Химия растительного сырья. 2026. №2. С. 143–149.
Khimiya rastitel'nogo syr'ya, 2026, no. 2, pp. 143–149.
DOI: 10.14258/jcprm.20260217881

UDC 582.52:581.4; 574.24

EXOGENOUS LIGNIN ENHANCES THE RESISTANCE OF *LEMNA MINOR* L. AQUATIC PLANTS TO COPPER STRESS

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Currently, there is a growing interest in preparations made from lignin, due to their various useful properties. These include biodegradability, biocompatibility, harmlessness, and a wide range of biological activities. For the first time, the fundamental possibility of using exogenous lignin to protect aquatic plant organisms from the negative effects of copper ions has been demonstrated in this work. Lignin from ledum (*Ledum palustre* L.) was tested as a chemoprotective agent. Presents the results of a study on the biological activity of isolated lignin on a laboratory culture of duckweed (*Lemna minor* L.) under the influence of a copper stress factor. During the experiments, we established the values of biomarkers for plant well-being (growth rate, level of damage, frond area, content of malondialdehyde and chlorophyll) and found that water-soluble lignin from ledum was not toxic to plant organisms. Preliminary cultivation of plants in aqueous lignin-containing media increased the total frond area, had a positive effect on growth rate, and reduced the level of damage to duckweed in copper-containing aqueous media. It was concluded that pre-treating duckweed with water-soluble lignin would increase the plant's resistance to copper stress. The data obtained confirm the opinion about the adaptive and protective properties of lignin under the influence of stress factors of various nature.

Keywords: lignin, duckweed, copper stress, antioxidant activity, biological activity.

For citing: Bodnar I.S., Karmanov A.P., Kocheva L.S., Cheban E.V., Raskosha O.V. *Khimiya Rastitel'nogo Syr'ya*, 2026, no. 2, pp. 143–149. (in Russ.). https://doi.org/10.14258/jcprm.20260217881.

Introduction

Lignins are among the most abundant biopolymers in the plant kingdom. Currently, interest is increasing in lignin-based products because of their various beneficial properties, such as biodegradability, biocompatibility, harmlessness and a wide range of biological activities. The biological functions of lignins in plants are very diverse [1]. They impart mechanical strength to plant tissue as a whole. The presence of lignin determines the moisture and light permeability of cell walls, which plays an important role in regulating various physical and biochemical processes. Tissue lignification increases plant resistance (adaptive function) to various environmental stresses, in particular extreme temperatures. These biopolymers protect plants from excess UV radiation and the harmful effects of free radicals. One of the functions of lignin is to perform antioxidant protection of plants [2–5]. Another important function of lignin is protection against various phytopathogens. Thus, lignification of plants ensures creating reliable physical, chemical and biological barriers that protect almost all plant elements, including stem, roots, branches, leaves and reproductive organs, from negative exogenous influences [1, 6].

These facts indicate uniqueness of lignin biopolymers, which perform protective functions according to various mechanisms and algorithms. The question arises: if native (endogenous) lignin has the ability to withstand negative stress factors, is it possible that lignin introduced into the system from the outside, that is, exogenous lignin, is able to perform certain protective functions? If this assumption is confirmed, it will provide more effective plant protection in some specific growing conditions, for example, when grown using vertical farming technologies, including hydroponics, aquaponics and aeroponics [7]. First of all, this is especially important for those species of aquatic plants and algae that, by their nature, do not have a lignification apparatus [8–10].

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As is known, some aquatic plants, in particular, plants of *Lemnaceae*, the duckweed family, are proposed for the remediation of polluted water bodies. Duckweed can absorb heavy metals and radionuclides, which is a necessary condition for the phytoremediation of water bodies [9]. At the same time, the plants themselves experience serious stress, often leading to their degradation and death. Biomedical properties of lignin are currently being actively studied in many laboratories, and almost all studies are carried out on animals that receive lignin preparations along with food or drinking water. Our data [10] indicates that lignin introduced into the body from the outside, i.e. exogenous lignin, brings positive results. As for plant organisms, the possibility of using exogenous lignin to protect them from an exogenous factor was first shown in work [11] using the example of the radiation stress factor.

One of the serious environmental problems that threatens both aquatic ecosystems [12] and humans is the pollution of water bodies with heavy metal ions, in particular, with copper ions [13]. This metal and its compounds are widely used in agriculture, semiconductors, sensors and other devices. Copper mining and wide application of copper-containing materials are accompanied by its increasing release into the environment. When copper enters the natural environment, it causes copper stress in plants [14], which can result in cell death [15].

This paper presents a novel attempt to use exogenous lignin to protect plant organisms from heavy metals using copper ions as an example. The aquatic flowering plant duckweed (*Lemna minor* L.) and the lignin of the widespread marsh plant ledum (*Ledum palustre* L.) were chosen as the main objects of our research.

Material and Methods

Obtaining a lignin sample and characteristics of lignin sample. Lignin isolated from the stems of ledum (*Ledum palustre* L.), was used in the experiments. The raw materials were harvested at the end of the growing season in a forest area near the city of Syktyvkar (Russia) (coordinates: latitude 61.50, longitude 50.61). The ledum lignin preparation was obtained by the Pepper method [16] by treating deresined plant raw materials with a water-dioxane mixture (9 : 1) at boiling temperature (~100 °C) for 1 hour. Lignin was purified by double reprecipitation from dioxane into diethyl ether. To obtain the finished sample, the freeze-drying method was used. The yield of the sample is 15.2% of the content of lignin Klason in the feedstock. Elemental analysis of the isolated preparations was carried out by the analyzer from Hewlett Packard (USA). C – 59.4±1.6; H – 6.4±0.6, O – 34.2. To quantify functional groups standard methods of wood chemistry were used. Phenolic hydroxyls 3.9±0.1%, carboxyl groups 3.5±0.2%, methoxy groups 16.3±0.3%. To study monomeric composition of samples by Py-GC/MS – methods was carried out with a single-shot pyrolyzer EGA/PY-3030D (Frontier lab, Japan) with liquid nitrogen-cooled cryo-trap (MJT-1030Ex, Japan) coupled with a GC–MS chromatograph. Monomeric composition of lignin samples according to Py-GC/MS data: G-units 22.2%, S-units 77.7%, H-units 0.1%. EPR spectra were obtained by RadioPAN SE/X-2547 X-band radio-spectrometer. The EPR spectrum of oat lignin is an intense narrow signal with a g-factor of 2.0042. The concentration of free radicals C is 2.7×10^{17}, spin/g.

Preparation of water-soluble lignin preparations. The method is based on the ability of lignin to dissolve in aqueous solutions of alkalis with subsequent conversion of the resulting compound into a water-soluble H-form using a cation exchange resin [17]. 1 g sample of lignin L-1 was poured into 40 ml of 0.1 N aqueous solution of NaOH (bidistillate) and left for 1 hour, then 40 ml of water (bidistillate) and 4 g of DIAION RCP160M cation exchange resin (Mitsubishi Chemical Corporation) were added. The process was carried out by infusion with stirring on a magnetic stirrer and with constant monitoring of the pH value using a pH meter (pH 3210 SET 2 (Germany) until pH = 7. Then the resin was filtered on a paper filter with a pore size (2–3 μm). A clear aqueous solution of lignin pH 7 without sediment was obtained.

Determination of antioxidant activity (AOA). Antioxidant activity was assessed by coulometric titration of electrically generated Br compounds [18]. We used an Ekspert-006 coulometric analyzer (Ekoniks-Ekspert Ltd., Russia) with glassy carbon electrodes. A semi-permeable membrane separated the cathode and anode compartments. The working electrodes were Pt. The amount of charge in coulombs that was consumed in the titration was calculated using equation $Q = (100 \times I \times t) / V_{al}$, where I was the current (amp); t was the time to reach the titration end point (s); V_{al} was the aliquot volume (ml). The lignin aqueous solution concentration was 2%. The AOA measurement units were kC/g of tested compound.

Plant material. A laboratory culture of duckweed was used in this work. Plants were grown in Steinberg's medium [19] under constant conditions (24±0.1 °C, 16 h light/8 h dark) maintained in a climate chamber (Binder, Germany).

Copper (Cu^{2+}) experiment. The plants were placed in a medium containing 10^{-5}% lignin for 24 hours. Then they were transferred to glass containers with a medium containing 3.15, 6.3, 12.6 μmol/L Cu^{2+}. A sterile $CuCl_2$ solution was used as a source of Cu^{2+}. These concentrations of heavy metal led to inhibition of growth rate, which was determined by us previously [20]. After 7 days, the specific growth rate, change in area and the presence of damage to the leaf-like blade in the form of chlorosis and necrosis were determined. The Cu^{2+} content in plant samples was determined after testing. The plants were washed with distilled water and dried. To prepare for analysis, the plants were destroyed by microwave mineralization with HNO_3 and H_2O_2. Elemental concentrations were determined by inductively coupled plasma atomic emission spectroscopy. The work was carried out by the eco-analytical laboratory of the Institute of Biology FRC Komi SC UB RAS.

*Determination of malondialdehyde (MDA).*For analysis, 50 mg wet weight of a laboratory culture of duckweed was ground with quartz sand, 1.5 ml of 20% trichloroacetic acid was added, and centrifuged for 15 min at 10.000 g. 0.5% thiobarbituric acid dissolved in 20% trichloroacetic acid was added to the supernatant. The resulting mixture was kept at 95 °C for 30 min, cooled and centrifuged. Next, the optical density was determined at wavelengths of 532 and 600 nm by Spectrumlab SS2107 spectrophotometer (LEKI Instruments, Finland). The MDA content was calculated by the formula [21]. The MDA content was determined four days after the start of the experiment.

Determination of a+b chlorophylls. To determine the level of photoassimilating pigments, the plants were ground with a small amount of quartz sand and calcium carbonate, then a 95% ethanol-water solution was added and kept for 30 minutes at a temperature of 4 °C. The resulting homogenate was centrifuged for 10 min at 13.000 g. The extract was poured into a clean test tube. An ethanol solution was added to the sediment and centrifuged again. Repeat until the sediment turns gray. The optical density of the samples was measured at wavelengths 470, 649, 664 nm by Spectrumlab SS2107 spectrophotometer (LEKI Instruments, Finland). The concentration of pigments was calculated according to [22].

Statistical Processing. The normality of distribution was tested by the Shapiro-Wilk test. To reliably determine differences between treatment groups, Student and Mann-Whitney tests were used. All experiments were carried out in triplicate. For statistical processing of the results, the Statistica 6.0 software package (StatSoft, USA) was used.

Results and discussion

Evaluation of the antioxidant activity of lignins. Previous works [2, 23, 24] found that isolated lignins had good antioxidant properties. However, the index of antioxidant activity (AOA) significantly depends on the botanical origin of lignin, which does not allow predicting its exact value. Figure 1 shows the results of the determination of the antioxidant activity of lignin from a number of different herbaceous plant species, as well as some wood lignins.

The presented results show that lignin from ledum *Ledum palustre* L. has the highest antioxidant activity. Comparing lignins with known antioxidant substances, we note that the AOA of ledum lignin is comparable to the antioxidant activity of drugs such as rutin (61.0 kC/g), and mitofen (92.6 kC/g) [23]. When discussing the problem of antioxidants, it is necessary to pay special attention to the fact that, unlike rutin and other recognized antioxidants, preparations based on lignins are high-molecular compounds that have all the characteristic features of polymers. Therefore, from the point of view of searching and selecting new means for protecting plant organisms from exogenous stress factors, the macromolecular nature of lignins is an undeniable advantage.

Considering that the sample from *Ledum* is characterized by a higher antioxidant activity, we can make a reasonable assumption that this lignin should have more pronounced bioactive properties. This circumstance served us as a main reason for choosing sample from Ledum as an exogenous lignin to protect plant organisms from copper stress.

Effect of lignin on plants under copper stress. We chose duckweed (*Lemna minor* L.) as the object of study. This is a flowering plant floating on the surface of reservoirs, which consists of a frond (the leaf-like surface) and a root (Fig. 2). A characteristic feature of duckweed is a rapid growth and reproduction, which is very important for scientific experiments. The most common method of propagation of this plant is vegetative, which allows conducting experiments on genetically homogeneous populations [25]. For this reason, duckweed is a practical model subject for biotesting and studying the effects of various toxicants on aquatic plants.

At this stage, studies were carried out to identify the effect of exogenous lignin on this plant under conditions of copper stress. Contamination of aquatic ecosystems with Cu^{2+} currently poses a serious problem from the point of view of the conservation of flora and fauna. On the other hand, Cu is one of the elements necessary for plants, since it is part of various enzymes and is involved in biochemical and physiological processes in plant cells [26]. However, even its slightly increasing concentration in water bodies negatively affects the life of aquatic plants [27].

This fact is confirmed by our data on the influence of copper on such an important indicator as the specific growth rate of plants. As can be seen from Figure 3, this indicator decreased by 1.3, 2.2 and 4.5 times relative to the control at Cu^{2+} concentrations of 3.15, 6.3, 12.6 μmol/L, respectively. It should be noted that copper content in plants increased in proportion to its content in the medium.

The concentration of Cu^{2+} in plants with and without precultivation on lignin at different concentrations of the element did not change (Table). As already noted, endogenous lignin in the xylem cell walls of typical higher plants plays an important role in neutralizing negative environmental factors. In particular, it was found that exceeding the normal level of Cu^{2+} in such higher plants leads to the launch of a number of processes aimed at changing the lignin content in the cell wall. Copper activates the biosynthesis of lignin enzymes L-phenylalanine ammonium lyase (PAL) and cinnamyl alcohol dehydrogenase [28]. As a result of this activation, the lignin content in the cell wall increases in plants growing under copper stress. Obviously, this fact should be considered as a protective reaction of plants aimed at increasing their survival under conditions of exposure to excess amounts of Cu^{2+}.

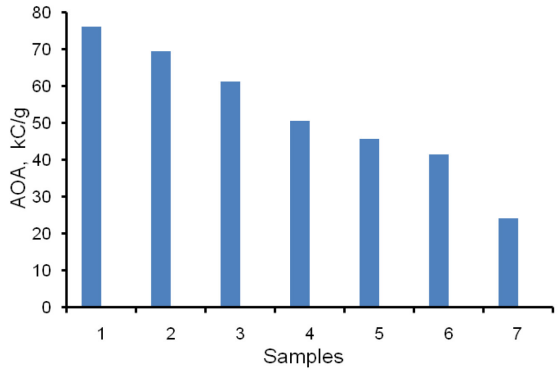
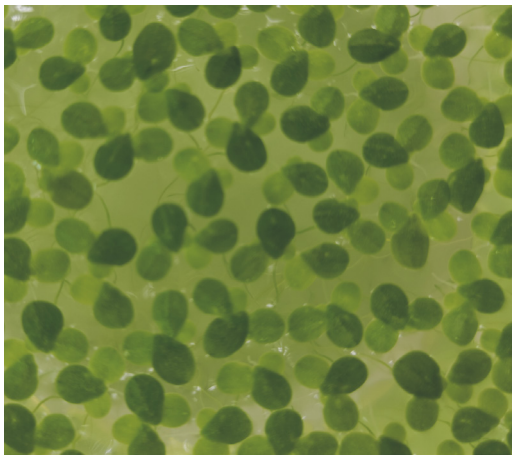


Fig. 1. Antioxidant activity of lignin samples from various plants: 1 – *Ledum palustre* L., 2 – *Avena sativa*, 3 –*Triticum sp.*, 4 – *Sorbus aucuparia*, 5 – *Larix sibirica*, 6 – *Festuca pratensis* Huds., 7 – *Brassica oleracea*



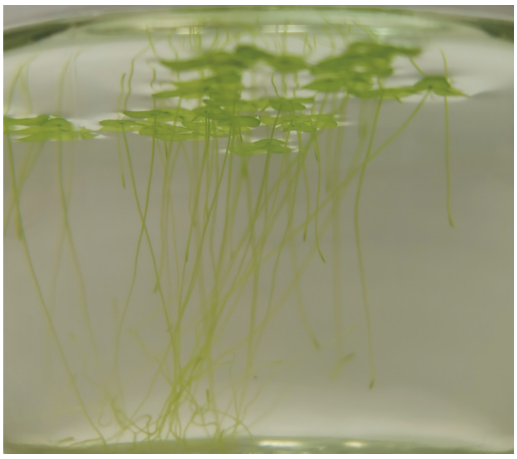


Fig. 2. The test subject – duckweed (*Lemna minor* L.)

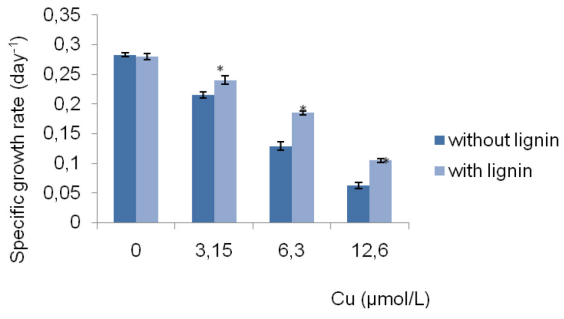


Fig. 3. Change in the specific growth rate of a laboratory culture of duckweed under the influence of Cu^{2+} without lignin treatment and with preliminary cultivation on a medium with lignin (10^{-5}%) for 24 hours. * – differences are reliable in relation to the plants grown on excess Cu^{2+} ($p \leq 0.05$, Student's test)

Copper content in aquatic medium and plants

Cu^{2+} in medium, μmol/L	Cu^{2+} in plants, mg/kg	
	without lignin	with lignin
3.15	28.7±1.2	29±3.8
6.3	79±4	72.3±3.3
12.6	293.3±39.3	286.7±41.8

As for the studied subject of duckweed, this plant, like some other aquatic plants, is not capable of synthesizing a sufficiently large amount of endogenous lignin to perform the entire range of protective functions inherent in typical terrestrial plants. In this regard, it is very important to evaluate the possibility of using exogenous lignin to perform protective functions, as well as to analyze its effect on plants under conditions of Cu^{2+} pollution in the aquatic environment. As the studies have shown (Fig. 3), pre-treatment of plants with an aqueous solution of lignin (concentration 10^{-5}%) for 24 hours actually had a positive effect on the growth rate of duckweed, i.e. increased its resistance to copper stress. For example, at a Cu^{2+} concentration of 3.15 μmol/L, the average growth rate in the population upon pretreatment with lignin increased by 11.6%, at 6.3 μmol/L – by 43.4%, at 12.6 μmol/L – by 66.7%. In the absence of Cu^{2+}, the specific growth rate with and without pretreatment with a lignin solution remained unchanged. Thus, it can be stated that exogenous lignin, although partially, neutralized the negative effect of Cu^{2+}, that is, it performed a chemical protective function. This conclusion is also confirmed by the results of assessing the level of damage to the fronds of plants subjected to copper stress.

Figure 4 shows median values of the level of damage to plant fronds. To calculate this indicator, the number of necrosis and chlorosis that appeared during the experiment was counted in plants. Necrosis is areas of dead plant tissue in the form of brown spots. Chloroses are known to be disorders of fronds with discoloration (yellowing) due to a lack of chlorophyll. In control plants, the level of damage to the fronds was 1%; pretreatment with water-soluble lignin did not change the value of this indicator.

Figure 5 presents results of experiments to study the effect of cupper stress on the total frond area of a laboratory duckweed culture. In the control experiment, the frond area was 1417±30 mm^2. Plants after lignin were characterized by a frond area of 1330 mm^2, which, in principle, did not differ from the control experiment. Under conditions of exposure to copper stress, there was a significant decrease in the area of the fronds, and the higher the Cu^{2+} concentration, the more significant the decrease was. In particular, at a copper concentration of 12.6 μmol/L, the frond area decreased to 199±3 mm^2, but pre-treatment with water-soluble lignin led to small but noticeable increase in this indicator to 245±6.5 mm^2, i.e. a noticeable increase in the value of the frond area was recorded. Similar results were observed at a concentration of 6.3 μmol/L Cu^{2+}. As a result, it can be stated that preliminary cultivation of plants in a lignin-containing medium had a positive effect on the total area of duckweed fronds under Cu^{2+} stress conditions.

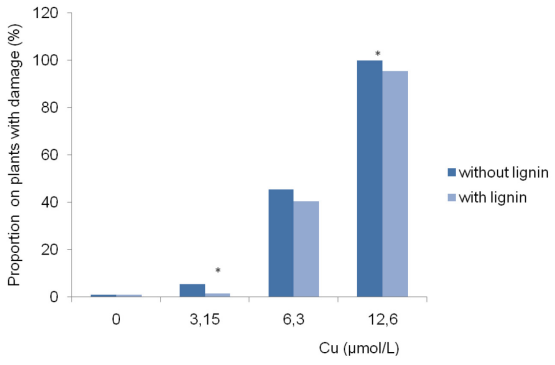


Fig. 4. Median values of the level of frond damage of plants with excess Cu^{2+} without pre-treatment with lignin and with pre-growth in a medium with lignin (10^{-5}%) for 24 hours. * – differences are reliable in relation to plants grown on excess Cu^{2+} ($p \leq 0.05$, Mann-Whitney test)

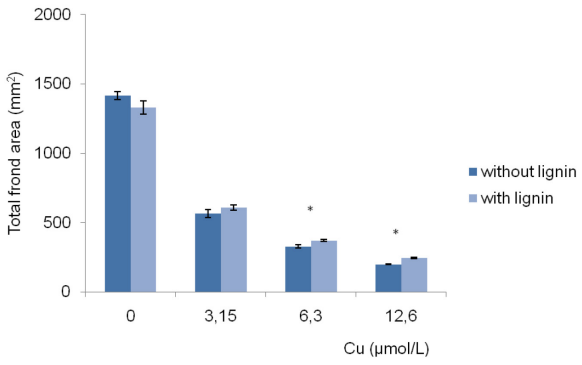


Fig. 5. Change in the total frond area of a laboratory culture of duckweed under conditions of exposure to Cu^{2+} stress without pre-treatment with lignin and with pre-growth in a medium with lignin for 24 hours. * – differences are reliable in relation to the positive control (plants grown on excess Cu^{2+}) ($p \leq 0.05$, Student's test)

The concentration of Cu^{2+} in plants with and without precultivation on lignin at different concentrations of the element did not change (Table). As already noted, endogenous lignin in the xylem cell walls of typical higher plants plays an important role in neutralizing negative environmental factors. In particular, it was found that exceeding the normal level of Cu^{2+} in such higher plants leads to the launch of a number of processes aimed at changing the lignin content in the cell wall. Copper activates the biosynthesis of lignin enzymes L-phenylalanine ammonium lyase (PAL) and cinnamyl alcohol dehydrogenase [28]. As a result of this activation, the lignin content in the cell wall increases in plants growing under copper stress. Obviously, this fact should be considered as a protective reaction of plants aimed at increasing their survival under conditions of exposure to excess amounts of Cu^{2+}.

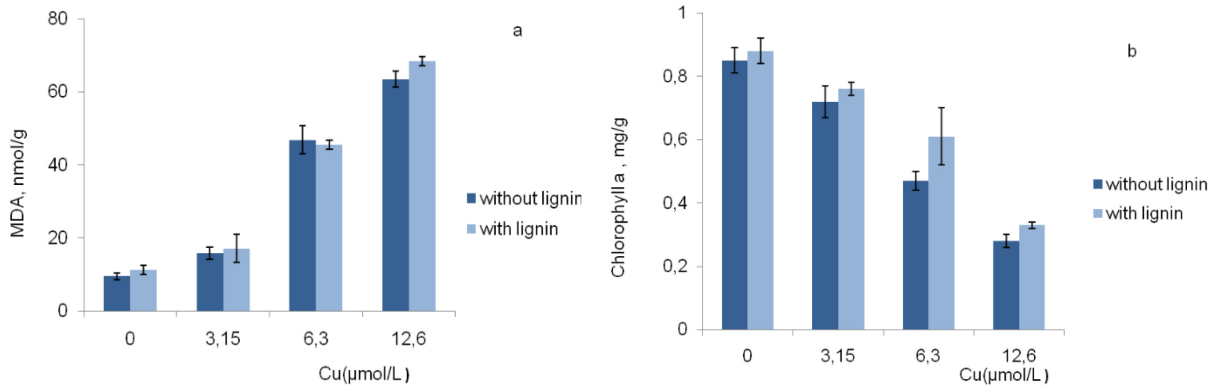


Fig. 6. Contents of MDA (a) and chlorophyll *a* (b) in plants without treatment and with pretreatment with aqueous lignin solution (10^{-5})

Conclusion

The basic possibility of using exogenous lignin to protect plant organisms from excessive amounts of copper is demonstrated using the example of the aquatic plant duckweed (*Lemna minor* L.). A lignin sample isolated from a marsh plant (*Ledum palustre* L.) was used as a protective biopolymer. The lignin studied has been shown to have good antioxidant activity. The values of the main biomarkers (growth rate, level of damage, frond area, content of malondialdehyde and chlorophyll) were determined. We determined that the specific growth rate of duckweed after pretreatment with water-soluble lignin increased in all variants of exposure with different Cu^{2+} concentrations relative to plants not treated with lignin. In addition, we showed that exposure to lignin could reduce the proportion of plants with chlorosis and/or necrosis. Since laboratory plants showed increasing total frond area, an increase in growth rate and a decrease in the level of damage, we concluded that treatment of duckweed with water-soluble lignin resulted in increasing plant resistance to copper stress at the population level. The obtained data indicate adaptive and chemical protective properties of lignin under conditions of exposure to the copper stress factor.

Funding

The study was carried out at the expense of a grant from the Russian Science Foundation No. 22-13-00196-P, https://rscf.ru/en/project/22-13-00196/.

Conflict of Interest

The authors of this work declare that they have no conflicts of interest.

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Received September 18, 2025

Revised October 15, 2025

Accepted November 24, 2025

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