

## THE EFFECT OF HEAVY METAL IONS ON THE PEROXIDASE ACTIVITY IN ARABIDOPSIS THALIANA

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*The biosphere pollution with the heavy metals (HM) has increased significantly in recent decades due to human activity. Plants can accumulate and concentrate HM, which negatively affects their growth, productivity and quality of agricultural products. Some HM, such as copper, belong to the group of biogenic elements that, in low concentrations, are essential for the normal functioning of plant organisms. Other HM such as cadmium are toxic even in low concentrations. The toxicity of HM is related to oxidative damage. In the plant cell, the antioxidant system provides protection against this kind of stress. However, data on changes in antioxidant enzyme activities in the early stage of the cellular response to HM-induced stress remain scarce. Therefore, we focused our research on studying peroxidase (POD) activity changes in Arabidopsis thaliana under conditions of rapid uptake of copper and cadmium ions into leaf tissue. For the experiments, 4.5–5-week-old A. thaliana plants were used. The plants were incubated on 0.5x MS liquid medium containing copper or cadmium chloride at concentrations of 0.1, 0.5 and 5 mM. The HM salt treatment was carried out in the dark at 20 °C for 2 (short-term stress) and 12 (long-term stress) hours. After that, the leaves were frozen and the POD activity was measured. Evaluation of the effects of Cd<sup>2+</sup> and Cu<sup>2+</sup> ions shows that these HM cause a decrease in POD activity after 2 hours and its increase after 12 hours of treatment. Therefore, modulation of POD activity is a component of the HM stress response in A. thaliana. Analysis of the available data revealed that the enzymes POD and CAT, which eliminate hydrogen peroxide, can partially replace each other and thus provide cellular protection in different phases of the stress response.*

*Key words: antioxidant enzymes, Arabidopsis thaliana, cadmium, copper, oxidative stress, heavy metals, peroxidase*

**Introduction:** In their natural environment, plants are continuously exposed to a variety of abiotic and biotic stresses. Among abiotic stressors, heavy metal salts (HM) play a significant role due to their detrimental effects on plant growth and function. Human activities, including fertilizer application and accumulation of waste from the mining industries, have significantly increased the influx of HM into the biosphere in recent decades (Ghori et al., 2019; Diaconu et al., 2020). This in turn leads to contamination of topsoil and groundwater. Plants, with their inherent tendency to bioaccumulate, absorb and concentrate HM in their tissues, which negatively affects their growth, productivity, and ultimately the quality of agricultural products (Yazlovitskaya et al., 1999; Dağhan & Ozturk, 2015; Afonne & Ifediba, 2020).

Heavy metals, such as iron, manganese, copper, molybdenum, nickel, and zinc belong to a group of biogenic elements that, in low concentrations, are essential for the normal functioning of plant organisms. Copper (Cu) is a particularly important element that plays a variety of roles in plants. Cu is a cofactor for many enzymes and plays a key role in ATP synthesis as it is a component of plastocyanins and cytochrome oxidase, which are included in the photosynthetic and respiratory electron transport chains. However, high concentrations of Cu<sup>2+</sup> ions

can increase the production of reactive oxygen species (ROS) and trigger oxidative stress in plants, which can cause significant damage to DNA, proteins and cell membranes (Badiia et al., 2020; Mir et al., 2021). Accordingly, Cu is considered one of the most toxic HM.

Some other HM, such as cadmium (Cd), are toxic even in low concentrations. Cd is often found in pesticides that are sprayed to protect plants from pathogens in the field. Plants exposed to Cd<sup>2+</sup> typically have stunted growth and chlorotic leaves. Cd<sup>2+</sup> binds to sulfhydryl groups of proteins, leading to their inhibition and/or misfolding, thereby disrupting their functions, including electron transfer in electron transport chains. The accumulation of Cd<sup>2+</sup> inhibits Fe (III) reductase, leading to Fe (II) deficiency, which in turn negatively affects photosynthesis. Additionally, photosynthesis is disrupted through decreased chlorophyll synthesis and inhibition of enzymes involved in CO<sub>2</sub> fixation. Cd<sup>2+</sup> also interferes with the absorption of Ca, P, K, Mg, and water, and inhibits nitrate reductase, thereby reducing the uptake and assimilation of nitrates (Ghori et al., 2019; Singh et al., 2019).

Disturbance of redox balance in the plant cell, excessive generation of ROS and associated oxidative stress are believed to be an important mechanism of the toxic action of HM. Plants have

various mechanisms to resist stress caused by HM. In particular, the cell has enzymatic and non-enzymatic antioxidant defense systems. The enzymatic system includes catalase, ascorbate, and other peroxidases that reduce the level of hydrogen peroxide (Ghori et al., 2019; Buzduga et al., 2022).

Class III peroxidases (PODs) catalyze the decomposition of hydrogen peroxide ( $H_2O_2$ ) using various phenolic compounds as substrates. The role of PODs in plant response to abiotic and biotic stresses has been demonstrated. For example, activation of expression of various class III POD genes under salt, heat stress, and drought has been shown for several plant species (Wang et al., 2015; Akbudak et al., 2018; Shahzad et al., 2019; Kidwai et al., 2020; Su et al., 2020; Raja et al., 2020; Lian et al., 2023). However, data on changes in antioxidant enzyme activities in the early stage of cellular response to HM-induced stress are still limited. Therefore, we focused our research on studying the POD activity in *A. thaliana* under conditions of rapid influx of Cu and Cd ions into leaf tissue.

**Materials and methods.** To study the effects of  $Cd^{2+}$  and  $Cu^{2+}$  ions, 4.5- to 5-week-old *Arabidopsis thaliana* (L.) Heynh plants were used. The plants were grown in soil in a cultivation chamber at a temperature of 20 °C and light intensity of 2.5 klx under 16-h photoperiod conditions. To obtain information about the early stage of the stress response and to clarify the primary reactions of the plant cell to the accumulation of  $Cd^{2+}$  and  $Cu^{2+}$  ions, the plants were treated under conditions that ensure the rapid uptake of these ions into the leaf tissues. It is known that the root system has a barrier function and selectively prevents the penetration of HM ions into the shoots (Rohozynskyj et al., 1998a; 1998b; Dixit et al., 2001). Therefore, to achieve rapid uptake of  $Cd^{2+}$  and  $Cu^{2+}$  ions into *Arabidopsis* leaves, the cut aerial parts of the plants were incubated on a liquid 0.5x MS medium containing copper or cadmium chloride at concentrations of 0.1, 0.5, and 5 mM. The treatment was carried out in the dark at a temperature of 20 °C for 2 (short-term stress) and 12 (long-term stress) hours. As our laboratory experience shows, 2 h is the minimum time in which the accumulation of the toxicants and the development of the stress response in the leaves can be expected. Control plants were incubated on a medium without the addition of copper and cadmium chlorides. Intact plants, which were frozen immediately after cutting, served as an additional control. For each experimental variant, a sample of 10-12 plants was pooled.

To measure the activity of POD, an extract of soluble proteins was obtained. For this purpose, the frozen plant material was homogenized in a mortar with liquid nitrogen. A buffer consisting of 50 mM

sodium phosphate (pH=7.0), 0.25 mM EDTA, 10% glycerol, 2% polyvinylpyrrolidone-25 and 0.5 mM ascorbate was used for protein extraction. Enzyme activity was determined spectrophotometrically by measuring the change in optical density of the sample at a wavelength of 470 nm (Amako et al., 1994; Buzduga et al., 2018). The reaction mixture contained 25  $\mu$ l of protein extract and 975  $\mu$ l of reaction buffer (25 mM sodium acetate buffer (pH 5.0), 8 mM guaiacol, and 9 mM  $H_2O_2$ ). The optical density of the samples was measured using an SF-46 spectrophotometer. Enzyme activity was expressed in micromoles of substrate oxidized in 1 min per 1 mg of protein. The amount of protein in the extract was determined according to the Bradford method (Bradford, 1976). The experiment was performed for five batches of plants. For each protein extract, enzymatic activity and protein content were measured three times. The significance of differences between the control and each treatment was assessed using the Tukey HSD test ( $P < 0.05$ ).

**Results and discussion.** Traditionally, when studying the response of plants to excessive concentrations of HM ions, long-term treatment with HM salts from 12 h to several days is used (Chen et al., 2000; Seneviratne et al., 2019; Giannakoula et al., 2021). Such chronic stress studies are important for understanding the mechanisms of the gradual adaptation of plants to elevated concentrations of HM. However, it is almost impossible to differentiate primary and secondary effects and changes that occur in a plant cell under stress. Accordingly, we decided to examine the effects that take place within hours of acute stress to better understand the early stage of the stress response.

In the group of control plants, incubated for 2 h on 0.5x Murashige and Skoog medium without HM salts, POD activity remained unchanged. However, after 12 h of incubation, the enzyme activity decreased by 32% (Figure 1).

Treatment of *Arabidopsis* plants with copper chloride for 2 h resulted in a dose-dependent decrease in POD activity, ranging from 30 to 43 % compared to the control group, which could be due to POD inactivation under  $Cu^{2+}$  stress without sufficient *de novo* synthesis of the enzyme.

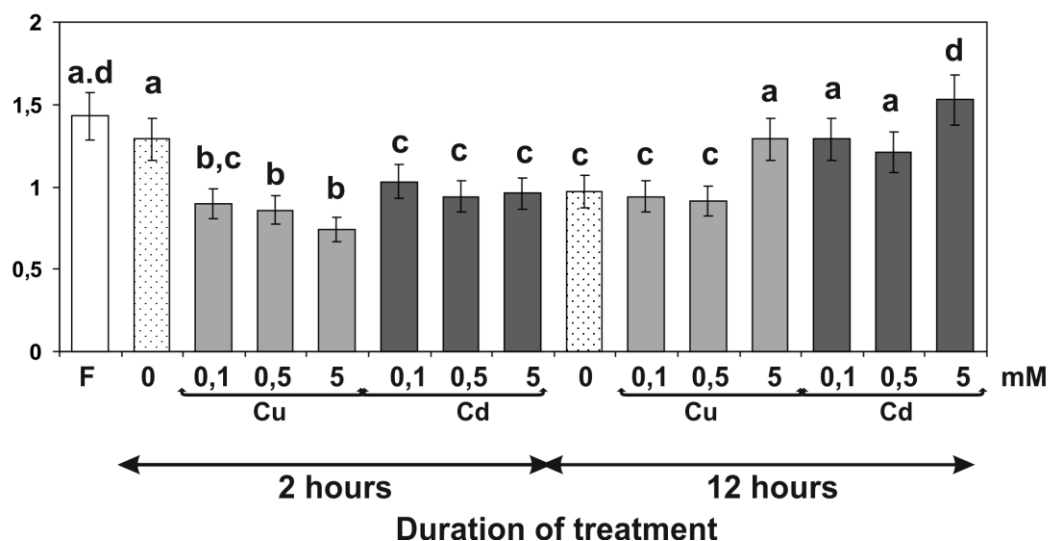
Our previous studies showed an increase in catalase (CAT) activity in *A. thaliana* after treatment with 0.1 and 0.5 mM (but not 5 mM) copper chloride (Doliba et al., 2012a). This suggests that other enzymes, particularly CAT, could functionally substitute POD providing  $H_2O_2$  decomposition upon short-term  $Cu^{2+}$  stress. However, when 5 mM copper chloride was applied, a decrease in activity of both POD (Figure 1) and CAT (Doliba et al., 2012a) was found. At the same time, under the influence of the highest tested concentration of the toxicant, a

significant increase in membrane lipid peroxidation was observed (Doliba et al., 2012b), indicating a serious oxidative damage in the cell. Taking together, the data show that the antioxidant system is unable to counteract such a high stress dose.

After treating *A. thaliana* with 0.1 and 0.5 mM copper chloride for 12 h, we observed a recovery of POD activity to control values, while treatment with 5 mM solution resulted in a 33 % increase over control (Figure 1). A comparison of our novel and previous data (Doliba et al., 2012b) shows that the increase in POD activity under the influence of 0.5

mM copper chloride correlates with a decrease in lipid peroxidation to control level. In contrast, the level of lipid peroxidation additionally increased after treating the plants with 5 mM copper chloride for 12 h.

Previous studies reported significant upregulation of peroxidase gene expression in rice and *Rhodiola crenulata* upon copper treatment (Sudo et al., 2008; Zhang et al., 2018). This suggests that the POD activation in *A. thaliana* observed in our study could be due to increased transcription of *Pod* genes.



**Fig. 1.** Peroxidase activity ( $\mu\text{mol}/\text{min mg}^{-1}$  protein) in arabidopsis leaves exposed to various concentrations of Cu or Cd chloride; F, fresh (untreated) leaves; error bars represent means  $\pm$  one standard deviation and different letters indicate significant differences between the values ( $P < 0.05$ ).

The expression of peroxidase genes has been shown to increase under salt, drought, cold, and heat stresses (Wang et al., 2015; Akbudak et al., 2018; Shahzad et al., 2019; Su et al., 2020; Raja et al., 2020; Lian et al., 2023). Transgenic plants with elevated expression of peroxidase genes show increased resistance to stress factors. For instance, overexpression of the *AtPRX62* gene provided tolerance to aluminum (Wu et al., 2017) and the *OsPRX38* gene to arsenic (Kidwai et al., 2019). Our new data indicate that POD in *A. thaliana* is also involved in the cell protection against oxidative stress caused by excessive concentrations of  $\text{Cu}^{2+}$  ions.

The next step of our research was to evaluate the effect of  $\text{Cd}^{2+}$  ions on Arabidopsis. After 2 h of cadmium stress, POD activity in Arabidopsis leaves decreases by 20 % and 26-27 % when treated with 0.1 mM and 0.5 or 5 mM cadmium chloride, respectively (Figure 1).

When the exposure time was extended to 12 h, an increase in POD activity of 33, 26, and 59 %, respectively, was observed with the application of

0.1, 0.5, and 5 mM cadmium chloride. Previously, it was reported that POD activity increased with long-term stress treatment in 10-day-old wheat seedlings grown on soil contaminated with cadmium and lead (Murtaza et al., 2019). However, in contrast to Arabidopsis, POD activity in tobacco leaves remained unchanged when the same experimental design was used for cadmium chloride treatment (Buzduga et al., 2022). It indicates the specificity of the stress response in plants of different taxonomic groups.

Our previous studies also showed a decrease in the activity of other antioxidant enzymes in Arabidopsis, CAT and ascorbate peroxidase, under the action of  $\text{Cd}^{2+}$  ions for 12 h, and the strongest decrease in CAT activity was found under the treatment with of 5 mM cadmium chloride (Doliba et al., 2011). In addition, our new results show that such treatment results in the greatest increase in POD activity. Therefore, these data further support our hypothesis that the antioxidative enzymes, e.g., POD and CAT, can functionally replace each other,

which ensures the reliability of the cell's defense mechanisms.

**Conclusions.** Analysis of the effects of  $\text{Cd}^{2+}$  and  $\text{Cu}^{2+}$  ions shows that these HM cause a decrease in POD activity after 2 h and its increase after 12 h of treatment. Therefore, modulation of POD activity is a component of the HM stress response in *A. thaliana*. Enzymes that split hydrogen peroxide, POD and CAT, can partially replace each other and thus provide cellular protection in different stages of the stress response.

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## ВПЛИВ ІОНІВ ВАЖКИХ МЕТАЛІВ НА АКТИВНІСТЬ ПЕРОКСИДАЗИ У *ARABIDOPSIS THALIANA*

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Надходження важких металів (ВМ) у біосферу за останні десятиліття суттєво зросло внаслідок діяльності людини. Рослини, як біоаккумулятори, можуть накопичувати та концентрувати ВМ, що негативно впливає на їхній ріст, продуктивність та якість сільськогосподарської продукції. Частина ВМ, а саме мідь, належить до групи біогенних елементів, які у низьких концентраціях є необхідними для нормального функціонування рослинного організму. Деякі інші ВМ, як от кадмій, є токсичними навіть у малих концентраціях. Токсичність ВМ пов'язана з окисдаційними пошкодженнями. У рослинній клітині захист від такого типу стресу забезпечує антиоксидантна система. Однак даних про зміни активності антиоксидантних ферментів на ранній стадії клітинної відповіді на стрес, викликаний ВМ, недостатньо. Тому у наших дослідженнях ми зосередили увагу на вивченні активності пероксидази (POD) *A. thaliana* за дії різних концентрацій міді та кадмію на ранніх етапах стресової відповіді. Для дослідження впливу іонів кадмію та міді використовували 4,5–5-тижневі рослини *Arabidopsis thaliana* (L.) Heynh. Рослини інкубували на рідкому середовищі 0,5х MS, яке містило хлорид міді або кадмію у концентраціях 0,1; 0,5 та 5 мМ. Обробку солями ВМ проводили у темряві за температури 20 °C протягом 2-х (короткотривалий стрес) та 12-ти (довготривалий стрес) год. Після цього листки заморозували та вимірювали активність POD.

Оцінка ефектів викликаних іонами Cd<sup>2+</sup> та Cu<sup>2+</sup> показує, що ці ВМ призводять до зниження активності POD через 2 години та її підвищення через 12 годин обробки. Таким чином, модуляція активності POD є компонентом відповіді на стрес викликаний ВМ у *A. thaliana*. Аналіз наявних даних показав, що ферменти POD і CAT, які знешкоджують перексид водню, можуть частково замінювати один одного і таким чином забезпечувати клітинний захист на різних фазах стресової відповіді.

**Ключові слова:** антиоксидантні ферменти, *Arabidopsis thaliana*, кадмій, мідь, окисдаційний стрес, важкі метали, пероксидаза.

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