Plant-Microbe Interactions in Flood Conditions

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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.

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1. 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 [1][2][3]. 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 the researchers should also note their works on flooding, which have shown that the main factor affecting plants is precisely oxygen deficiency [4][5][6].

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% [7]. Hypoxic conditions are created when aerobic respiration is limited to an oxygen concentration in the range of 1–5% [8]. Although plant hypoxia can occur under a variety of conditions, it is most acute for roots or seeds in overwatered soils [9]. 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 [10]. The growth processes tend to slow down with a limited oxygen supply, while the response to hypoxia is immediate [11]. The root system suffers first and foremost, which is mainly expressed in the inhibition of the growth of primary roots [12]. 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 [13]. Adventitious roots improve nutrient uptake and plant adaptability, especially during prolonged flooding [14]. The formation of adventitious roots under flooding can occur either de novo, or from preformed primordia, or by a simultaneous combination of these two [15][16][17][18]. 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 [17], and only seven days later with an average temperature of 12.9 °C [19]. If plants are flooded, the direction of root growth changes, i.e. the roots begin to exhibit aerotropism [12]. 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 [20]. Aerenchyma is divided into primary and secondary, depending on the way it is formed [21][22]. The primary aerenchyma is formed in the primary tissue of some grains, such as rice [23] and corn [24][25], 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 [26].

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* [27] and agricultural plants such as rice [28] use this strategy of accelerated shoot growth. Some plants use a quiescence strategy based on the inhibition of growth during flooding [29]. 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 [30].

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. [31].

2. 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 [32] 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 [33], 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 [34], 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 [35]. 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 [3].

The microbial communities, aside from hypoxic conditions, react keenly to changes in pH resulting from flooding [36]. Numerous authors consider pH change to be a key determinant of soil microbiota composition in a wide range of ecosystems [37][38].

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 [39]. Flooding increases the diversity of bacteria from the genera *Geobacter* and *Clostridium*, which are strictly anaerobic bacteria characteristic of waterlogged soils [40].

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. [41] 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 [42].

3. 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 [43]. The rhizosphere microbiome directly affects plant growth and health [44]. In turn, plants affect the composition, ratio, and activity of rhizosphere microflora via root exudates and rhizodeposits [45][46]. Plants release into the rhizosphere about 11% of the carbon taken up during photosynthesis [47]. Root exudates include sugars, amino acids and amides, organic acids, and aromatic and phenolic acids [48]. 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 [49][50]. This may be a determining factor leading to a difference in the microbial communities of the rhizosphere in different plant varieties [51].

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 [52][53]. A common consequence is a reduction in potentially beneficial microorganisms for plants [39]. In this research 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 [39].

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 [54]. 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 [55]. 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 [56][57]. While leaf microflora tends to be seasonally dependent, even such a factor as soil composition can affect it [58][59][60]. A recent study has shown that flooding negatively affects wheat leaf microflora in the early stages of its development [58]. 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.

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