et al., 2000; Jardim-Messeder et al., 2023).

Many studies have reported that oxidative stress causes lipid peroxidation, damages nucleic acids and proteins, and alters carbohydrate metabolism, leading to cell dysfunction and death (Scandalios, 2002; Hasanuzzaman et al., 2019).

The destruction of ROS in the cell is known to be carried out by the antioxidant defense system, which involves a number of enzymes and substrates. Various enzymatic and non-enzymatic antioxidant components eliminate ROS, inhibit the development of the peroxidation process, and prevent DNA fragmentation (Hasanuzzaman et al., 2019).

Foyer and Noctor (2009) consider ROS to be important mediators involved in the transmission of cellular signals that regulate gene expression and adaptive responses of plants to stressors. A significant amount of ROS can be formed under the action of stressors in mitochondria and apoplast. The apoplast is believed to be the compartment in which stress signal sensors and the transmission system to regulatory proteins are located. ROS generation in the apoplast is due to the activity of NADP oxidase (Sagi and Fluhr, 2006; Shao et al., 2007). Kolesnikov et al. (2023) showed that NADPH oxidases are involved in the response to drought and other abiotic stressors.

Plants have several ROS detoxification mechanisms. First, these are low-molecular antioxidants, enzymes, and complex systems that intercept ROS, protecting cells. The main antioxidant enzymes are ascorbate peroxidase (APO), catalase, and glutathione peroxidase. Together with the antioxidants ascorbic acid and glutathione, these enzymes provide an effective mechanism for ROS detoxification (Willekens et al., 1997; Scandalios, 2002; Jardim-Messeder et al., 2023).

Catalase was found to be an enzyme of the class of oxidoreductases, located mainly in peroxisomes and cytosol (Willekens et al., 1997; Guan and Scandalios, 2000; Doliba et al., 2010). Under normal physiological conditions, the role of the enzyme is to regulate the content of H_2O_2 in the organism, preventing its toxic effect and plays an important role in the plant aging process. Catalase catalyzes the reaction by which hydrogen peroxide is decomposed to water and oxygen without using a reducing substrate (Doliba et al., 2010). The increase in catalase activity depends on the degree of drought (Secenji et al., 2010; Caverzan et al., 2012). Drier-resistant wheat (Zhang et al., 2013), corn (Ivanov et al., 2001), and rice (Hussain et al., 2016) have been shown to have high catalase activity, while catalase deficiency leads to ROS accumulation and increased susceptibility to severe stress in tobacco leaves (Romero-Puertas et al., 2006).

In the antioxidant protection system, low-molecular antioxidants of a non-enzymatic nature, such as ascorbate, glutathione, and tocopherol, also play an important role. They are redox buffers that interact with numerous cellular components and cofactors of enzymes (Foyer, 2005). Their role is not limited to antioxidant protection; they are able to influence the growth and development of the plant organism by modulating processes ranging from mitosis and cell elongation to aging and death (de Pinto and de Gara, 2004; Potters, 2004).

To protect cells from ROS effects, in addition to enzymes, several substrates are involved. Ascorbic acid is an important low-molecular antioxidant, the main function of which is the reduction of ROS. It has the ability to interact with ROS radical ROS, singlet oxygen, and hydrogen peroxide. The protective effect of ascorbic acid is that intermediate radicals and molecules formed during its oxidation are chemically less active compared to ROS (Gill and Tuteja, 2010; Bil'chuk and Rossikhina-Galycha, 2012).

Glutathione is a low molecular weight hydrophilic and lipophilic organic compound with reducing properties (Foyer and Noctor, 2011). It contains a sulfhydryl group and can interact with hydrogen peroxide and participate in the reduction of dehydroascorbate (Foyer and Shigeoka, 2011). For the permanent removal of hydrogen peroxide, it is necessary that the levels

of reduced ascorbic acid and glutathione be sufficiently high. For this, several enzymes act together in the so-called ascorbate-glutathione cycle to neutralize H_2O_2 . This cycle consists of interconnected redox reactions involving ascorbate, glutathione, and NADPH.

Ascorbate peroxidase is an important component of the enzymatic antioxidant system of plants, has a high affinity for ascorbate, and catalyzes the oxidation of ascorbate with hydrogen peroxide (Foyer and Noctor, 2000). It neutralizes H_2O_2 by oxidizing ascorbate to monodehydroascorbate, which can be reduced by monodehydroascorbate reductase in the presence of NADPH (Potters, 2004). It follows that the basic function of ascorbate peroxidase is to scavenge excess ROS produced within the plant cell as a result of oxidative burst under stress conditions, therefore a decrease in its activity often results in a large accumulation of ROS (Kausar et al., 2012).

At high concentrations of H_2O_2 , catalase activity is important. The specificity of catalase is its localization in peroxisomes and its participation in catabolism processes that are activated in the cell destruction process. A molecule of catalase can convert about six million molecules of H_2O_2 into H_2O and O_2 in 1 min (Petrov and Breusegem, 2012; Chakrabarty et al., 2016).

Today, biologically active substances and natural antioxidants are used in the field of horticulture to treat grain crops to increase their resistance to various stressors, including drought, and to increase yields. Metabolically active substances (tocopherol, ubiquinone-10, methionine, magnesium sulfate, parahydroxybenzoic acid) and their combinations (Kurylenko and Kuchmenko, 2022), which are highly effective in small concentrations and are not toxic to human and animal health, can be promising regulators of the growth of grain crops under drought conditions.

Ali et al. (2020) found that spraying corn leaves (*Zea mays* L.) with a solution of α -tocopherol increased the activity of antioxidant enzymes and played an important role in protecting cell membranes from oxidation.

Liu and Lu (2016) demonstrated that the use of ubiquinone-10 can increase the vegetation period and improve the structure of the wheat crop by inhibiting ROS production due to its antioxidant activity. Ubiquinone-10 is also able to restore oxidized forms of other antioxidants (α -tocopherol, ascorbic acid).

The search for active compounds that reduce the negative effect of drought and stimulate metabolic processes in grain crops is an urgent problem today. Therefore, the study aimed to investigate the effect of metabolically active compounds on reducing the negative effects of drought and stimulating physiological and biochemical processes in spring wheat of the Provintsialka variety.

Material and Methods

Plant material and stress treatments

Uniform soft wheat seeds (*T. aestivum*) of the Provintsialka variety were selected. This variety is one of the most suitable varieties for growing high-quality food grains in the forest-steppe and Polissia zones and is characterized by high resistance to drought. According to the Ukrainian State System of Variety Testing, Provintsialka wheat has good yield indicators (32-34.8 dt·ha⁻¹), high grain quality, resistance to shedding (8.9-9 points), lodging (8.6-9

points), drought (6.6-8.0 points), major diseases (7.5-9 points) (Ministry of Agrarian Policy and Food of Ukraine, 2022). The soft wheat of the Provintsialka variety is the result of breeding at the Nosivska Selection and Experimental Station of the V.M. Remeslo Myronivka Institute of Wheat National Academy of Agrarian Sciences of Ukraine.

A solution of high molecular weight nonionic polymer polyethylene glycol 6000 (PEG) with a concentration of 12% was used to simulate the water deficit. According to studies (Kolesnikov et al., 2023), the indicated concentration of PEG is optimal to assess drought resistance.

PEG is used in experiments to simulate drought because of its ability to block water from entering cells, mimicking the effects of soil drying and causing plasmolysis. Furthermore, PEG is not absorbed by the plant and has no toxic effect (Kolesnikov et al., 2023).

After processing, wheat seeds were transferred to Petri dishes on filter paper (40 pieces per cup), poured with 20 mL of 12% PEG solution, and germinated at a temperature of 20-21°C (Figure 1). The study was organized as a completely randomized design with 10 treatments and four replicates.

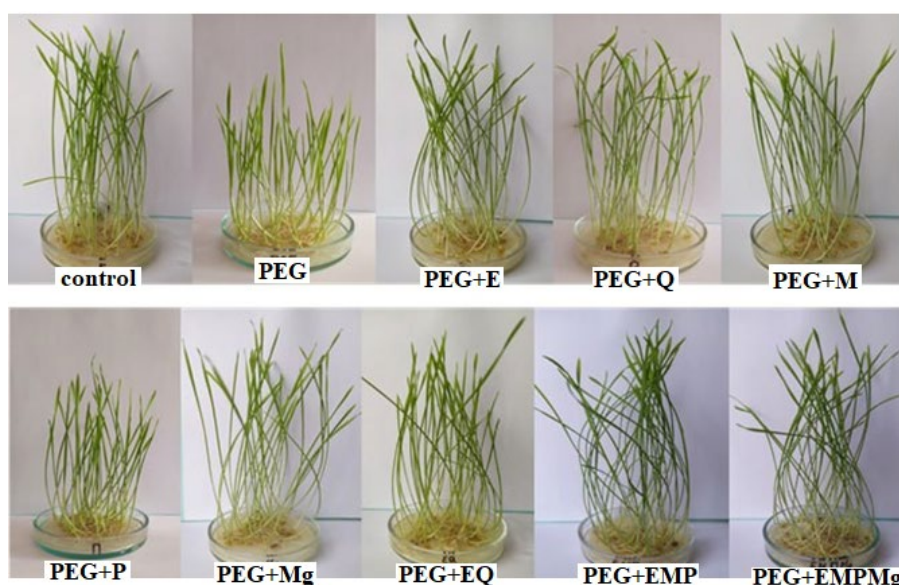


Figure 1. 10-day seedlings of common wheat variety (*T. aestivum*) Provintsialka under water deficit conditions simulated using PEG under the action of metabolically active substances

Determination of antioxidant system components in common wheat seedlings under water deficit

The study of the components of the antioxidant system in 10-day-old seedlings of soft wheat of the Provintsialka variety under water deficit, simulated with PEG, was carried out

with determination of ascorbate peroxidase and catalase activities, ascorbic acid and glutathione content with ten repetitions.

Determination of ascorbate peroxidase activity

The activity of ascorbate peroxidase (EC 1.11.1.11) in wheat seedlings was measured according to the method (Nakano and Asada, 1981). Leaf samples (0.15 g) were homogenized with a mortar and pestle on ice with a small amount (3 mL) of 0.05 M phosphate buffer (pH 7.8). The homogenate was centrifuged for 10 min at 11,180 x g. The supernatant was transferred to a test tube and kept on ice to prevent loss of activity. Enzyme activity was determined at a temperature of 37°C. 2.25 mL of phosphate buffer, 0.1 mL of ascorbic acid solution, 0.1 mL of hydrogen peroxide solution, and 0.05 mL of EDTA solution were added to the cuvette. The reaction was started by adding 0.5 mL of the supernatant. The mixture was quickly shaken, and the change in optical density at 290 nm was measured on a spectrophotometer. Enzyme activity was expressed in μmol of ascorbate per 1 g of raw mass for 1 min.

Determination of ascorbic acid content

The ascorbic acid content in the wheat seedlings was measured according to the method of Hewitt et al. and Dickes et al. (Antonenko et al., 2016). Leaf samples (0.25 g) were homogenized with mortar and pestle with 2.5 mL of 2% metaphosphoric acid. The homogenate was transferred to a volumetric flask and the volume was brought to the mark of 12.5 mL with a mixture of 2% HPO_3 and 0.21 M Na_3PO_4 in ratio 3:2 (V/V, pH 7.3 – 7.4). The extract was centrifuged for 15 min at 3000 rpm, and the extinction of the solution was measured spectrophotometrically at 265 nm. The content of ascorbic acid was expressed in $\text{mmol} \cdot \text{g}^{-1}$ of raw mass (Alam et al., 2014).

Determination of catalase activity

Catalase activity (EC 1.11.1.6) in wheat seedlings was determined using the method described by (Aebi, 1984). Leaf samples (0.2 g) were homogenized with a mortar and pestle on ice with a small amount (2 mL) of 0.1 M Tris-HCl buffer pH 7.4. The homogenate was centrifuged for 20 min at 5000 x g. The supernatant was transferred to a clean test tube and kept on ice to prevent loss of activity. 2 mL of 0.03% hydrogen peroxide was added to 0.2 mL of the supernatant and incubated for 10 min at 37°C. After that, 1 mL of 4% ammonium molybdate was added. Catalase activity was determined spectrophotometrically at 410 nm. Catalase activity was expressed in μmol per 1 g of raw mass for 1 min.

Determination of glutathione content

Reduced glutathione (GSH) in wheat seedlings was determined according to the method (Yu et al., 2003) with our modifications. Leaf samples (0.5 g) were homogenized with a mortar and pestle, poured with 2.5 mL of a 5% solution of trichloroacetic acid, and homogenized. Subsequently, the homogenate was poured into a measuring cylinder and brought to the mark of 12.5 mL with a 5% solution of trichloroacetic acid. The homogenate was then shaken for 5 min and filtered, and 4 mL of 0.3 M Na_2HPO_4 solution, 0.5 mL of 0.02% 5,5'-

dithio-bis-2-nitrobenzoic acid and 1 mL of supernatant were added to the cuvette. The change in optical density at 412 nm was measured spectrophotometrically. GSH content was determined from a standard curve.

Statistical analysis

Statistical analysis was performed using Statistica 13.3 software (TIBCO, Santa Clara, CA, US). The normality of the data distribution was assessed using the Shapiro-Wilk test and the significance of the mean was determined using the Tukey test. The significance of the mean was determined using the Tukey test, at a significance level of $p < 0.05$.

Results and Discussion

The results of our research showed that the treatment of wheat seeds with metabolically active compounds and their combinations affects the activity of the antioxidant protection components of seedlings under water deficit conditions.

The use of simulated drought conditions in our study using PEG induced an increase in ascorbate peroxidase activity by 58.9% compared to the control (Figure 2). This is confirmed by studies conducted on soybeans, in which an increase in the amount and activity of ascorbate peroxidase was observed with increasing drought stress conditions, detected by western blotting, enzyme activity assay, and biophoton emission techniques (Kausar et al., 2012). In our study, this indicator indicates the development of oxidative stress and the increase in H_2O_2 content in seedlings. Treatment of wheat seeds with the metabolically active compound vitamin E (PEG+E) increases the activity of ascorbate peroxidase, exceeding the control rate by 65.4% and by 6.5% compared to the rates of seedlings whose seeds were in simulated drought conditions (treated with PEG).

Ascorbate peroxidase activity indicators of wheat seedlings after seed treatment with Mg (PEG+Mg), PEG+M, ubiquinone-10 (PEG+Q), PEG+P and a combination of vitamin E and ubiquinone-10 (PEG+EQ) exceed control values by 46.7%, 43.9%, 33.6%, 31.8% and 29.9%, respectively, but do not exceed PEG. This indicates that these substances have a protective effect under water deficit conditions, but do not completely remove the inhibitory effect of PEG.

The increase in ascorbate peroxidase activity is dependent on the accumulation of H_2O_2 in seedling tissues. The activity of ascorbate peroxidase in the seedlings observed is associated with an increase in the concentration of H_2O_2 , which leads to the activation of the enzyme. Vitamin E activates antioxidant enzymes and non-enzymatic antioxidants, stimulates the synthesis of ascorbate peroxidase, as an enzyme of the antioxidant system, which is necessary for the formation of drought resistance (Ali et al., 2020). Under drought stress conditions, ascorbate peroxidase activity has a negative correlation with the intensity of photosynthesis of wheat leaves. That is, oxidative stress causes a decrease in the activity of the photosynthetic apparatus, but antioxidant enzymes prevent their final inhibition (Ashraf and Harris, 2013).

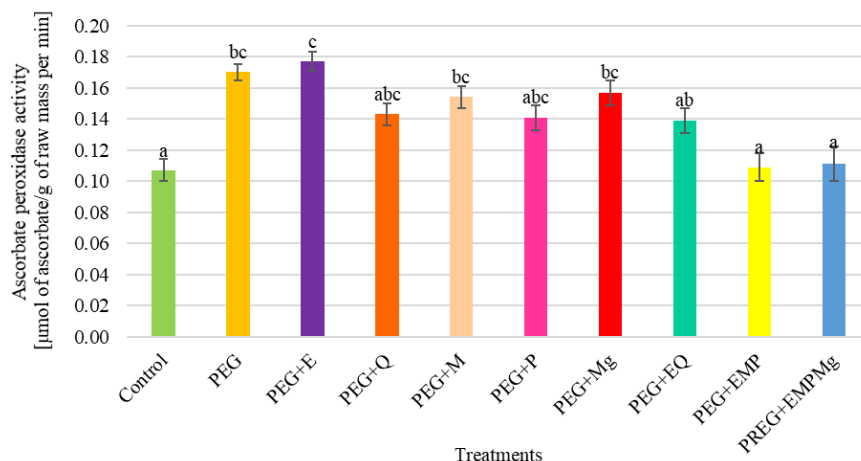


Figure 2. Ascorbate peroxidase activity in 10-day-old soft wheat seedlings (*T. aestivum*) under water deficit due to treatment with metabolically active substances. Means followed by different lowercase letters indicate statistically significant differences at $p < 0.05$. Bars indicate the standard deviations ($\pm SD$). PEG - PEG-6000; PEG+E - PEG-6000 + vitamin E ($10^{-8}M$); PEG+Q - PEG-6000 + ubiquinone-10 ($10^{-8}M$); PEG+M - PEG-6000 + methionine (0.001%); PEG+P - PEG-6000 + para-hydroxybenzoic acid (POBA) (0.001%); PEG+Mg - PEG-6000 + $MgSO_4$ (0.001%); PEG+EQ - PEG-6000 + vitamin E ($10^{-8}M$) + ubiquinone-10 ($10^{-8}M$); PEG+EMP - PEG-6000 + vitamin E ($10^{-8}M$) + methionine (0.001%) + POBA (0.001%); PEG+EMPMg - PEG-6000 + vitamin E ($10^{-8}M$) + methionine (0.001%) + POBA (0.001%) + $MgSO_4$ (0.001%)

We showed that under PEG-induced drought, catalase activity increased, exceeding the control indicator by 8.5% (Figure 3). Numerous studies have confirmed that increased catalase activity is often positively correlated with the degree of drought to which plants are subjected (Mittler et al., 2011; Pinheiro and Chaves, 2011; Sofo et al., 2015).

Studies of the influence of metabolically active substances on catalase activity in soft wheat seedlings showed that Mg seed treatment (PEG + Mg) reduces catalase activity more effectively under conditions of water deficit by 3.1% compared to the control and by 11.6% compared to PEG. The effectiveness in reducing catalase activity was also noted when using the combination of metabolically active substances (PEG+EMPM) – catalase activity decreases by 2.8% compared to the control and by 11.3% compared to PEG. Catalase activity in wheat seedlings in groups PEG+Q, PEG+P, PEG+EQ and PEG+EMP are close to the control, and seed treatment with vitamin E (PEG+E) and methionine (PEG + M) exceeds control values but does not eliminate the negative effect of drought. Kolupaev et al. (2019) indicated that the connection between drought resistance of plants and catalase activity is not obvious, as the activity of this enzyme depends on the species, variety of plants, and their characteristics regarding drought resistance. Additionally, catalase serves as a biochemical marker of the stress state of plants and participates in protecting the plant organism against oxidation by free radicals of biomolecules (Popovych, 2018). It is possible that such minor changes in catalase activity are related to the compensatory effect of other components of

antioxidant protection, in particular, to an increase in the activity of other antioxidant enzymes and the content of antioxidants of low molecular weight.

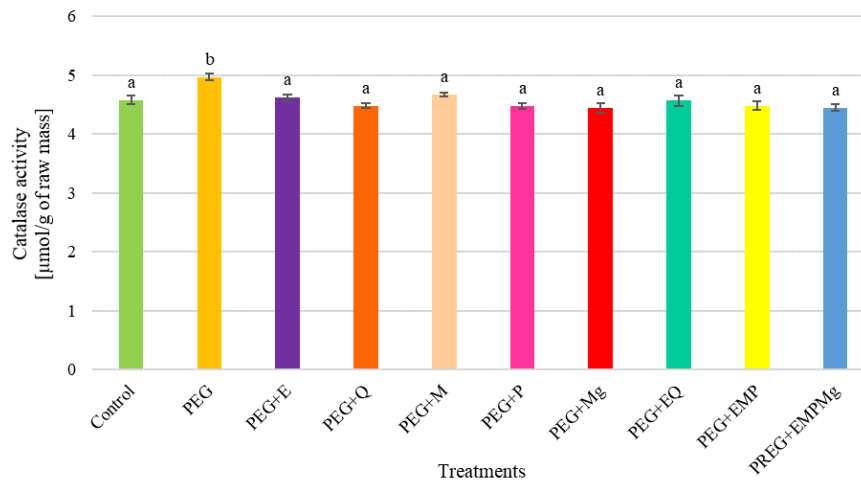


Figure 3. Catalase activity in 10-day-old soft wheat (*T. aestivum*) seedlings under water deficit due to treatment with metabolically active substances. Means followed by different lowercase letters indicate significant differences at $p < 0.05$. Bars indicate the standard deviations ($\pm$ SD). PEG - PEG-6000; PEG+E - PEG-6000 + vitamin E (10^{-8} M); PEG+Q - PEG-6000 + ubiquinone-10 (10^{-8} M); PEG+M - PEG-6000 + methionine (0.001%); PEG+P - PEG-6000 + parahydroxybenzoic acid (POBA) (0.001%); PEG+Mg - PEG-6000 + $MgSO_4$ (0.001%); PEG+EQ - PEG-6000 + vitamin E (10^{-8} M) + ubiquinone-10 (10^{-8} M); PEG+EMP - PEG-6000 + vitamin E (10^{-8} M) + methionine (0.001%) + POBA (0.001%); PEG+EMPMg - PEG-6000 + vitamin E (10^{-8} M) + methionine (0.001%) + POBA (0.001%) + $MgSO_4$ (0.001%)

The results of the study of the influence of metabolically active substances on the content of ascorbic acid in wheat seedlings with a water deficit are presented in Figure 4. Under the PEG-induced water deficit, the accumulation of ascorbic acid in seedling tissues exceeded the control values by 29.1%. Under treatment of wheat seeds with different metabolically active substances, the ascorbic acid content increased in the PEG + Q, PEG + EMPMg, PEG + EMP, PEG + M and PEG + EQ groups by 46.3%, 24.2%, 17.3%, 16.1% and 3.8% respectively, compared to PEG.

Ascorbic acid in plant cells is an important substrate for the reduction of H_2O_2 , due to which the functioning of the ascorbate-glutathione cycle plays an important role in the antioxidant protection system (Foyer and Noctor, 2011; Konturska and Palladina, 2012). The protective effect of ascorbic acid is based on the fact that intermediate radicals and molecules formed during their oxidation are chemically less active compared to ROS radicals. The reduced form of ascorbic acid is able not only to interact directly with ROS, but also to participate in the reduction of other low molecular weight antioxidants (α -tocopherol, glutathione) in enzymatic and nonenzymatic reactions (Kausar et al., 2012; Kaur et al., 2021). The results obtained from the research allow us to conclude that the metabolically active compounds mentioned above, and their combinations cause an increase in the accumulation of ascorbic

acid to ensure a pro- and antioxidant balance for the restoration of metabolism. Treatment of seeds with vitamin E (PEG+E) and Mg (PEG + Mg) leads to a decrease in the ascorbic acid content compared to PEG. The decrease in ascorbic acid content occurred in the background of an increase in ascorbate peroxidase activity and may be associated with the active use of ascorbic acid as a substrate in the reaction catalyzed by this enzyme (Foyer and Noctor, 2011; Kausar et al., 2012; Kaur et al., 2021).

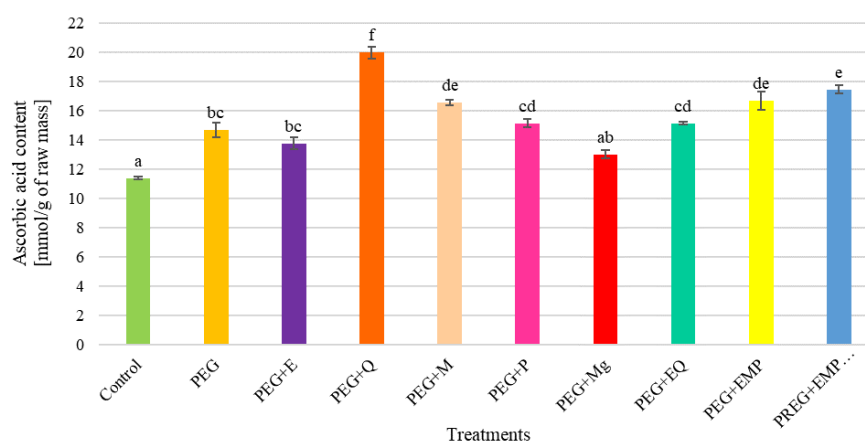


Figure 4. Ascorbic acid content in 10-day soft wheat (*T. aestivum*) seedlings under water deficit due to treatment with metabolically active substances. Means followed by different lowercase letters indicate significant differences at $p < 0.05$. Bars indicate the standard deviations ($\pm$ SD). PEG - PEG-6000; PEG+E - PEG-6000 + vitamin E (10^{-8} M); PEG+Q - PEG-6000 + ubiquinone-10 (10^{-8} M); PEG+M - PEG-6000 + methionine (0.001%); PEG+P - PEG-6000 + parahydroxybenzoic acid (POBA) (0.001%); PEG+Mg - PEG-6000 + MgSO_4 (0.001%); PEG+EQ - PEG-6000 + vitamin E (10^{-8} M) + ubiquinone-10 (10^{-8} M); PEG+EMP - PEG-6000 + vitamin E (10^{-8} M) + methionine (0.001%) + POBA (0.001%); PEG+EMPMg - PEG-6000 + vitamin E (10^{-8} M) + methionine (0.001%) + POBA (0.001%) + MgSO_4 (0.001%)

Under simulated drought conditions, a decrease in glutathione content was observed in wheat seedlings (Figure 5). Treatment of wheat seeds with vitamin E (PEG+E) and a combination of metabolically active substances (PEG+EMP) increased the content of GSH in seedlings by 31.4% and 30.7%, respectively, compared to the control and by 59.9% and 59.2%, respectively, compared to drought (PEG). High efficiency of the content of GSH was also observed in wheat seedlings under drought in the PEG + Mg and PEG + EMPMg groups. The GSH content in groups PEG+Q, PEG+M, PEG+P, and PEG + EQ does not exceed control but neutralizes the negative effect of PEG. The metabolically active substances investigated stimulated an increase in glutathione content in seedlings in drought. The increased glutathione content indicates its active participation in the detoxification of hydrogen peroxide (Strohm, 1995; Foyer and Noctor, 2011; Konturska and Palladina, 2012).

In general, the ascorbate-glutathione cycle is the central antioxidant mechanism in plants, responsible for the detoxification of H_2O_2 and is crucial to the formation of tolerance to drought (Bil'chuk and Rossikhina-Galycha, 2012; Konturska and Palladina, 2012). The AsA-

GSH cycle not only precisely regulates ROS concentrations but also contributes to maintaining cellular AsA and GSH pools (Smirnov, 2018).

Glutathione is regenerated from oxidized glutathione dimers (GSSG) by NADPH-dependent GR (Farooq et al., 2019). Glutathione participates in nonenzymatic detoxification of the superoxide radical, is a donor of reducing equivalents in the ascorbate-glutathione cycle (Strohm, 1995; Foyer and Noctor, 2011; Zhuk, 2011; Bil'chuk and Rossikhina-Galycha, 2012; Konturska and Palladina, 2012). It can interact with H_2O_2 and participate in the reduction of dehydroascorbate (Strohm, 1995; Foyer and Noctor, 2011; Zhuk, 2011; Konturska and Palladina, 2012). For constant removal of H_2O_2 , it is necessary that the level of reduced ascorbate and glutathione be sufficiently high (Strohm, 1995; Foyer and Noctor, 2011). Noctor et al. (2017) showed that during drought stress, more GSH is oxidized, and cells export GSSG to the extracellular environment to restore the redox imbalance.

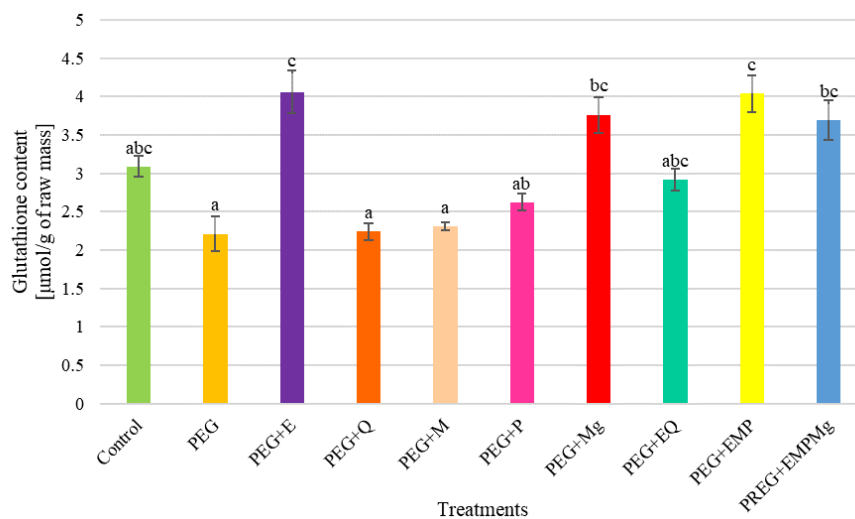


Figure 5. Glutathione content in 10-day-old soft wheat (*T. aestivum*) seedlings with a water deficit due to treatment with metabolically active substances. Means followed by different lowercase letters indicate significant differences at $p < 0.05$. The bars indicate the standard deviations ($\pm SD$). PEG - PEG-6000; PEG + E - PEG-6000 + vitamin E (10-8M); PEG+Q - PEG-6000 + ubiquinone-10 (10-8M); PEG + M - PEG-6000 + methionine (0.001%); PEG+P - PEG-6000 + parahydroxybenzoic acid (POBA) (0.001%); PEG + Mg - PEG-6000 + $MgSO_4$ (0.001%); PEG+EQ - PEG-6000 + vitamin E (10-8M) + ubiquinone-10 (10-8M); PEG + EMP - PEG-6000 + vitamin E (10-8M) + methionine (0.001%) + POBA (0.001%); PEG + EMPMg - PEG-6000 + vitamin E (10-8M) + methionine (0.001%) + POBA (0.001%) + $MgSO_4$ (0.001%)

The results of our research show that plants can support biochemical processes by activating antioxidant defense enzymes to avoid the negative effects of drought stress.

The pretreatment of soft wheat seeds (*T. aestivum*) with metabolically active substances had a clear stimulatory effect on the antioxidant defense system. This is because α -tocopherol is one of the most important antioxidants. It interacts with polyunsaturated acyl groups and

protects polyunsaturated fatty acids from lipid peroxidation by scavenging lipid peroxyradicals and quenching ROS. During this process, tocopherols donate their phenolic hydrogen to lipid free radicals, thus neutralizing the radical. The latter tocopherol radicals are more stable and less reactive and, more importantly, they can be converted to the corresponding tocopherol by reaction with other antioxidants such as ascorbate or glutathione. In addition, α -tocopherol is capable of deactivating singlet oxygen, which oxidizes membrane lipids, proteins, amino acids, nucleic acids, nucleotides, and carbohydrates. The chemical reaction of α -tocopherol with singlet oxygen leads to the formation of the corresponding tocopherol quinones (and other derivatives), some of which are powerful antioxidants (Sattler et al., 2004; Ali et al., 2020).

One of the most important antioxidant properties of ubiquinone is its ability to regenerate other antioxidants such as alpha-tocopherol and ascorbic acid (Dziuba and Kuchmenko, 2017). Ubiquinone, in turn, can not only act as an antioxidant but also be a pro-oxidant.

Methionine is a key metabolite in plant cells and plays a role in the antioxidant system by contributing to glutathione biosynthesis (Matthews, 1999; Martinez et al., 2017).

Hydroxybenzoic acid regulates the activity of a complex of antioxidant enzymes, that is, it activates enzymes of the antioxidant system, such as NADPH oxidases, peroxidases, and SOD (Barkosky and Einhellig, 2003).

Sulfur, as a component of MgSO_4 , participates in the synthesis of enzymes, proteins, in the redox processes of cells through glutathione and its derivatives, increasing the resistance to drought of plants (Guo et al., 2015).

Conclusions

Metabolically active compounds and their combinations activate antioxidant protection enzymes of wheat seedlings of the Provintsialka variety. They also contribute to reducing the manifestations of oxidative processes, which are the inevitable consequences of drought. Treatment of the seeds with vitamin E best stimulated the activity of ascorbate peroxidase in wheat seedlings, exceeding control and drought. The treatment of seeds with Mg most effectively reduced catalase activity in wheat seedlings, which correlates with increased ascorbate peroxidase activity and indicates the compensatory effect of enzymes of the antioxidant system.

The ascorbate-glutathione cycle is a key antioxidant mechanism in plants and plays a crucial role in tolerance to drought. The treatment of wheat seeds with ubiquinone-10 most effectively increased the ascorbic acid content in the seedlings by 46.3% compared to the seedlings whose seeds were in water-deficient conditions. An increase in the ascorbic acid content in wheat seedlings was also observed after treating wheat seeds with combinations of EMP and EMPMg. The highest levels of glutathione in drought-sown seeds were found when the seeds were treated with vitamin E and the combination of EMP, exceeding the control and PEG. This confirms the prospect of using metabolically active substances for plant adaptation under conditions of slow water supply.

Therefore, seed treatment with vitamin E, combinations of EQ, EMP, and EMPMg enhances the activity of enzymes and the content of components of the antioxidant defense system of soft wheat seedlings that participate in the neutralization of reactive oxygen species

under water deficit conditions. These metabolically active substances can be used to produce new modern preparations to increase the resistance of grain crops to drought.

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BIOCHEMICZNE MECHANIZMY ODPORNOŚCI NA SUSZĘ NASION PSZENICY JAREJ PRZY MODELOWANYM NIEDOBORZE WODY ORAZ APLIKACJI SUBSTANCJI METABOLICZNIE CZYNNYCH

Streszczenie. Niedobór wody jest jednym z najistotniejszych czynników stresowych ograniczających produkcję roślinną. Celem badań była ocena wpływu związków aktywnych metabolicznie na łagodzenie skutków suszy oraz stymulację procesów fizjologicznych i biochemicznych w pszenicy jarej odmiany Provintialka. W eksperymencie nasiona pszenicy moczone w roztworach zawierających różne substancje: PEG-6000 (PEG); PEG-6000 z dodatkiem witaminy E (PEG+E); PEG-6000 z ubichinonem-10 (PEG+Q); PEG-6000 z metioniną (PEG+M); PEG-6000 z kwasem parahydroksybenzoesowym (PEG+P); PEG-6000 z siarczanem magnezu (PEG+Mg); PEG-6000 z witaminą E i ubichinonem-10 (PEG+EQ); PEG-6000 z witaminą E, metioniną i kwasem parahydroksybenzoesowym (PEG+EMP); PEG-6000 z witaminą E, metioniną, kwasem parahydroksybenzoesowym i siarczanem magnezu (PEG+EMPMg). Następnie nasiona poddano działaniu 12% roztworu PEG, symulując deficyt wody,

po czym przeprowadzono proces kiełkowania. W badaniu analizowano aktywność peroksydazy askorbinianowej i katalazy oraz zawartość kwasu askorbinianowego i glutationu. Stwierdzono, że traktowanie nasion pszenicy związkami aktywnymi metabolicznie oraz ich kombinacjami wpływa na aktywność enzymów antyoksydacyjnych w siewkach w warunkach deficytu wody. Najsilniejsze obniżenie aktywności katalazy zaobserwowano po zastosowaniu roztworu $MgSO_4$, w porównaniu z siewkami poddanymi symulowanej suszy. Najsilniejszą aktywację aktywności peroksydazy askorbinianowej uzyskano po zastosowaniu witaminy E (PEG+E), co skutkowało wzrostem o 65,5% względem kontroli oraz o 2,4% w porównaniu z siewkami poddanymi symulowanej suszy. Spadek aktywności katalazy korelował ze wzrostem aktywności peroksydazy askorbinianowej, co wskazuje na efekt kompensacyjny enzymów układu antyoksydacyjnego. Największy wzrost zawartości askorbinianu w siewkach (o 46,3% względem siewek z grupy deficytu wody) zaobserwowano po zastosowaniu ubichinonu-10 (PEG+Q). Podobny efekt odnotowano po traktowaniu nasion kombinacjami EMP (PEG+EMP) oraz EMPMg (PEG+EMPMg). Najwyższy poziom glutationu w siewkach poddanych suszy uzyskano po zastosowaniu witaminy E (PEG+E) oraz EMP (PEG+EMP), przekraczając wartości kontrolne odpowiednio o 31,4% i 30,7%, a wartości uzyskane dla PEG – o 59,9% i 59,2%. Wyniki te potwierdzają potencjał substancji aktywnych metabolicznie w adaptacji roślin do warunków ograniczonego dostępu do wody.

Słowa kluczowe: właściwości przeciwutleniające, susza, substancje metabolicznie czynne, pszenica jara