Л.Н. Гумилев атындағы Еуразия ұлттық университетінің ХАБАРШЫСЫ.
BULLETIN of L.N. Gumilyov Eurasian National University.
ВЕСТНИК Евразийского национального университета имени Л.Н. Гумилева.
ISSN: 2616-7034. eISSN: 2663-130X

IRSTI 34.31, 34.31.27
https://doi.org/10.32523/2789-4320-2026-154-1-120-136
Research article

Biochemical mechanisms of the effects of heavy metals on barley (Hordeum vulgare L.)

M.K. Beisekova[†1], A.S. Satu[†2], K.D. Kumargazy[†3], M. Mambetova[4], A. Samat[5], A.Zh. Bekturova[6], M.T. Myrzabayeva[7], A.Zh. Akbassova[8], Zh.K. Masalimov*[9], A.B. Kurmanbayeva*[10]

[1,2,3,4,5,6,7,8,9,10]L.N. Gumilyov Eurasian National University, Astana, Kazakhstan

*E-mail: [1]mk.beisekova@gmail.com, [2]alekasatu@gmail.com, [3]karinakumargazy5@gmail.com, [4]mambetova022@gmail.com, [5]abay.samatuli07@gmail.com, [6]bekturova_az@enu.kz, [7]malikamyr@gmail.com, [8]akbassova_azh@enu.kz, *[9]masalimov@gmail.com, *[10]kurmanbayeva.assylay@gmail.com*

Abstract. Heavy metal pollution poses a major threat to ecosystems and the health of living organisms. In the present study, we investigated the effects of zinc and copper by applying $ZnSO_4$ and $CuSO_4 \cdot 6H_2O$ solution on the physiological and biochemical processes in barley (Hordeum vulgare L.) cv. Astana-2000 seedlings, 1 mM solutions of $ZnSO_4$ and $CuSO_4 \cdot 6H_2O$ were used. Sulfite oxidase (SO) is an enzyme that contains molybdenum and that contributes to sulfite detoxification and the regulation of redox reactions. The present research focuses on the impact of Zn and Cu on the enzyme SO activity. Zn and Cu treatments apparently induce moderate stress by stimulating SO activity, thereby enhancing sulfite detoxification and maintaining cellular redox balance. These results suggest that Zn and Cu differently affect the SO regulatory mechanism, also showing the participation of SO in the early regulation of redox balance and defense mechanism in barley under heavy metal stress. These findings support the importance of studying heavy metal interactions to develop strategies for enhancing plant tolerance to Zn, Cu, and similar stress conditions.

Keywords: zinc, Copper, barley, sulfite oxidase, catalase, heavy metals

Introduction

The heavy metal pollution has been identified as a global threat since the beginning of the Industrial Revolution. Heavy metal exposure due to its toxicity poses serious health and environmental problems [1]. Its toxicity adversely impacts physiological and morphological characteristics by reducing the absorption of essential nutrients and disrupting metabolism, thus inhibiting growth and biomass accumulation [2]. Common morphological symptoms are

Received: 12.02.2026. Accepted: 30.03.2026. Available online: 31.03.2026.

**Corresponding author*
[†]These authors contributed equally to this work

reduced root and shoot growth, which decrease respiration and photosynthetic processes, along with typical symptoms of heavy metal exposure in plants, such as chlorosis and necrosis [3]. Moreover, heavy metals such as Fe, Mn, Cu, Ni, Co, Cd Zn and Hg stimulate the production of reactive oxygen species (ROS) such as superoxide radical (O·−2), hydroxyl radical (OH) and hydrogen peroxide (H2O2), which causes lipid peroxidation, resulting damage of cell membrane and enzymatic activity at the cellular level [4]. However, many heavy metals at low concentrations function as enzyme cofactors and promote antioxidative defense that ultimately increases plant growth and its resistance to stress [5].

This dual nature of heavy metals plays a critical role in sustainable agriculture and in environmental protection. Some of the heavy metals, such as Cu, Fe, Mn, Mo, Ni, and Zn, function as essential micronutrients for plant growth when present in small amounts [6]. Among these, Cu and Zn often act as cofactors or activators in numerous enzymatic reactions. Zinc ions (Zn^{2+}) play a crucial role in various metabolic pathways, supporting the activity of enzymes such as RNA polymerase, superoxide dismutase, alcohol dehydrogenase, and carbonic anhydrase, as well as contributing to protein synthesis and the metabolism of lipids, carbohydrates, and nucleic acids. Also, Zn is a structural component of Zn-finger chain transcription factors, which regulate cell proliferation and differentiation [7]. Similarly, copper is crucial for photosynthesis, respiration, and lignin biosynthesis. However, at high concentration it impairs nutrient homeostasis, photosynthesis, and inhibits plant growth and productivity by causing oxidative stress [8]. Thus, a balance between deficiency and toxicity determines whether heavy metals act as growth promoters or stress inducers.

Copper and zinc illustrate this duality among various heavy metals. As reported by Azooz et al. (2012), Cu in wheat (*Triticum aestivum* cv. Hasaawi) promoted plant growth by enhancing the biosynthesis of free amino acids, proline, and antioxidant enzyme activity [9]. However, excessive Cu stress was shown to reduce photosynthesis, chlorophyll, leaf area, and grain yield [10], demonstrating its delicate boundary between beneficial and harmful levels. In spring barley (*Hordeum vulgare*), co-treatment with Cd and Zn suppressed plant growth, disrupted root and leaf morphology, and induced ultrastructural impairment in chloroplasts and mitochondria [11]. Similarly, excessive Zn concentration in cereals can inhibit growth and induce chlorosis, which is a sign of impaired chlorophyll synthesis often associated with impaired iron uptake and cellular damage [12]. In rice (*Oryza sativa*), high Cu exposure inhibited root and shoot growth, and accumulated excessive Cu, but when Zn was combined with Cu, the plant was improved, oxidative stress was reduced, antioxidant enzyme activity was increased and Cu uptake was limited [13]. Although, despite its beneficial role in trace amounts, copper becomes toxic at elevated concentrations, causing growth inhibition and morphological changes in various plant species. Copper reduces root growth, plant mortality, biomass, and seed production in Rhodes grass (*Chloris gayana*), black bindweed (*Polygonum convolvulus*), and bean (*Phaseolus vulgaris*) [14].

Given the specificity of crop responses to Zn and Cu, barley (Hordeum vulgare) was chosen as the model species for this study. Barley is the fourth-most widely grown cereal crop worldwide, after maize, rice, and wheat, and this cereal is widely used as feed and malt. For the experiment, we used the Astana-2000 cultivar of Hordeum vulgare L., which was previously used as a reference variety in field trials of Kazakhstan and demonstrated good adaptation to steppe and continental climates [15, 16].

Sulfite oxidase (SO) is a molybdenum cofactor-containing enzyme that catalyzes the oxidation of sulfite to sulfate. Because sulfite is a toxic nucleophile, its concentration must be strictly

managed [17]. It has been isolated from several plant species, including Spinacia oleracea, Malva sylvestris, Nicotiana tabacum, and Arabidopsis thaliana [18]. SO plays a vital role in the detoxification of sulfite formed during the degradation of sulfur-containing amino acids in plants, as well as excess sulfite derived from atmospheric SO2. Thus, SO contributes to both sulfur metabolism and protection against sulfite-induced oxidative stress. Recent evidence suggests that SO is not only responsible for sulfite detoxification but also influences wider metabolic and stress pathways. For example, Oshanova et al. (2021) demonstrated that variations in SO activity affect sulfur, carbon, and nitrogen metabolism, while modulating oxidative stress resistance [19]. Similarly, overexpression of SO in maize enhanced drought tolerance by reducing oxidative damage, highlighting the enzyme's role in maintaining cellular redox homeostasis under stress conditions [20]. These findings suggest that SO activity is sensitive to disturbances in cellular redox balance, which is also a characteristic feature of heavy metal stress.

Heavy metals such as Zn, Cu, and Cd are known to disrupt cellular homeostasis by inducing excessive formation of ROS and interfering with enzymatic redox regulation [21]. At the biochemical level, heavy metals can affect molybdoenzymes, including SO, through two main mechanisms: firstly, altering the redox signaling pathways that regulate their transcription and activity, and secondly, inhibiting enzyme function directly through inappropriate metalation or replacement of essential cofactors [21-23]. Neumann et al. (2008) demonstrated that heavy metal ions can inhibit molybdoenzymes by binding to sulfur ligands or directly interfering with Moco incorporation, offering a feasible mechanism responsible for SO inhibition during metal toxicity [23].

Therefore, although direct studies of SO under heavy metal stress remain limited, data from studies of oxidative stress and molybdoenzymes support the hypothesis that the effect of Zn and Cu on SO activity may vary according to their concentrations. At physiological trace metal levels, these metals can indirectly stimulate SO activity through redox signaling and the induction of antioxidant defenses. However, heavy metals can inhibit SO at elevated concentrations by disrupting Moco biosynthesis or directly interacting with its catalytic center. This dual mechanism of action highlights the importance of studying the role of SO in plant responses to heavy metal stress conditions, particularly Zn and Cu, which are both essential trace elements and potential toxicants at high concentrations.

The production of H2O2 directly links sulfite metabolism to the generation of ROS [24], establishing SO as both a detoxifying agent and an oxidative stressor in the plant mechanism. Furthermore, SO activity indirectly influences ROS and increases catalase (CAT) activity, thereby enhancing the antioxidant defense network. ROS, which are byproducts of various metabolic processes, play dual roles in plants as signaling molecules and potential agents of oxidative damage [25]. CAT normally detoxifies the H2O2 that comes from SO at low sulfite levels, but at higher concentrations, the accumulated H2O2 may non-enzymatically oxidize extra sulfite. The class III peroxidases might be a backup detoxification system in SO-deficient plants [24, 26]. Moreover, Xia et al. (2012) provided evidence that sulfite alone is capable of generating ROS and causing oxidative stress. As a result, SO contributes to the protection of plants by not allowing the peroxisomal CAT that is involved in the detoxification to be inhibited during excess sulfite in plants [20]. Hence, SO is a pivotal factor that not only connects sulfite metabolism but also redox signaling and defense pathways in conditions of oxidative stress.

The interconnection between antioxidant enzymes and SO activity in plants under heavy metal stress is crucial for the preservation of cellular redox homeostasis and for the alleviation of ROS-induced oxidative damage. Heavy metal stress is the major cause of oxidative stress

in plants, leading to the accumulation of ROS, which in turn requires an effective antioxidant response to be able to protect cellular structures and functions. Moreover, this increase often contributes to the activation of different antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), which have a very important role in detoxification of ROS and protection of biological macromolecules against oxidative damage [9]. These antioxidant enzymes not only detoxify ROS production, but also stabilize the redox environment, which is necessary for maintaining SO activity. Increased antioxidant activity limits oxidative modifications that can degrade SO, while SO itself promotes detoxification of ROS by converting sulfite to sulfate and also supporting glutathione (GSH) biosynthesis. Studies show that overexpression of SO in plants improves drought tolerance by increasing GSH levels, which enhances the SO-dependent antioxidant system and reduces H2O2 accumulation, thereby scavenging ROS and minimizing oxidative damage [20]. Furthermore, Yadav (2010) demonstrated that modulation of key enzyme activity participated in sulfur acquisition, the ascorbate-glutathione cycle (ASA-GSH), and phytochelatin (PC) synthesis promotes Cu detoxification [27]. This tightly coordinated interaction reflects a complex yet effective plant response to oxidative stress.

This study demonstrates that SO functions at the intersection of sulfur metabolism, ROS regulation, and antioxidant defense, making it susceptible to damage during heavy metal stress. By studying the responses of barley (*Hordeum vulgare* L.) cv. Astana 2000 to Zn and Cu, we aim to determine whether SO activity varies within coordination, stimulating defense at the micronutrient level but inhibiting it under toxic conditions.

Materials and research methods

Growth conditions

Barley seeds (Hordeum vulgare L.) were sterilized on the surface by immersing in a 3% hydrogen peroxide solution and constantly stirring for 5 minutes. After sterilization, the seeds were washed three times with double-distilled water (DDW) to completely remove the hydrogen peroxide. The seeds were placed in Petri dishes lined with filter paper soaked in 10 ml of 1 mM ZnSO4 or CuSO4 ·6H2O solutions for germination. The dishes were kept in the dark for 72 hours and then transferred to the light. Seedlings were grown in a controlled chamber under long-day conditions (16 h light/8 h dark) at a relative humidity of 75-80% and an air temperature of 22 to 27 °C. Lamps with spectral outputs of 2700 K and 6400 K, arranged alternately to stimulate optimal growth conditions, provided artificial lighting. The plants were watered with 15-20 ml of DDW at the same time each day. Seven-day-old seedlings were used for further experiments.

Preparation of samples for the experiment

To prepare samples, fresh leaves of seven-day-old seedlings were harvested and immediately processed to prevent enzymatic degradation. Leaf material was thoroughly homogenized using a pre-cooled mortar and pestle with the addition of extraction buffer. The extraction buffer was freshly prepared and contained 250 mM sucrose, 3 mM EDTA (pH 8.3), 250 mM Tris-HCl, L-cysteine, molybdenum solution, dithiothreitol (DTT), and DDW. This composition was chosen to stabilize proteins and enzymes, prevent oxidation, and maintain the structural integrity of biomolecules during homogenization. The homogenate was transferred to pre-cooled centrifuge tubes and centrifuged at 10,000 rpm for 25 minutes at 4°C. Centrifugation at low temperature was used to reduce the risk of protein denaturation and enzymatic activity. After centrifugation,

the supernatant, which contained soluble proteins and metabolites, was gently separated from the pellet, which consisted mainly of cellular debris and intact tissue. The obtained supernatants were immediately used for further biochemical analysis. Protein concentration was measured using the Bradford method [28].

Determination of chlorophyll content

Chlorophyll pigments were determined by taking about 20 mg of fresh leaf tissue from each sample and homogenized in 1 ml of 90% (v/v) ethanol using a pre-cooled mortar and pestle. The homogenates were put in centrifuge tubes and spun at 10,000 rpm for 10minutes at 4°C to separate cellular debris. The supernatant, containing the extracted pigments, was carefully collected for subsequent analysis. Chlorophyll concentrations were analyzed with a spectrophotometer through absorbance measurement at a specific wavelength. Chlorophyll a content was measured at 664 nm, and chlorophyll b at 649 nm. 90% ethanol served as a blank standard during the measurements. Chlorophyll concentrations were calculated using the following equations based on the studies of Lichtenthaler and Wellburn et. al. (1983) [29].

Determination of ROS generation

Barley seedling leaves were analyzed to establish ROS components, particularly H2O2. To quantify H2O2, samples were homogenized in 50 mM phosphate buffer (pH 7.5) at a 1:8 (w/v) ratio and centrifuged twice at 10,000 rpm for 10 minutes at 4°C. The resulting supernatants were used for analysis. The reaction mixture for H2O2 detection consisted of 0.85 mM 4-aminoantipyrine (AAP), 3.4 mM 3,5-dichloro-2-hyroxybenzene sulfonate (BHS), and 4.5 U/ml horseradish peroxidase (HRP) dissolved in 2 ml of 50 mM phosphate buffer (pH 7.5), prepared based on the method of Yesbergenova et. al. (2005) [30]. Samples were incubated in the reaction mixture and after 5 minutes, the absorbance at 515 nm was recorded using a spectrophotometer. The H2O2 concentration was identified by comparison with a standard calibration curve.

Determination of CAT activity

CAT activity was assessed according to the method originally described by Aebi et. al. (1984) with minor modifications. After electrophoresis, CAT isoenzyme bands were visualized by incubating the gel in 0.03% H2O2 solution for 10 minutes. Then, enzyme activity was detected by staining the gel with a freshly prepared solution containing 1% potassium ferricyanide [K3Fe(CN)6] and 1% ferric chloride (FeCl3) [31].

SO activity measurement

SO activity was evaluated according to the method of Kurmanbayeva et. al. (2017) [37]. To separate proteins, 500 µl of the plant extract supernatant was introduced to a Sephadex G25 column pre-equilibrated with sulfate buffer (0.5 M Na2SO4 in 0.1 M Tris-HCl, pH 8.0). The samples were applied to completely absorb onto the G25 matrix. To separate proteins from low-molecular-weight metabolites, 1 ml of sulfate buffer was then added to the column and completely absorbed into the matrix. The first 1 ml of eluate, containing the protein fraction, was collected and used for subsequent SO activity measurements.

Statistical analysis

All experiments were repeated at least three times to confirm the reliability of the results. Seedling shoot height was measured for each treatment, and the data were analyzed using GraphPad Prism software (version 8.02). Comparative analysis of arithmetic means was

performed, and the statistical significance of the differences between treatments was determined using one-way analysis of variance (ANOVA) followed by Turkey's multiple comparison test. Data from three independent replicates were converted to numerical values (±SD), and ImageJ was used to quantify enzyme activity intensity.

Results

Effect of Zn and Cu on seed germination and morphological parameters

To quantify the morphological responses to applied metal stress, shoots and root lengths of barley seedlings were measured by using a standard ruler (cm) under identical growth conditions. The data have shown the effect of Zn and Cu on barley growth and development. Figure 1 revealed a noticeable enhancement in seedling growth under Zn treatment compared with the control plant. It is characterized by a slight increase in shoot length and developed leaf structure. Overall, seedlings exposed to Zn treatment have maintained normal development. On the other hand, Cu treated ones showed a significant decline in growth, the shoot length decreased remarkably, and leaves became thinner compared with Zn-treated and control plants. Those leaves have shown several symptoms of stress, including pale green color and slightly curly morphology. Overall, seedlings were smaller, and the difference in height was clearly visible.

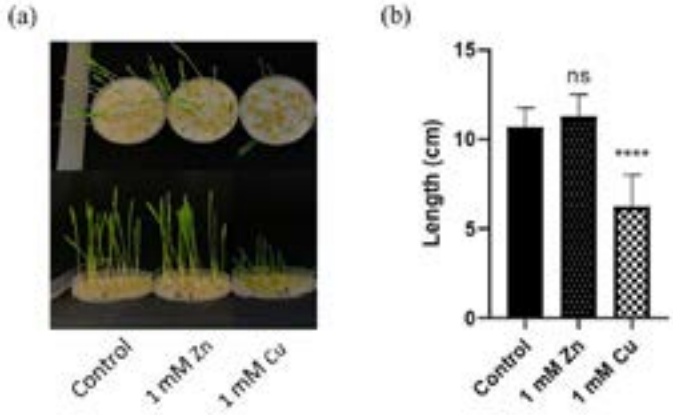

Figure 1. Heavy metal-induced changes in growth and development of barley leaves. (a) Effect of Zn and Cu on the morphology of barley; (b) Effect of Zn and Cu treatments on barley shoot length. The graph shows the average shoot length (cm) of barley seedlings grown under control, 1 mM Zn, and 1 mM Cu conditions. Asterisks in the graph "***" indicate a very significant ($P < 0.01$); "ns" – an insignificant ($P < 0.05$) difference in the presented data. Statistical analysis (Student's test) was performed using GraphPad Prism software (v.8.02). Data are presented in relative units.

Quantitative measurements confirmed these visual observations. As illustrated in Figure 1 (b), compared to the control, one Zn treatment resulted in a slight increase in shoot length, reaching approximately 6%, but this difference was not statistically significant. In contrast, shoot length significantly reduced to approximately 39% of the control value. Our results demonstrate the opposite effect of Zn and Cu on barley morphology; Zn treatment showed a moderate stimulating effect, whereas Cu significantly inhibited growth and elongation processes. Overall, morphological analysis has demonstrated contrasting physiological effects on barley seedlings. Zn acts as a micronutrient and moderately stimulates shoot growth, whereas Cu showed a phytotoxic effect even during relatively low concentrations.

The change in chlorophyll content under Zn and Cu treatment

Chlorophyll a and b contents were measured in barley seedlings to assess the effects of Zn and Cu exposure. The chlorophyll content of seedlings was differently affected by Zn and Cu treatments, as shown in Figure 2.

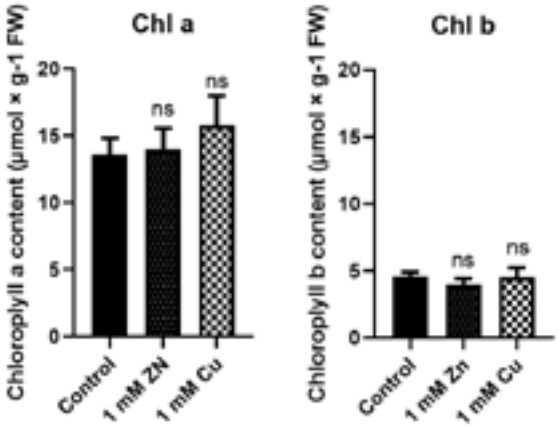

Figure 2. Determination of chlorophyll a and b contents. Asterisks in the graph "***" indicate a very significant (P < 0.01); "ns" – an insignificant (P < 0.05) difference in the presented data. Statistical analysis (Student's test) was performed using GraphPad Prism software (v.8.02). Data are presented in relative units

Compared with the control, exposure to 1 mM Zn resulted in a slight increase in chlorophyll a content by 3%; however, the effect of 1 mM Zn solution on chlorophyll b content was opposite, resulting in a 14% decrease. In contrast, seedlings treated with 1mM Cu exhibited a marked increase in chlorophyll a by 16%, showing the most pronounced enhancement. The effect of a 1 mM Cu solution on the chlorophyll b content was not remarkable. These findings indicate that Zn stress negatively influences pigment accumulation, whereas Cu at high concentration appears to stimulate chlorophyll a biosynthesis under the tested conditions.

Reactive oxygen species (ROS) accumulation under heavy metal stress

To evaluate the oxidative response of barley under heavy metal stress, ROS activity was quantified after exposure to 1 mM Zn and 1 mM Cu. As shown in Figure 3, the results clearly indicate that the two metals have distinct and opposing effects on ROS, reflecting the different mechanisms by which they influence plant oxidative balance.

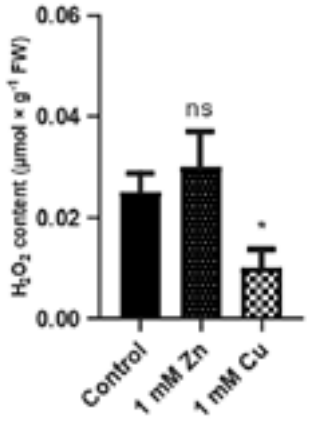

Figure 3. ROS content in leaves of barley seedlings treated with 1 mM Zn and 1 mM Cu. Asterisks in the graph "***" indicate a very significant (P < 0.01); "ns" – an insignificant (P < 0.05) difference in the presented data. Statistical analysis (Student's test) was performed using GraphPad Prism software (v.8.02). Data are presented in relative units.

Significant differences were observed between the experimental groups. In control seedlings, ROS formation was maintained at a stable baseline level, consistent with the normal oxidative state of untreated plants. Compared with untreated or control ones, seedlings exposed to Zn treatment increased ROS generation. It was approximately 20% of the control group, revealing a tendency for the ROS level to increase under these stress conditions. Although the increase was not statistically significant, the data consistency showed slightly higher ROS values in Zn-treated plants across all replicates. In contrast, Cu treatment significantly reduced ROS accumulation compared to both the control and Zn-treated groups. Cu treatment led to a decrease in ROS accumulation to 40% of that in the control group, which reveals a statistically significant change. This result was repeated in all biological replicates, confirming the inhibitory effect of Cu treatment on ROS generation. Comparing Zn, Cu treated and untreated groups, the lowest accumulation of ROS was detected in Cu-exposed plants, whereas Zn-treated ones showed the lowest values. Barley plants under Cu treatment showed significantly lower ROS levels compared with those during Zn stress conditions, which indicates a remarkable difference between treatment with Zn and Cu.

These results demonstrate a remarkable contrast in oxidative responses under the influence of the two metals. Zn and Cu treatments have led to different oxidative responses in barley seedlings. Zn exposure caused a small increase in ROS level, whereas Cu exposure significantly increased ROS production, demonstrating greater potential to disrupt cellular redox balance and lead to oxidative damage.

The role of the CAT enzyme in plants under zinc and copper stress

To better understand the antioxidant defense responses of barley seedlings under metal stress, CAT activity was reported, as CAT is one of the key enzymes responsible for the breakdown of H2O2 and protecting cells from oxidative damage. The dynamics of CAT activity, visualized as band intensities on the gel, are shown in Figure 4.

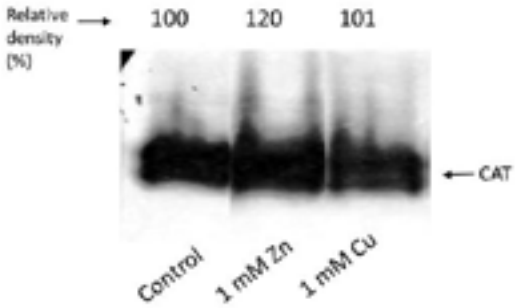

Figure 4. Catalase activity in barley leaves

The control group has determined a distinct band, indicating basal CAT activity during normal physiological conditions. Under Zn treatment, the CAT band intensity remarkably increased compared to the control plant. It reveals increased enzyme activity. Quantitative analysis of the relative band density revealed a significant increase compared to the control value. This increase shows that Zn moderately stimulated the antioxidant defense system, which is correlated to the adaptive reaction in order to maintain redox balance under moderate oxidative stress induced by Zn ions. On the other hand, Cu exposure led to a similar band intensity as in the control plant; it showed no significant increase, as shown in Figure 4. It implies that stress related to the Cu

exposure may exceed the antioxidant capacity or dysregulate the CAT enzyme activity, resulting in an imbalance between ROS generation and detoxification.

Overall, the results obtained showed that Zn treatment led to a moderate increase in enzymatic CAT activity as a defense response, whereas Cu treatment caused in minimal enzymatic change, indicating weaker or possibly suppressed antioxidant defense against Cu-induced oxidative stress in barley leaves.

Role of Sulfite oxidase (SO) stimulation under heavy metal stress

To subsequently investigate the enzymatic antioxidant responses of barley seedlings to Zn and Cu, SO activity was measured, as this enzyme plays a key role in sulfur metabolism and the detoxification of sulfite to sulfate, thereby reducing oxidative stress. Relative SO activity levels are shown in Figure 5.

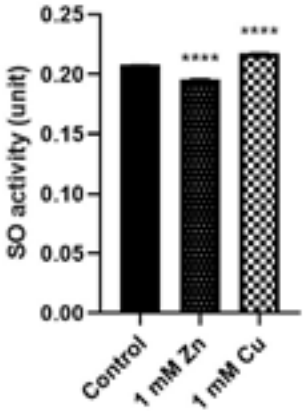

Figure 5. SO activity in barley grown with 1 mM Zn and 1mM Cu treatments. Asterisks in the graph "***" indicate a very significant (P < 0.01); "ns" – an insignificant (P < 0.05) difference in the presented data. Statistical analysis (Student's test) was performed using GraphPad Prism software (v.8.02). Data are presented in relative units

Figure 5 demonstrates that SO activity occurs in untreated barley seedlings. During 1mM Zn treatment, the enzymatic activity of SO has slightly decreased and is reduced to 6% compared to the control plant. Stress related to Zn exposure didn't significantly affect sulfur-related oxidative metabolism, since no huge decrease in SO activity was detected, indicating a weak inhibitory effect. On the other hand, during Cu treatment, seedlings showed a moderate increase in SO activity, approximately 15% of the control plant. It indicates a moderate activation of SO, possibly related to a compensatory response to the increased oxidative pressure generated by Cu ions. Neither Zn nor Cu treatments have led to a significant change compared to the control plant in SO activity; in other words, it was relatively stable. Whereas, a slight decline in activity under Zn and an increase under Cu treatment reveal that So is a stable enzyme and has a crucial role in preserving the redox and sulfur balance in barley leaves during early metal stress.

Discussion

This study shows the different influences of Zn and Cu on barley growth and development. According to the morphological data, in seedlings exposed to a 1mM Zn solution, shoot length hasn't demonstrated a remarkable change; on the other hand, 1mM Cu-treated ones demonstrated a significant decline. This demonstrates that the applied concentration, Zn, did

not significantly impair growth, while Cu caused substantial growth inhibition. These findings align with previous observations on the effect of high concentrations of Cu on barley that showed a notable decline in biomass accumulation and overall plant growth. The study by Leite et al. (2024) found that Cu treatment during early development and barley seed germination declined seedling length and biomass, confirming strong growth inhibition [33]. Similarly, the study by Gao et al. (2008) reported that an increase in Cu concentrations in Jatropha curcas seedlings significantly reduced growth and biomass while changing antioxidant enzyme activities, inducing oxidative stress, and activating the defense mechanisms [34]. In contrast, Zn treatment on barley plants in the study by Mazurek et al. (2024) showed a clear inhibitory effect on shoot elongation and overall growth, demonstrating the negative effect of excessive Zn concentrations on morphological development [35]. Our findings of a non-significant decline under Zn suggest that the Zn level used may lie near the threshold between slight stimulation and inhibition, or that barley seedlings tolerate 1mM Zn under our experimental conditions. The much stronger morphological inhibition by Cu underscores the greater toxicity potential of Cu compared to Zn in barley early development.

Cu and Zn are elements with an important role in plant growth and development at low concentrations; however, they are toxic at high concentrations [36]. Cu treatment increased the content of chlorophyll a and b, since it was used at low concentrations. However, a significant decrease in chlorophyll content and photosynthesis rate was observed in other studies using higher concentrations of Cu. In the study by Panou-Filotheou et al. (2001), the effect of high Cu concentrations on oregano (*Origanum vulgare subsp. hirtum*) leaves was studied, and many structural and ultrastructural damages in chloroplast and mesophyll tissues were detected [37]. In another study, Cambrollé et al. evaluated the tolerance of wild grapevine (*Vitis vinifera L. subsp. sylvestris*) to copper toxicity by assessing physiological and biochemical responses to excess Cu exposure [38]. On the other hand, Essa et al. (2021) explored the effects of biogenic copper nanoparticles synthesized from *Avicennia marina* leaves on wheat seedlings, demonstrating that these nanoparticles influenced seed germination, chlorophyll content, detoxification enzyme activity, and copper uptake [39]. Zn had slightly different effects on chlorophyll a and b, since it was used at low concentrations (1mM). In the study by Singh, on *Cajanus cajan (L) Millsp*., at 500 and 1000 mg kg-1 concentrations of Zn, resulted in a dramatic decline in chlorophyll pigments [40]. In another study on *Triticum aestivum* L. at 900 mg kg-1 concentration, inhibition in chlorophyll and total sugar contents was detected [41].

Results of ROS generation showed that Zn treatment increased ROS accumulation compared to the control, whereas Cu treatment markedly decreased ROS activity. This is somewhat unexpected because many studies report increased ROS under heavy metal stress, particularly with Cu. According to Juknys et al. (2012), both Zn and Cu exposure in spring barley increased oxidative stress markers, with Cu causing a stronger accumulation of ROS and greater lipid peroxidation than Zn, indicating that Cu exerts a more severe oxidative effect on plant tissues [42]. The decrease in ROS under Cu exposure in our experiment may result from a few possible mechanisms: (1) Cu stress may have suppressed ROS-producing processes (e.g., inhibited electron transport or metabolic activity), (2) there may have been a strong up-regulation of ROS scavenging systems (even if we did not detect large increases in CAT or SO), or (3) severe damage may have reduced overall metabolic activity and thus ROS generation. In contrast, the mild increase under Zn aligns with the idea that Zn may generate a mild oxidative damage. Interestingly, a barley metal toxicity study found that Zn acted antagonistically in Cu + Zn mixtures and reduced oxidative stress biomarkers in some combinations [43]. Our data thus suggest that under the conditions of our experiment, Cu caused strong growth inhibition but

without the expected ROS elevation, possibly because ROS generation was suppressed or rapidly scavenged, whereas Zn provoked a minor ROS increase consistent with a low-level stress or signalling response. In leaves of barley seedlings, CAT activity under Zn treatment slightly increased compared to the control, while under Cu treatment it remained nearly unchanged. According to Song et al. (2014), exposure of barley seedlings to heavy metal stresses led to an increase in CAT activity, indicating activation of the antioxidant defense system in response to metal-induced oxidative stress [44]. Another barley study under copper stress (200 μmol CuCl2) found an increase in CAT activity compared with the control, demonstrating strong induction under Cu toxicity [45]. The modest increase in our Zn treatment is thus consistent with a mild protective response, whereas the near-control level under Cu suggests that, in our experimental conditions, catalase induction was minimal, perhaps due to enzyme inhibition or oxidative damage overwhelming the CAT-mediated detoxification. This may help explain why morphological growth was so severely reduced under Cu stress despite only moderate CAT induction.

In the present study, the activity of sulfite oxidase (SO) in barley leaves showed differential responses under Zn and Cu stress, being slightly lower under Zn and slightly higher under Cu compared to the control. The slight reduction in SO under Zn treatment suggests that moderate Zn exposure may not strongly disrupt sulfur metabolism, while the increase under Cu indicates a stress-induced activation of SO as part of the plant's defense system. This detoxifying role is the most studied in Arabidopsis plants, where SO enzymatic activity results in disruption of sulfur and carbon metabolism; moreover, it leads to the decline in biomass and increased oxidative stress [19]. In the same manner, a transgenic tobacco plant with overexpression of SO was shown to elevate sulfate and glutathione (GSH) levels; furthermore, it results in reduced ROS accumulation and improvement of stress tolerance [20]. These findings support the interpretation that the increase in SO activity observed under Cu stress in barley reflects a protective adaptation to elevated oxidative load. Brychkova et al. (2007) showed that SO-deficient Arabidopsis and tomato plants accumulate toxic levels of sulfite and suffer from growth inhibition and metabolic disturbances, indicating that SO has a key detoxification function under stress conditions [46]. Furthermore, according to Sun et al. (2023), exposure to heavy metals such as Cu and Zn alters sulfur metabolism in plants by regulating key enzymes, including sulfite oxidase (SO), whose enhanced activity contributed to detoxification of sulfite and improved tolerance to metal-induced oxidative stress [47]. Thus, the metal-specific modulation of SO observed in this study likely represents an adaptive mechanism to sustain sulfur metabolism and mitigate ROS accumulation under Cu and Zu toxicity. These findings align with reports that heavy metals can modulate sulfur assimilation pathways and SO-related defense mechanisms [46,47], highlighting that SO activation plays a crucial role in mitigating sulfite toxicity and maintaining redox homeostasis under metal stress.

Although this study revealed that Cu and Zn differently influence sulfite oxidase activity in barley seedlings, it was limited to short-term exposure and basic biochemical parameters. Future research should include longer exposure periods, different plant stages, and a wider range of metal concentrations to better understand how SO activity contributes to plant tolerance under metal stress.

Conclusion

This study demonstrated that copper and zinc differently affect the growth, chlorophyll content, and enzyme activity of barley seedlings, especially SO. Zinc treatment slightly increased

SO and catalase activities and maintained chlorophyll levels, suggesting that plants can activate these protective mechanisms under mild stress. In contrast, copper caused stronger growth inhibition with only a small change in SO and other physiological parameters, indicating that the enzyme and associated processes were partly suppressed under Cu stress. Overall, these results show that SO, along with other cellular and physiological responses, plays an important role in mitigating the harmful effects of heavy metals, with the response depending on metal type and concentration. Considering that Kazakhstan has regions with elevated Cu and Zn levels in agricultural soils due to industrial activity, understanding how barley responds to these metals is especially relevant for improving crop tolerance and maintaining soil health. Further studies on SO regulation and overall physiological responses under different metal stress conditions will be useful for developing strategies to enhance stress resistance in crops grown in Kazakhstan and other countries or regions facing comparable agricultural and environmental challenges.

Author Contributions

M.B., Zh.M., and **A.K.** – conceptualization; **A.S., K.K., A.S., A.A.** – data curation; **M.B., A.S.,** and **A.K.** – formal analysis; **M.B., M.M.,** and **A.Zh.** – investigation; **M.B., A.K., A.S.** and **Zh.M.** – methodology; **M.B.** – visualization; **M.B., A.S.** and **A.K.** - writing – original draft; **M.B., A.S., A.K., A.B., A. Zh., M.M.,** and **Zh.M.** – writing – review & editing; **M.M.,** and **Zh.M.** – project administration; **M.B., A.K.** and **Zh.M.** – supervision; **A.K., Zh.M.** - funding acquisition and resources. All authors have read and agreed to the published version of the manuscript.

Funding

This work was supported by the AP19676731 "Investigation of the role of signaling molecules to create new strategies for increasing the stress tolerance of grain crops".

Conflicts of Interest

The authors declare no conflicts of interest.

Compliance with ethical standards

This article does not contain a description of studies performed by the authors involving people or using animals as objects.

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Ауыр металлдардың арпаға (Hordeum vulgare L.) тигізітен әсерінің биохимиялық механизмдері

М.К. Бейсекова[†1], А.С. Сату[†2], К.Д. Құмарғазы[†3], М.Мамбетова[4], А. Самат[5], А.Ж. Бектурова[6], М.Т. Мырзабаева[7], А.Ж. Акбасова[8], Ж.К. Масалимов*[9], А.Б. Курманбаева*[10]

[1,2,3,4,5,6,7,8,9,10]*Л.Н. Гумилев атындағы Еуразия ұлттық университеті, Астана, Қазақстан*

Аңдатпа. Экожүйенің тұтастығына және тірі организмдердің денсаулығына төнетін негізгі қауіптердің бірі – ауыр металдардың ластануының улы әсері. 1 мМ ZnSO4 және $CuSO_4 \cdot 6H_2O$ ерітінділері түрінде қолданылатын мырыш және мыс арпаның (Hordeum vulgare L.) Астана-2000 сорты өскіндеріндегі физиологиялық-биохимиялық процестерге дифференциалды әсер етеді. Сульфитоксидаза (СО) құрамында молибден бар фермент, ол сульфитті детоксикациялау мен тотығу-тотықсыздану процестерін реттеуге қатысады, алайда ауыр металл стрессіне оның реакциясы әлі де жеткілікті зерттелмеген. Бұл зерттеудің мақсаты сульфитоксидаза белсенділігінің модуляциясына Zn және Cu әсерін зерттеу болды. Zn және Cu әсерлері орташа стресс тудырып, СО белсенділігін арттыратыны байқалды, бұл сульфиттің детоксикациясын күшейтіп, жасушалардың тотығу-тотықсыздану тепе-теңдігін сақтауға ықпал етуі мүмкін. Бұл нәтижелер Zn және Cu СО реттелуіне әртүрлі әсер ететінін және СО ферментінің ауыр металл стрессі кезінде арпадағы ерте тотығу-тотықсыздану реттелуіне және қорғаныш реакцияларында қатысатыны дәлелдейді. Алынған деректер Zn және Cu өсімдіктермен өзара әрекеттесуін зерттеудің маңыздылығын көрсетіп, ауылшаруашылық дақылдарының Zn және Cu және басқа да стресс факторларына төзімділігін арттыру стратегияларын әзірлеу үшін негіз бола алады.

Түйін сөздер: мырыш, мыс, арпа, сульфитоксидаза, ауыр металдар

Биохимические механизмы воздействия тяжелых металлов на ячмень (Hordeum vulgare L.)

М.К. Бейсекова[†1], А.С. Сату[†2], К.Д. Кумаргазы[†3], М. Мамбетова[4], А. Самат[5], А.Ж. Бектурова[6], М.Т. Мырзабаева[7], А.Ж. Акбасова8, Ж.К. Масалимов*[9], А.Б. Курманбаева*[10]

[1,2,3,4,5,6,7,8,9,10]*Евразийский национальный университет имени Л.Н. Гумилева, Астана, Казахстан*

Аннотация. Одна из главных угроз целостности экосистем и здоровью живых организмов связана с токсическим воздействием загрязнения тяжелыми металлами. В данном исследовании для изучения влияния Zn и Cu на физиологические и биохимические процессы в ростках ячменя (Hordeum vulgare L.) сорт «Астана-2000» использовались 1 мМ растворы $ZnSO_4$ и $CuSO_4 \cdot 6H_2O$. Сульфитоксидаза (СО), молибденсодержащий фермент, играющий ключевую роль в детоксикации сульфитов и регуляции окислительно-восстановительных процессов, недостаточно изучена в

условиях стресса, вызванного тяжелыми металлами. Поэтому целью данного исследования было изучение влияния Zn и Cu на активность сульфитоксидазы. Обработка Zn и Cu, по-видимому, вызывает умеренный стресс, стимулирующий активность СО, что потенциально усиливает детоксикацию сульфита и поддерживает окислительно-восстановительный баланс клеток. Эти результаты свидетельствуют о том, что Zn и Cu оказывают различное воздействие на регуляцию СО, что, в свою очередь, указывает на участие СО в ранней окислительно-восстановительной регуляции и защитных реакциях ячменя при стрессе, вызванном тяжёлыми металлами. Полученные данные подчёркивают важность изучения взаимодействия тяжёлых металлов с растениями для разработки стратегий повышения устойчивости сельскохозяйственных культур к воздействию Zn и Cu и других аналогичных стрессовых условий.

Ключевые слова: цинк, медь, ячмень, сульфитоксидаза, тяжёлые металлы

Сведения об авторах:

Бейсекова Молдир Кудиярбековна – магистр технических наук, постдокторант, старший преподаватель кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Сату Альбина Саматқызы – студент 4 курса бакалавриата кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Қумаргазы Карина Дауренқызы – студент 4 курса бакалавриата кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Мамбетова Мадина – бакалавр естественных наук, магистрант 2 курса кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н.Гумилева, 010000, Астана, Казахстан.

Самат Абай – магистр естественных наук, PhD студент кафедры общей биологии и геномики Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Бектурова Асемгуль Жамбуловна – PhD, доцент кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Мырзабаева Малика Төлендіқызы – PhD, старший преподаватель кафедры общей биологии и геномики Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Акбасова Алуа Жолдасбаевна – PhD, ассоциированный профессор кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Масалимов Жаксылык Каирбекович – автор для корреспонденции, кандидат биологических наук, PhD, ассоциированный профессор, заведующий кафедрой биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Курманбаева Асылай Бактыбаевна – автор для корреспонденции, PhD, ассоциированный профессор кафедры биотехнологии и микробиологии Евразийского национального университета имени Л.Н. Гумилева, 010000, Астана, Казахстан.

Авторлар туралы мәлімет:

Бейсекова Молдир Кудиярбековна – техника ғылымдарының магистрі, постдокторант Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының аға оқытушысы, 010000, Астана, Қазақстан.

Сату Альбина Саматқызы – Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының 4 курс бакалавр студенті, 010000, Астана, Қазақстан.

Қумарғазы Карина Дауренқызы – Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының 4 курс бакалавр студенті, 010000, Астана, Қазақстан.

Мамбетова Мадина – жаратылыстану ғылымдарының бакалавры, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының 2 курс магистр студенті, 010000, Астана, Қазақстан.

Самат Абай – жаратылыстану ғылымдарының магистрі, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің жалпы биология және геномика кафедрасының PhD студенті, 010000, Астана, Қазақстан.

Бектурова Асемгуль Жамбуловна – философия ғылымдарының докторы (PhD), Л.Н. Гумилев Атындағы Еуразия Ұлттық Университетінің Биотехнология және Микробиология Кафедрасының доценті, 010000, Астана, Қазақстан.

Мырзабаева Малика Төлендіқызы – PhD, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің жалпы биология және геномика кафедрасының аға оқытушысы, 010000, Астана, Қазақстан.

Акбасова Алуа Жолдасбаевна – PhD, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының доценті, 010000, Астана, Қазақстан.

Масалимов Жаксылык Каирбекович – хат-хабар авторы, биология ғылымдарының кандидаты, PhD, қауымдастырылған профессоры, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының меңгерушісі, 010000, Астана, Қазақстан.

Курманбаева Асылай Бактыбаевна – хат-хабар авторы, PhD, Л.Н. Гумилев атындағы Еуразия ұлттық университетінің биотехнология және микробиология кафедрасының қауымдастырылған профессоры, 010000, Астана, Қазақстан.

Authors' information:

Beisekova Moldir Kudiyarbekovna – MSc, postdoctoral student, senior lecturer, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Satu Albina Samatkyzy – 4th year undergraduate student, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Kumargazy Karina Daurenkyzy – 4th year undergraduate student, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Mambetova Madina – Bachelor of Natural Sciences, 2nd year master's student, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Samat Abay – MSc, PhD student, Department of General Biology and Genomics, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Bekturova Assemgul Zhambulovna – PhD, Associate Professor, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Malika Myrzabayeva – PhD, senior lecturer, Department of General Biology and Genomics, L.N.Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Akbassova Alua Zholdasbaevna – PhD, Associate Professor, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Masalimov Zhaksylyk Kairbekovich – Corresponding author, Candidate of biological sciences, PhD, Associate Professor, head of the Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.

Kurmanbayeva Assylay Baktybaevna – Corresponding author, PhD, Associate Professor, Department of Biotechnology and Microbiology, L.N. Gumilyov Eurasian National University, 010000, Astana, Kazakhstan.