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Review

Plant–Microbe Interactions under the Action of Heavy Metals and under the Conditions of Flooding

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Abstract: Heavy metals and flooding are among the primary environmental factors affecting plants and microorganisms. This review separately considers the impact of heavy metal contamination of soils on microorganisms and plants, on plant and microbial biodiversity, and on plant–microorganism interactions. The use of beneficial microorganisms is considered one of the most promising methods of increasing stress tolerance since plant-associated microbes reduce metal accumulation, so the review focuses on plant–microorganism interactions and their practical application in phytoremediation. The impact of flooding as an adverse environmental factor is outlined. It has been shown that plants and bacteria under flooding conditions primarily suffer from a lack of oxygen and activation of anaerobic microflora. The combined effects of heavy metals and flooding on microorganisms and plants are also discussed. In conclusion, we summarize the combined effects of heavy metals and flooding on microorganisms and plants.

Keywords: interaction of plants and microorganisms; flooding; heavy metals; phytoremediation

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1. Introduction

Unfavorable environmental factors have a negative impact on living organisms. One of the serious consequences of unfavorable environmental factors is the reduction of biodiversity and changes in the relationships between plants and microorganisms. Currently, global warming is of particular concern, which, according to most environmental scientists, may exacerbate other environmental problems [1,2].

According to one hypothesis, global warming can lead to variable rainfall patterns, causing floods or droughts in different regions of the planet [1]. However, there are serious concerns about climate change caused by the rise in the world ocean level, which will result in the flooding of adjacent areas with cities and settlements located on them [2]. Indeed, according to several authors, anthropogenic climate change led to an increase in flooded areas of northern Eurasia and other regions in 2010–2013 [3]. The flooding of the largest cities on Earth, such as London, New York, Tokyo, St. Petersburg, and others, as well as increasing storm surges and the frequency of flooding are all very real [4].

A number of scientists believe that flooding can increase average concentrations of heavy metals in the soil [5]. Floods have been shown to have different effects on heavy metal content in the soil; however, regular floods can contaminate the entire ecosystem, making it less suitable for agricultural activities [6]. Thus, the problems of flooding and soil contamination with heavy metals are becoming increasingly urgent.

The aim of this review was to study the effects of heavy metals and flooding on plants and microorganisms and their interactions with each other.

2. Effects of Heavy Metals on Plants and Microorganisms

The prolonged influence of heavy metals in the environment poses a threat to various populations of plants and microorganisms affecting biocenoses and putting the integrity of ecosystems at risk. High concentrations of heavy metals are typical not only for the soils of areas of ore metal deposits but also for other ecosystems. For instance, heavy metals, along with deicing agents, are priority pollutants of the soil in urban ecosystems and have an adverse effect on plants [7,8].

Contamination by Cu, Pb, Zn, and Cd is common in urban soils and urban road dust [9,10]. Heavy metals reduce ornamental qualities and significantly limit the diversity of plant species and varieties used in urban areas. This is a serious ecological problem, so issues of increasing plant tolerance to the urban environment are an important field of biological sciences [11,12].

Plants that are not resistant to heavy metals show altered metabolism, reduced growth, biomass production, and yields [13]. High concentrations of heavy metals in the soil have a strong negative impact on plant biodiversity. The number of cereals, legumes, and compositae is decreasing, while other species (including ruderals) are affected to a lesser extent [14].

When studying the effects of various mining land restoration measures on plant diversity, eight families and 10 species of surviving plants were observed, with most of them being herbs [15,16]. Heavy metal pollution can also affect microbial communities causing changes in their structure and biodiversity [17].

Differences in the abundance of fungi, as well as in the composition of communities and the relationship of soil bacterial and fungal communities between the soils of urban and suburban parks were noted. Soil-available Zn played an important role in the formation of bacterial and fungal community structures in the park soils of Shanghai [18].

The metal resistance depends on the type of microorganism and the specific metal. Bacterial communities show different reactions to soil contamination depending on the metal. A negative dose-dependent response was found for Cu but not for Cd on the diversity of bacteria in the environment [19].

Consortia may show greater tolerance to heavy metals than pure cultures [20].

3. The Influence of Heavy Metals on Plant–Microorganism Interactions

There are various works describing the interaction between plants and microorganisms under the high content of heavy metals in the soil.

Plants release a variety of compounds that attract and stimulate soil microbial communities. *C. ambrosioides* feeds a diverse bacterial community in its rhizosphere soils [21]. *Pseudomonas* and *Arthrobacter* predominated among the metal-resistant bacteria [21]. Plant root exudates are useful sources of nutrients and energy for soil microorganisms [22].

Some microorganisms stimulate plant growth in soils through the production of important substances for the growth of plants, including the solubilization/transformation of minerals (phosphorus, potassium nitrogen, and iron), synthesis of phytohormones, siderophores and specific enzymes, as well as indirectly by controlling plant pathogens or inducing systemic plant resistance to them [22,23].

Plant growth-promoting microorganisms can modify the bioavailability of metals in the soil through different mechanisms, such as acidification, precipitation, chelation, complexation, and redox reactions [22].

Studies are being conducted to show the effects of microorganisms on plant growth. Copper-resistant rhizobacteria isolated from *Elsholtzia splendens* exhibit growth-enhancing features [24].

Bacterial isolates from *Bacillus cereus*, *B. atrophaeus*, *B. pumilus*, *B. amyloliquefaciens*, *B. tropicus*, *B. subtilis*, *B. halotolerans*, *B. vallismortis*, and *Enterococcus mundtii* have plant growth promoting properties and can improve soils contaminated with heavy metals [25].

Rhizobacteria produce siderophores that promote the uptake of trace elements by the rhizosphere and the production of organic and inorganic acids, thereby affecting the bioavailability of trace elements and plant-induced systemic tolerance to limit metal accumulation in the crops [26].

Siderophore-producing bacteria actually supply plants with nutrients, especially iron. The benefits of combining metal-tolerant siderophore-producing bacteria with plants in order to remove metals from contaminated soils are demonstrated. Perhaps the bacterial root microbiota stimulated by secreted coumarins is an essential mediator of plant adaptation to iron-deficient soils [27,28].

A number of isolated rhizosphere bacteria from the mine tailings containing high concentrations of heavy metals capable of stimulating plant growth showed the greatest capacity for nitrogen fixation and produced indolylacetic acid, gibberellins, siderophores, and lytic enzymes [29]. An improvement in plant growth with the presence of heavy metals in the soil is possible due to the bacterial enzyme 1-aminocyclopropane-1-carboxylate deaminase. It was revealed that the inoculation of plants with the bacteria-producers of 1-aminocyclopropane-1-carboxylate deaminase had a positive effect on their growth under stress [30].

Therefore, plant growth-promoting bacteria play a key role in growth regulation through the synthesis of phytohormones, plant nutrient uptake, and the relief of abiotic and biotic stress, which helps plants to tolerate high concentrations of heavy metals [31].

4. Interaction between Plants—Hyperaccumulators of Metals and Microorganisms

A plant's resistance to metals depends on the type of plant and the specific metal. For centuries, plants in biogeochemical provinces have been adapting to metals. Metallophytes are plant species that are able to survive in metal-rich soils.

Some plant species are capable of hyperaccumulating metals or metalloids to several orders of magnitude higher than other species. Metallophytes are often found in mining areas where soils are enriched with metals. There are many works on studying these plant species. Three species of metallophytes from mineral wastes in the copper–cobalt zone of Zambia were studied: *Persicaria capitata*, *P. puncata* (Polygonaceae), and *Conyza cordata* (Asteraceae) [32].

Silene vulgaris is a metallophyte of calamine, cupreous, and serpentine soils throughout Europe [33]. The roots of metallophytes are effective absorbers of trace elements via interactions in the rhizosphere. Bacteria and fungi in the rhizosphere of the hyperaccumulator can exhibit increased tolerance to metals, stimulate plant growth, and have a significant effect on plant micronutrient concentrations [34]. The rhizosphere of metallophytes can provide a nutrient-rich microenvironment that allows certain microbial communities to thrive or contribute to metal tolerance [35]. *Pseudomonas fluorescens* accelerates the reverse and distant transport of cadmium and sucrose in the hyperaccumulator plant *Sedum alfredii* [36].

One of the solutions to the problem of heavy metal pollution could be a proper understanding of hyperaccumulator plants and their interactions with microbes [37].

5. The Use of Plant–Microbe Interactions in Phytoremediation

The effect of microorganisms on plant metal accumulation varies. Sunflower plants grown in soils with bacteria adapted to heavy metals are able to accumulate about 1.7–2.5 times more Zn and Cd, respectively, in shoots [38]. A study of the interaction between plants and *Aspergillus awamori* showed that the fungus had no effect on cotton's Cd uptake [39]. It has been concluded that cotton is classified as a Cd-excluding plant [39].

Tungsten-resistant bacteria increased the tungsten transfer from root to shoot in lettuce (*Lactuca sativa* L.) [40]. The interactions between plants and beneficial rhizosphere microorganisms can increase biomass production and plant resistance to heavy metals, making microorganisms an important component in phytoremediation technology [35].

Phytoremediation is a plant-based method of cleaning soil, water, and atmospheric air. In recent years there has been a great deal of interest in phytoremediation for the purification of soil from toxic metals using plant growth-promoting bacteria. Such phytoremediation includes rhizosphere bacteria, endophytic bacteria, and bacteria facilitating phytoremediation by other means [41]. Rhizosphere bacteria are involved in the process of metal absorption. For example, ten rhizosphere isolates (*Janthinobacterium*, *Streptomyces*, *Agromyces*, and others) derived from heavy metal accumulating willows were analyzed. *Streptomyces* AR17 increased Zn and Cd uptake. *Agromyces* AR33 stimulated plant growth and, as a result, increased Zn and Cd uptake from the soil [42]. Another option for bioremediation is to reduce the toxicity of heavy metals by transferring (converting) them from one valence to another, as in the case of chromium, in which the Cr (VI) valence is more toxic to living organisms than Cr (III) [43].

Here are more examples of interaction between plants and microorganisms to decontaminate soil from heavy metals. For example, due to improper phosphate mining strategies, wastelands containing significant amounts of residual insoluble phosphate and various heavy metals such as lead (Pb), chromium (Cr), cadmium (Cd), and arsenic (As) occur. The use of plant–microbe interactions is optimal for soil improvement under these conditions. In Zheng et al. [44], the combined use of *Bacillus megaterium* PMW-03 and *Pteris vittate* led to a decrease in Cr (VI) content. In addition, the PMW-03 strain also promoted *Pteris vittata* growth by secreting indoleacetic acid (IAA) and siderophores, stimulating chlorophyll production in *Pteris vittata*, increasing soluble phosphate concentration, and reducing Cr(VI) concentration in the roots [44]. The lead content reduction was achieved by combining the *Pseudomonas* sp. LA strain coupled with ryegrass (*Lolium perenne* L.) and sonchus (*Sonchus oleraceus* L.) [45]. In the other study, the excessive phosphate content was eliminated with two native phosphate-solubilizing microorganisms (PSM) (*Trichoderma asperellum* LZ1 and *Serratia* sp. LX2) and two native plants (*Lolium perenne* L. and *Lactuca versicolor*) [46].

Alfalfa coinoculated with *Paenibacillus mucilaginosus* and metal-resistant rhizobium *Sinorhizobium meliloti* can increase plant growth and copper uptake in the soil [47].

Arabidopsis halleri accumulated more cadmium and zinc when grown in untreated soil than in a gamma-irradiated one (gamma irradiation changed the composition of the soil microbial community strongly) [48]. Plant–microbe interaction can be applied to the elimination of various metals from the soil.

The integration of plants and microbes increased total Cd removal without hindering plant growth while improving photosynthetic capacity [49]. An understanding of the bacterial rhizobiome of hyperaccumulators may contribute to the development of optimized phytoextraction for metal-contaminated soils [50].

The usage of plant–microbe interaction for the transfer of chemical compounds into a less mobile and active form (phytostabilization) is highly relevant. Phytostabilization can be used as an environmentally friendly and cost-effective method of mine rehabilitation and ecological restoration [51]. An increase in plant species diversity is possible due to phytostabilization. *Erica australis*, for example, can promote the rooting of less resistant *Nerium oleander* species by phytostabilization [51]. The application of phytostabilization can also increase microbial diversity [52].

Phytostabilization of mine tailings contaminated with heavy metals is of great interest. Unvegetated open mine tailings are a global environmental problem and a source of pollution for nearby communities [53].

The arbuscular mycorrhizal fungus *Funneliformis mosseae* (Nicol. and Gerd.) Gerd and Trappe, the native bacterium *Bacillus cereus* Frankland and Frankland in combination with an organic additive can be used to phytostabilize *L. spartum* cultivated on a tailing dump, due to the ability of increasing plant tolerance to heavy metals [54].

Lead phytoextraction is not a viable recovery option, however, but phytostabilization can be an effective recovery tool under a variety of conditions [55].

Plant-growth-stimulating rhizobacteria proved to be effective in reducing Pb mobility and can be effectively used for its phytostabilization [56].

A saprophy fungus *Lewia* sp. can improve the Pb-phytostabilization of *D. viscosa* in soils contaminated with soluble and insoluble forms of Pb [57]. The use of plant–microbial interaction makes it possible to reduce the amount of fertilizers during phytoremediation.

The application of legume–rhizobium symbiosis for phytoremediation increases plant coverage (and then phytostabilization) of contaminated areas without requiring costly nitrogen fertilization of the soil [58] The studies on crop combination and its effect on phytoremediation are of current interest. The effect of crop matching systems *Brassica napus* L., *Brassica juncea* L., and *Sedum alfredii* using 16S rRNA gene sequencing on rhizosphere microbiota composition and cadmium accumulation in shoots was shown.

The use of heavy-metal-resistant, plant-stimulating microbes and their interaction with plants for the remediation of contaminated soil may be a relevant approach moving forward [59].

The economic importance of using phytoremediation to clean up agricultural areas should be noted. Phytoremediation is of great interest to many farmers affected by soil contaminated with heavy metals, which was confirmed by a survey according to which farmers in China were willing to remediate contaminated soil and preferred phytoremediation [60].

There is a possibility of combining phytoremediation and the cultivation of agricultural crops, which increases its economic attractiveness. Yet combinations of soil types, plant species/varieties, and agronomic practices must be taken into account, along with the careful monitoring of contaminants [61].

Thus plant–microbe interactions can significantly increase the efficiency of phytoremediation (Table 1) and have important practical applications (Table 2).

Table 1. Possible influences of microorganisms on plants in phytoremediation technologies.

Effect on plant growth
Reducing the toxicity of heavy metals
Increasing plant resistance to heavy metals
Effect on the accumulation of heavy metals

Table 2. Examples of the practical use of plant–microbe interactions in phytoremediation of soils.

Increasing plant species diversity
Phytoremediation of mine tailings
Phytoremediation of agricultural soils

6. The Effect of Flooding on Plants

Most of the pore spaces in the soil surrounding the soil particles are filled with air. There is a free gas exchange between the soil and the atmosphere, which allows oxygen to diffuse rather quickly into the root system of plants. During flooding, water penetrates through the pores, displacing air from them. Since oxygen in water is 30 times less than in the air and its diffusion coefficient in water is 10,000 times less than in a gas atmosphere, the oxygen disappears from the soil water within a few hours or a number of days when it is flooded [62–64]. The activity of aerobic microorganisms also contributes to the rapid removal of oxygen from the soil. This leads to the development of hypoxia and normal breathing of the roots and other underground organs becomes impossible. Here we should also note our works on flooding, which have shown that the main factor affecting plants is precisely oxygen deficiency [65–67].

Normal growth and development of various plant species are usually possible at an oxygen concentration above 10% and the limit of existence is restricted to 5% [68]. Hypoxic conditions are created when aerobic respiration is limited to an oxygen concentration in the range of 1–5% [69]. Although plant hypoxia can occur under a variety of conditions, it is most acute for roots or seeds in overwatered soils [70]. Since in most cases plants react negatively to flooding, it leads to the fact that in some years there is the mass death of both agricultural plants and plants of wild flora, which causes significant economic damage. Thus, the loss of a wheat crop due to flooding can be up to 50%, which, however, depends on the duration of the flood, wheat genotype, stage of growth, and soil composition [71]. The growth processes tend to slow down with a limited oxygen supply, while the response to hypoxia is immediate [72]. The root system suffers first and foremost, which is mainly expressed in the inhibition of the growth of primary roots [73]. Along with the retardation of the length growth of the main root, there are morphological changes in the root system: the growth of adventitious roots is stimulated and the growth of lateral roots is inhibited [74]. Adventitious roots improve nutrient uptake and plant adaptability, especially during prolonged flooding [75]. The formation of adventitious roots under flooding can occur either de novo, or from preformed primordia, or by a simultaneous combination of these two [76–79]. Apart from the intensity and duration of flooding, the growth rate of adventitious roots is also affected by ambient temperature. Hence, the formation of adventitious roots in *Solanum dulcamara* began 2–3 days after the beginning of partial immersion with an average flood water temperature of 20 °C [78], and only seven days later with an average temperature of 12.9 °C [80]. If plants are flooded, the direction of root growth changes, i.e. the roots begin to exhibit aerotropism [73]. The adaptive value of this phenomenon is obvious; the roots begin to grow laterally, which allows them to avoid the deeper, and therefore less oxygenated, layers of the soil. One of the key morphophysiological modifications that promote plant adaptation to flood conditions is the formation of aerenchyma. Aerenchyma is a plant tissue that forms spaces in leaves, stems, and roots, providing a gas exchange. The formation of aerenchyma is the mechanism with which the internal supply of oxygen can be significantly increased, as oxygen diffuses much faster in the gas atmosphere of the aerenchyma cavity than in the liquid medium [81]. Aerenchyma is divided into primary and secondary, depending on the way it is formed [82,83]. The primary aerenchyma is formed in the primary tissue of some grains, such as rice [84] and corn [85,86], and is further classified into two types depending on its formation (lysigenous and schizogenous). Lysigenous aerenchyma is formed as a result of programmed cell death, while schizogenous aerenchyma is formed as a result of cell division and differentiated cell expansion. Secondary aerenchyma is a tissue of secondary origin and differentiates from phellogen (cork cambium), cambium, or pericycle, and can produce either a porous secondary cortex or aerenchymatous phellema in stems, hypocotyls, and roots. The formation of secondary aerenchyma in adventitious roots and root nodules of some legumes, such as soybean, has been well studied [87].

The flooding of the root system indirectly affects the growth and development of the above-ground parts of plants. In this case, the impact depends on the strategy of the plant to maintain viability in these adverse conditions. Under flooding, several plants accelerate their shoot growth by elongating their coleoptiles, petioles, and stems. In this way, at least a part of the plant remains above water. Both wild plants such as *Rumex palustris* [88] and agricultural plants such as rice [89] use this strategy of accelerated shoot growth. Some plants use a quiescence strategy based on the inhibition of growth during flooding [90]. This strategy allows the plant to reduce energy requirements, delay carbohydrate starvation and maintain viability until the normalization of growing conditions, which is especially critical during temporary total immersion [91].

To conclude this section, it is necessary to say that the flooding of agricultural areas causes significant damage not only to wildlife but also to farms. Farmers have currently developed a number of measures to help reduce the negative effects of flooding. These measures include changing crop varieties, changing the timing of sowing and harvesting, creating shelterbelt forests, etc. [92].

7. Effects of Flooding on Microorganisms

Populations of soil microorganisms are very sensitive to abiotic disturbances including soil flooding. Low oxygen content leads to the activation of anaerobic microflora [93] since microorganisms can use not only oxygen but also other compounds as a terminal electron acceptor. As a result of anaerobic metabolism, CH_4, H_2, H_2S, SO_2, CO_2, and low-molecular organic acids are formed. At the same time, CH_4 emissions from flooded soils are of global environmental significance. Thus, according to some authors [94], CH_4 emissions from submerged rice fields alone can account for up to a quarter of total biogenic CH_4. Since

CH_4 is one of the major greenhouse gases [95], its uncontrolled release carries possible risks associated with global warming. In turn, global warming could lead to an increase in extreme rainfall events, resulting in an increase in the frequency and duration of floods [96]. As a result of the activity of denitrifying bacteria, a large amount of nitrogen is lost due to its conversion into molecular nitrogen and nitrogen oxide compounds [64].

The microbial communities, aside from hypoxic conditions, react keenly to changes in pH resulting from flooding [97]. Numerous authors consider pH change to be a key determinant of soil microbiota composition in a wide range of ecosystems [98,99].

These factors lead to a change in the quantitative and qualitative ratio in the soil microbiota, significantly increasing the number of bacterial taxa capable of anaerobic respiration within the *Firmicutes* and *Desulfobacterota* phyla, and reducing the proportion of representatives of the *Actinobacteria* and *Proteobacteria* phyla [100]. Flooding increases the diversity of bacteria from the genera *Geobacter* and *Clostridium*, which are strictly anaerobic bacteria characteristic of waterlogged soils [101].

Nevertheless, it is believed that changes in the population ratios of soil microorganisms, as well as the appearance of new, or disappearance of a number of previously typical taxa during temporary flooding, do not lead to a disturbance of the stability of the soil microbiota in the long term. Thus, the work of Shah et al. [102] illustrates the complete recovery of the taxonomic composition of soil microflora within three weeks after the completion of the 15-day flooding. One of the mechanisms that provide such stability may be the process of formation of endospores by bacteria and the switch to anaerobic respiration for facultative anaerobes [103].

8. The Effect of Flooding on the Interaction of Plants and Microorganisms

The soil microbiome is represented by the coexistence of diverse populations of microorganisms, some of which play various roles in plant life. There are microorganisms that stimulate plant growth, perform nitrogen fixation, increase the amount of available nutrients by degradation of hard-to-degrade polymers, inhibit the development of phytopathogens, or, conversely, are phytopathogens themselves [104]. The rhizosphere microbiome directly affects plant growth and health [105]. In turn, plants affect the composition, ratio, and activity of rhizosphere microflora via root exudates and rhizodeposits [106,107]. Plants release into the rhizosphere about 11% of the carbon taken up during photosynthesis [108]. Root exudates include sugars, amino acids and amides, organic acids, and aromatic and phenolic acids [109]. The quantity and quality of root excretions depend on the age, health, environmental conditions, abiotic or biotic stresses, and variety of different species and even plant cultivars [110,111]. This may be a determining factor leading to a difference in the microbial communities of the rhizosphere in different plant varieties [112].

The significant morphophysiological changes mentioned above and largely related to the root system occur in plants under the influence of flooding. Root system stress, in turn, leads to changes in the quantity and quality of exudates, resulting in changes in the composition of the plant soil microbiome [113,114]. A common consequence is a reduction in potentially beneficial microorganisms for plants [100]. In this paper it was shown that flooding led to a decrease in the root microflora of various potentially useful taxa of microorganisms, such as: *Streptomyces*, *Spinghomonas* and *Flavobacterium*, able to dissolve phosphates, secrete siderophores, affect the production of phytohormones; *Saccharimonadia*, capable of increasing nitrogen assimilation efficiency, *Massilia*, producing proteases, siderophytes and auxins [100].

Structural changes in soil microflora can also have a direct impact on plants during flooding. Some species of the *Clostridium* genus have been shown to cause soft rot disease in some vegetable crops, and their numbers are greatly increased during heavy rains and floods [115]. The other changes in the soil microbiota can affect plants indirectly. Thus, substances like CH_4, H_2S, and SO_2 produced by anaerobic microflora during flooding can be phytotoxic, and their accumulation in the soil can lead to damage to the root system.

Plant–microbe interactions are not limited only to the root system. Microorganisms colonizing leaves and other niches can also affect the change in plant phenotype [116]. This impact is not limited to pathogens infecting the leaves. Some leaf microorganisms can have a positive effect on plants, namely to stimulate their growth and immune system and to increase their resistance to biotic and abiotic stresses [117,118]. While leaf microflora tends to be seasonally dependent, even such a factor as soil composition can affect it [119–121]. A recent study has shown that flooding negatively affects wheat leaf microflora in the early stages of its development [119]. Meanwhile, the bacterial communities of leaves of both flooded and control variants at later stages of growth had a high degree of similarity. Possible reasons for this could be a more severe suppression of young plants during flooding, or that in young plants the leaf microbiota is still in its formative stage. However, the detailed mechanisms of this relationship have yet to be elucidated.

9. Effects of Heavy Metals and Flooding on Plants and Microorganisms

According to a number of studies, flooding increases the content of heavy metals in the soil, as a result of its erosion. However, first of all, it is necessary to take into account the resistance of plants to flooding if we are speaking about plants that are resistant to flooding and forming aerenchyma, through which the transport of oxygen to the parts of the plant located underwater takes place. This airflow can be so intense that an aerobic zone is created around the roots, in which aerobic microorganisms are multiplied, thereby reducing the toxic effects of heavy metals on the plants [113,122].

Particular attention was paid to plant exudates, which can affect both negatively and positively the mobility of metals and the ability of plants to absorb them [123]. Exudates (various organic compounds) of a number of plants create conditions for the development of microorganisms under flooding conditions [123]. It should be noted that many aquatic plants such as *Phragmites australis* [124], *Typha latifolia*, *Typha angustifolia* [125], and *Cyperus articulatus* L. [126] have a high ability to accumulate heavy metals. Plants typically use two pathways of phytoremediation: phytostabilization, when heavy metals are stored in the roots, and phytoextraction, when heavy metals accumulate in the above-ground part of the plant [127].

It is worth mentioning that the interaction between plants and microorganisms in conditions of flooding and heavy metals has not been studied enough. However, such studies are necessary within the context of global climate change.

10. Conclusions

High concentrations of heavy metals and flooding have adverse effects on plants and microorganisms in the soil. Plants release a variety of compounds that attract and stimulate soil microbial communities.

A number of microorganisms stimulate plant growth in the soil by producing essential substances for it, reducing the adverse effects of heavy metals, and increasing tolerance to them. In this way, the interaction of plants and microorganisms can significantly improve the effectiveness of phytoremediation. The study of the interaction between plants and microorganisms at high concentrations of heavy metals in the soil is not only of great scientific ecological importance, it can also be used for practical purposes. Remediation of polluted soils by reducing heavy metal concentrations increases the diversity of plant species, whereas the number of cultivated species increases considerably on agricultural soils. One of the leading trends in bioremediation can be soil purification from heavy metals by the interaction of plants and microorganisms.

Plants and microbes in the conditions of flooding are primarily affected by the lack of oxygen and activation of anaerobic microflora. Flooding can cause both environmental and economic damage. The problem of soil flooding is becoming more urgent as a result of global warming. This environmental problem is becoming a worldwide one. For that reason, studying the effects of flooding on plants and microorganisms and their interactions is of great interest to modern ecology.

Flooding and heavy metals, as environmental hazards, can be interlinked. Flooding can increase the heavy metal content in the soil, thus increasing the negative impact on plants. The interaction of plants and microorganisms under conditions of flooding and exposure to heavy metals has not been studied sufficiently. However, such research is needed in the context of global climate change and is the closest research.

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