Plant–Microbe Associations in Phytoremediation

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Abstract

Microorganisms are important partners with plants in phytotechnology applications. Plant–microbe relationships in phytoremediation include those of rhizobacteria which colonize root surfaces and biodegrade organic contaminants and other organic matter; endophytic bacteria that colonize the inner surface of plant stems and biodegrade organic compounds; and plant growth-promoting bacteria (PGPB) that have beneficial effects for plants. Plants produce organic substrates for the microbial populations. Because of root exudates, there are healthy numbers of bacteria near root surfaces that help with nutrient cycling and other ecosystem services. There is an emphasis on plant–microbe associations with *Miscanthus*; studies are conducted with and without PGPBs in soils contaminated with metals. Effects of PGPBs on bioconcentration factor and translocation factor are reported for *Miscanthus* growing in metal-contaminated soil.

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Microorganisms play key roles in soil ecosystem functions and supply important services, especially organic matter mineralization, nutrient cycling, and contribution to formation of humic substances (Blagodatskaya & Kuzyakov, 2013). Microorganisms associate with all parts of plant and form various interactions (Arora, 2013), and the term holobiont is used to stress the ubiquity of plant–microbe interactions (Hassani et al., 2018). The plant–microbe cooperation can be classified by various criteria, and the crucial benchmark is the profit which plant gains from such interactions which usually are neutral or positive (with mutualistic or symbiotic microorganisms); however, sometimes they could be negative (with parasitic or pathogenic microorganisms).

The symbiotic microorganisms can be classified as endosymbionts (living inside plant) or exosymbionts (living on the surface of plant). Symbiosis is a both-side positive relationship; nevertheless it is always described as “give cheap and take expensive”, i.e., partners invest their surpluses and cover insufficiencies from the partner. Plants, as photoautotrophic organisms, mainly supply organic substances produced during photosynthesis. Indeed, microbial partners, often heterotrophic, consume them, provide to plants mineral nutrients (like fixed nitrogen or available phosphate), and protect against parasites or regulatory substances (Arora, 2013).

The effectiveness of phytoremediation depends on soil contamination level and historical background of soil exploitation. It also depends on the presence and accessibility of contaminants in the rhizosphere, their bioavailability to plant’s root system, and the ability of plant–microbe association to intercept, absorb, accumulate, and/or degrade the contaminants (Vangronsveld et al., 2009). The plant–microbe associations are used to increase contaminant bioavailability and mobility in different environmental matrices (soil, water, wetlands, etc.) (Alkorta et al., 2004; Chu & Chan, 2003; Epelde et al., 2008; Mukherjee & Zimmerman, 2013). Contaminants inhibit plant growth and development and thereby reduce the phytoremediation effectiveness (Thion et al., 2013). In order to overcome this reduction, the plant–microbe partnership is used (Mitter et al., 2016). For example, the use of the C65 strain allowed *Populus euphratica* to more efficiently extract zinc from the contaminated environment, facilitating growth inhibition caused by heavy metals (Zhu et al., 2015).

7.1 Role of Plant–Microbe Association in Phytoremediation

The numerous studies are focused on using microorganisms (rhizo- and endophytic bacteria) for increasing the efficiency of phytoremediation technology and stimulating the plant development (Mitter et al., 2016). The main part of the research has been done in greenhouse conditions, while *in situ*

field experiments have been rare (Glick, 2010; Guo & Chi, 2014; Kidd et al., 2017; Muratova et al., 2003a; Ren et al., 2019).

Rhizobacteria colonize the roots' surface while endophytic bacteria colonize the inner surface of stem without harming the plant, and both of the microorganisms are susceptible to biotic and abiotic factors. Another advantage of endophytes is that microorganisms are able to degrade the organic pollutants commonly widespread in endophytic populations. Endophytes can reduce the pollutants' phytotoxicity and the evaporation of volatile organic compounds (Shehzadi et al., 2014). Since endophytes are present inside the plant, they can interact more closely with the host plant in comparison with rhizobacteria. Before entering to plant, endophytes have to settle in rhizosphere and to attach to root surface. Organic compounds, i.e., root exudates, act as signals for the chemotactic movement of bacteria. During the transition from the plant rhizosphere to the endosphere, colonizing bacteria have to be able to quickly adapt to very different environment, i.e., pH, osmotic pressure, carbon source, and oxygen availability. They also have to overcome the plant's protective response to invasion, that is, the reactive oxygen species production, which causes stress for invasive bacteria. The important advantage of applying the endophytic degraders in phytoremediation technology is that any toxic xenobiotic absorbed by the plant can decompose inside the plant, thereby reducing the phytotoxic effect and eliminating any toxic effects on the herbivorous fauna living in or near contaminated sites (Ryan et al., 2008).

7.1.1 Endophytic Bacteria

Endophytic bacteria were first used to clean soil contaminated with organochloride herbicide 2,4-dichlorophenoxyacetic acid (Germaine et al., 2006). They reduced the accumulation of organic compounds in plant tissues and transpiration value. The improved degradation of pollutants was correlated with increasing the quantity of bacteria which were able to decompose pollutants in the plants. Woody plants: poplar and willow have been used to clean soil contaminated with various organic chemicals (Newman & Reynolds, 2005); inoculation of these plants with endophytic bacteria enhanced plant growth and degradation of various organic compounds. The partnership of different plant species and endophytes has been studied (Afzal et al., 2012; Germaine et al., 2006; Kang et al., 2012; Wang et al., 2010; Weyens et al., 2009; Yousaf et al., 2011), i.e., willow and *Burkholderia* sp. HU001, *Pseudomonas* sp. HU002 for Cd accumulation; poplar and *Enterobacter* sp. PDN3; multiflorum chaff (*L. multiflorum* var. Taurus) and *Pseudomonas* sp. ITRI53, *Pseudomonas* sp. MixRI75 with hydrocarbon degradation; multiflorum chaff (*L. multiflorum* var. Taurus), horned chaff (*L. corniculatus* var. Leo), alfalfa (*M. sativa* var. Harpe) and *Enterobacter ludwigii* with hydrocarbon degradation; poplar and *Pseudomonas putida* W619-TCE; lupine yellow and *Bacillus cepacia* VM1468; corn and wheat and *Burkholderia cepacia* FX2; peas (*Pisum sativum*) and *Pseudomonas putida*; wheat (*Triticum* sp.) and corn (*Z. mays*) and *Enterobacter* sp.

12J1; peas (*Pisum sativum*) and *Pseudomonas putida* VM1450 with the destruction of 2,4-dichlorophenoxyacetic acid. The potential of endophytic bacteria to enhance phytoremediation of soil contaminated with diesel fuel was compared with the potential of rhizobacteria (Afzal et al., 2012; Andria et al., 2009). Endophytes showed higher levels of colonization, especially in roots and shoots, and higher levels of expression of alkane-cleaving genes (alkB and CYP153) than the rhizobacterial strain. Inoculated endophytes colonize both the rhizosphere and the endosphere but are also metabolically active with respect to the decomposition of organic pollutants in soil and in plant itself (Afzal et al., 2014).

7.1.2 Rhizobacteria

The significant role of rhizobacteria in plant life is illustrated (Adesemoye & Kloepper, 2009; Afzal et al., 2014; Hayat et al., 2010; Mitter et al., 2016; Ortíz-Castro et al., 2009; Simpson et al., 2011). Active secretion by root cells of various substances, such as sugars, polysaccharides, amino acids, tricarboxylic acids, oxalic, malic, succinic and citric acids, fatty acids, sterols, phenols, enzymes and proteins, provides nutrients to microorganisms: inside root tissues and to root surfaces (rhizoplane) as well as to rhizosphere in close surroundings of roots (Döbereiner, 1989; Fan et al., 2018; Mitter et al., 2016). Plant exudates contribute to xenobiotic degradation through the following actions (Anderson & Coats, 1995):

- selective increasing in microorganisms destructors;
- increasing metabolism associated with growth;
- induction of joint metabolism with some microorganisms that have genes and plasmids responsible for degradation of pollutants.

Microorganisms secrete phytohormones, small molecules, or volatile compounds that can act directly or indirectly activate plant immunity or regulate plant growth and morphogenesis (Bhattacharyya & Jha, 2012; Glick, 2003; Ortíz-Castro et al., 2009). Indirect stimulation of plant growth is caused by reduction or preventing the harmful influence of phytotoxic compounds. It may include reducing iron prepared for phytopathogens in the rhizosphere; synthesis of enzymes that lyse fungal cell walls; competition with harmful microorganisms for their location on plant roots surface. Direct stimulation of plant growth by bacteria is caused by following factors (Dimkpa et al., 2008; Glick, 2003; Loper & Henkels, 1999; Rodríguez et al., 2006):

- providing plants with substances that are synthesized by bacteria (e.g., microbial nitrogen fixation);
- synthesis of siderophores, which can dissolve and accumulate iron from soil and supply it to plant cells;

- production of various phytohormones, including auxins (e.g., indole-3-acetic acid, cytokinins, and gibberellins) that affect growth;
- dissolution of minerals such as phosphorus which become readily available to plant;
- production of compounds which can influence growth and development, for example, 1-aminocyclopropane-1-carboxylic acid.

In the presence of pathogenic microorganisms, rhizosphere bacteria can synthesize various biocontrol agents (antibiotics, enzymes, siderophores, etc.) that suppress the growth of unwanted microbiota (Loper & Henkels, 1999; Mitter et al., 2016). Being developed on roots, the rhizosphere microbiomes affect plants by converting complex organic substances into accessible forms which stimulate growth and affect the morphology and physiology of plants; production of other specific metabolites, for example, ethylene, which causes early flowering (Glick, 2006).

Plant growth-promoting rhizobacteria (PGPR) are useful free-living rhizosphere bacteria that stimulate the plant's growth and are in association with them; they are found inside and around plant roots (Kloepper & Schroth, 1981; Belimov et al., 2005, 2009). These microorganisms are involved in complex ecological interactions in the rhizosphere, where they can influence plant health, growth, and stress response under unfavorable conditions, since some of them have a high destructive potential for pollutants (Glick, 2003; Hayat et al., 2010; Mitter et al., 2016).

PGPR have been widely used for improving crop development as biologically friendly fertilizers (Adesemoye & Kloepper, 2009; Ortiz-Castro et al., 2009; Simpson et al., 2011; Singh et al., 2011). Later the area of PGPRs application expanded, and they are considered for use in soil bioremediation, since many rhizosphere bacteria belonging to the PGPR group are resistant to pollutants (Costa et al., 2014). PGPRs are involved in processes of metal migration and have converted them to biologically available and soluble forms through effects of siderophores, organic acids, biosurfactants, biomethylation, and redox processes as part of the designed plant-microbial complexes (Ali et al., 2013; Belimov et al., 2005; Oh et al., 2015; Zhu et al., 2015). Effectiveness of phytoremediation depends on the activity of plant microbiome (Afzal et al., 2014; Weyens et al., 2009).

Campanella and Paul (2000) suggested that the root system of *Cucurbita pepo* secretes exudates of protein origin, which play an important role in the biodegradation of organochlorine compounds. Microbial degradation of pesticides mediated by enzyme systems is a promising approach for destruction of these toxic substances (Pascal-Lorber & Laurent, 2011) and assisted in the degradation of 4,4'-dichlorodiphenyl trichloroethane. Due to root exudates, the plant ensures the stable functioning of microorganisms, and they, in turn, contribute to the growth and development of the plant (Doornbos et al., 2012). Synergistic effects caused by interaction of plants and microorganisms

stimulated the phytoremediation of soil contaminated by trace elements and organics: oil, polyaromatic hydrocarbons, polychlorinated biphenyls, organochlorine, nitroaromatic, and organophosphate compounds (Guo & Chi, 2014; Kidd et al., 2017; Muratova et al., 2003b). Through the inoculation of *Populus euphratica* by PGPR strain *Phyllobacterium* sp. C65, which produced auxin, assisted *Populus euphratica* to extract Zn more efficiently (Zhu et al., 2015).

7.2 Impact of PGPB Isolated from Contaminated Soil to Phytoremediation with *Miscanthus*

In order to increase the biomass harvest of *Miscanthus* while growing in contaminated soils (Ben Fradj et al., 2020; Nsanganwimana et al., 2014; Pacheco-Torgal & Jalali, 2011), two main approaches can be used:

- soil treatment by different amendments such as fertilizers, sludge, biosolids, citric acid, Ethylenediamine tetraacetic acid (EDTA), and fungi (Antonkiewicz et al., 2019; Damodaran et al., 2013; Han et al., 2018; Hu et al., 2018; Alasmay, 2020);
- plant rhizome treatment by co-composting, plant growth regulators, and microorganisms (Khan et al., 2017; Leech et al., 2020; Nebeská et al., 2019).

The effectiveness of PGPB in the phytoremediation of metal contaminated soils can be explained by their ability to facilitate the adaptation of host plants to suboptimal soil conditions during stress state; promote plant growth; vary the bioavailability; relieve phytotoxicity in soil by producing amino acids, proteins, and antibiotics; and increase contaminant translocation within the plant (Oves et al., 2013). Also, PGPB can reduce the metals harmful effect by reduction, oxidation, methylation or de-methylation, compartmentalization, and conversion to a less toxic state (Hassan et al., 2017). Zeng et al. (2020) investigated the positive role of extracellular polymeric substances produced by *Bacillus* sp. S3 to detoxify different metals. Ndeddy Aka and Babalola (2016) showed that inoculation of soil by PGPB: *Pseudomonas aeruginosa* KP717554, *Alcaligenes faecalis* KP717561, and *Bacillus subtilis* KP717559 increased the amount of soluble Ni, Cd, and Cr in the soil by 51%, 50%, and 44%, respectively. Ma et al. (2015) researched the phytostabilization potential of PGPB in relation to metal contaminated soils: inoculation by *Pseudomonas* sp. A3R3 improved plant biomass production while *Psychrobacter* sp. SRS8 inoculation increased the accumulation of metals by plants. PGPB and *Miscanthus* sp. association in the metal contaminated soil was researched by Babu et al. (2015) and Schmidt et al. (2018). An endophytic PGPB *Pseudomonas koreensis* was explored for enhancing the production of *Miscanthus sinensis* growing in soil contaminated by As, Cd, Cu, Pb, and Zn (Babu et al., 2015).

Bacillus altitudinis KP-14 (*B. altitudinis* KP-14) is a plant growth-promoting bacterium isolated from postmining metal contaminated soil (Pranaw et al., 2020). The microbiological profile of *B. altitudinis* KP-14 is shown in Figure 7.1. The inoculation of *M. × giganteus* rhizomes by this PGPB led to increasing of plant morphological parameters: aboveground (leaves and stems) and roots biomass increased by 23%, 86%, and 76%, respectively. In addition, artificially contaminated by Pb soil the increase in the root dry weight was detected.

The analysis of metal behavior in artificially contaminated by Pb soil is presented in Table 7.1. Increasing of Pb concentration in soil led to decreasing in Zn and Cu accumulation in roots. The inoculation of *M. × giganteus* rhizomes resulted in increasing uptake of metals from the research soil: Mn (by 103%) > Zn (by 65%) > Sr, Pb (by 50%) > Cu (by 40%). These results can be explained by the ability of PGPB to mitigate metals tolerance (Babu et al., 2015; Schmidt et al., 2018). The metals tolerance mitigation process can be reached by their transformation into bioavailable and soluble form, organic acids, and siderophore production, diminishing phytotoxicity and altering the phytoavailability in contaminated soils (Ma et al., 2016).

The inoculation of *M. × giganteus* rhizomes by the PGPB *B. altitudinis* strain KP-14 significantly enhanced plants' bioparameters and influenced the phytoremediation parameters: increased bioconcentration factor (BCF) and decreased translocation factor (TLF) while it was grown on the metal-contaminated soil. The increasing of BCF values can be explained by the rising of metals mobility; nevertheless, the phytoremediation process that

FIGURE 7.1

The tolerance profile and plant growth-promoting properties of *Bacillus altitudinis* strain KP-14. (Modified from Pidlisnyuk et al., 2020.)

TABLE 7.1

Trace Element Behavior in *M. × giganteus* Tissues during Growth in Artificially Contaminated by Pb Soil

Trace Element	Without <i>B. altitudinis</i> KP-14	With <i>B. altitudinis</i> KP-14
Pb	Mainly accumulated in roots.	Mainly accumulated in roots; translocation to aboveground biomass decreased.
Zn	Mainly accumulated in roots; the share accumulated in aboveground biomass increased from 13% to 20%.	The share accumulated in aboveground biomass increased from 16% to 22%; the share accumulated in roots decreased by 25.4% while the lead content in roots increased.
Cu	Mainly accumulated in roots; Accumulation in stems increased with increasing Pb concentrations in soil.	The share accumulated in stems remained almost the same (2%, 8%, and 4%) with increasing Pb concentration in soil. accumulation in roots increased by 58%–295%. total uptake increased as well (by 60%–238%).
Mn	Mainly accumulated in the aboveground biomass; the share in aboveground biomass (leaves in stems) was varied from 66% to 86%.	The total uptake increased, with increasing Pb concentration in soil, the effect decreased from 62% to 26%; accumulation in aboveground biomass decreased from 64% to 52%.
Sr	It evenly distributed throughout the plant; highest accumulation was in stems; the share in aboveground biomass varied from 50% to 69%.	It evenly distributed throughout the plant; highest accumulation was in the roots; accumulation in aboveground biomass (leaves and stems) reduced from 46% to 27%.

Source: Modified from Pidlisnyuk et al. (2020).

occurred could still be characterized as phytostabilization. The *M. × giganteus* root biomass increased with increasing Pb concentrations to tackle the Pb toxicity in the soil. With regard to the places of accumulation, the metals were divided into three groups: Pb, Zn, and Cu were predominantly accumulated in the roots; the Sr distribution was almost equal within the whole plant; and Mn predominantly accumulated in the leaves and stems.

7.3 Influence of Rhizobacteria Isolated from *Miscanthus* Rhizosphere to Phytoremediation of Trace Elements Contaminated Soil

The rhizosphere plays a significant role in phytoremediation of soil contaminated with trace elements (Jing et al., 2007). PGPRs are of interest among rhizosphere microorganisms (Shrivastava, 2017), because they facilitate the

adaptation of host plants to suboptimal soil conditions during stressful conditions and increase the efficiency of phytoremediation (Hassan et al., 2017; Oves et al., 2013).

The PGPR strain *Agrobacterium* sp. Zn1-18 was used as an inoculant to increase the efficiency of phytoremediation of trace elements contaminated soil using *M. × giganteus* plants. The strain was isolated during the germination period from the rhizosphere of *M. × giganteus* when crop was cultivated in trace elements contaminated postindustrial soil (Table 7.2). Isolated strain showed PGPR properties: the ability to fix atmospheric nitrogen, to dissolve hard-to-reach phosphates, to synthesize siderophores, to produce phytohormone indolacetic acid (IAA), and ability to grow in medium that contains Zn ions up to 4.0 mmol L⁻¹ and Pb ions up to 2.5 mmol L⁻¹.

Agrobacterium sp. Zn1-18 showed a significant effect on the bioparameters of *M. × giganteus* plants: the aboveground biomass of treated crop increased by 50%; the biomass of roots decreased by 77.3% on comparison with control untreated crop. Upon inoculation of *M. × giganteus* rhizome the roots' dry weight decreased by 34.8% while the dry weight of the aboveground biomass, on the contrary, increased by 7.1%. When comparing *M. × giganteus* grown on control and contaminated soils in the presence of PGPR, results revealed that the *Agrobacterium* sp. Zn1-18 increased the productivity of aboveground biomass by 7.1% while reduced the root dry weight. Thus, *Agrobacterium* sp. Zn1-18 promoted the growth and development of *M. × giganteus* on trace elements contaminated post-industrial soils.

TABLE 7.2

The Trace Element Concentrations in the Research Soils

Trace Element	MPC (mg kg ⁻¹)	The Total Trace Element Concentration in Soil (mg kg ⁻¹)	
		Control Soil	Contaminated Soil
V	150	50.5 ± 3.5	60.0 ± 12.0
Cr	6	35.0 ± 2.8	44.0 ± 7.1
Mn	1500	690.0 ± 56.5	810.0 ± 42.4
Fe	n/a	19,600 ± 424	21,450 ± 2,757
Co	5	14.5 ± 0.7	18.0 ± 1.4
Ni	4	32.0 ± 5.6	39.2 ± 2.8
Cu	3	31.0 ± 2.8	31.5 ± 7.7
Zn	55	101.0 ± 12.7	180.0 ± 14.1
As	2	11.5 ± 0.7	22.5 ± 4.9
Sr	7	66.0 ± 1.4	81.3 ± 0.8
Ba	0.1	125.0 ± 21.2	210.1 ± 28.2
Pb	32	20.0 ± 21.2	230.0 ± 44.2
U	n/a	0.8 ± 0.1	1.3 ± 0.2

Depth of soil sampling: 0–60 cm.

MPC, maximum permissible concentration.

The analysis of the abovementioned trace elements content in the roots and aboveground biomass of *M. × giganteus*, when growing on contaminated and control soil with and without inoculation of *Agrobacterium* sp. Zn1-18, showed changes in the phytoremediation process (Figure 7.2). When crop grew in contaminated soil without inoculation of As, Pb, Co, Cr, Cu, V, and U accumulated mainly in the roots; Zn, Mn, and Sr—in the aboveground biomass; Ba and Ni accumulated uniformly in roots and aboveground biomass. When rhizomes were inoculated, phytoremediation potential of *M. × giganteus* changed: content of Zn, Mn, As, Pb, Co, Cr, V, U, and Sr increased in roots, Ni accumulated in all plant parts, Cu accumulated mainly in the aboveground biomass, and for this trace elements accumulation increased by 41% compared to uninoculated system.

The calculated bioaccumulation factor and TLF coefficients (Nurzhanova et al., 2019) showed that inoculation of *M. × giganteus* rhizomes with strain *Agrobacterium* sp. Zn1-18 increased the crop potential to extract As, Mn, Ba, Cu, Cr, Zn, and Sr from soil to aboveground biomass. The TLF values for Mn, Sr, Ba, Zn were ≥ 1 , while for As, Cu, Pb, Co, Ni, V, Cr it was < 1 (Figure 7.2).

Overall using strain *Agrobacterium* sp. Zn1-18 reduced the total content of trace elements in plant tissues which may be due to decreasing of root dry weight which decreased adsorption surface and changed phytoremediation parameters.

FIGURE 7.2
Influence of PGPB on the migration of elements from the *M. × giganteus* root system to the aboveground biomass.

7.4 Changing of Soil Microbial Communities during *Miscanthus* Production at the Contaminated Military Land

The soil from the former military site (Sliač, Slovakia) contaminated by different trace elements was under investigation. *M. × giganteus* showed good growth in this soil during two vegetation seasons (Pidlisnyuk et al., 2018). The changes in soil microbial community, physiological state of soil microorganisms, and metabolic activities were investigated; rhizosphere and bulk soils were distinguished from each other (Nebeská et al., 2018).

During two-years growing period, the most significant changes could be attributed to time: comparison of first growing season vs. second growing season (Table 7.3). The indicators showed slight positive influence of *M. × giganteus* to soil and microbial community, which was documented by increased soil respiration, proportion of the fungal biomass, and decreased microbial stress indicators (*trans/cis* PLFA and *cy/pre* PLFA).

TABLE 7.3

Summary of the Changes of Soil Nutrients, Microbial Community Characteristics and Metabolic Activities during 2-Years Vegetation of *M. × giganteus* in Sliač Soil

Parameter	First Growing Season vs. Second Growing Season	Rhizosphere × Bulk Soil
Available P [mg kg ⁻¹ dwt]	0.27	1.02
Available K [mg kg ⁻¹ dwt]	1.90	0.00
Available Ca [mg kg ⁻¹ dwt]	0.03	0.32
Available Mg [mg kg ⁻¹ dwt]	1.72	2.82
S [%]	9.75↓ ***	2.15
N _{tot} [%]	5.78↓ **	0.67
TOC [%]	0.14	0.08
Phosphatases [U g ⁻¹ dwt]	55.71↓ ***	2.52
Arylsulfatases [U g ⁻¹ dwt]	2.54	0.48
Proteases [U g ⁻¹ dwt]	12.42↑ ***	0.01
Oxidases [U g ⁻¹ dwt]	18.55↓ ***	0.51
Peroxidases [U g ⁻¹ dwt]	117.98↑ ***	0.16
Respiration [U g ⁻¹ dwt]	8.03↑ ***	0.94
PLFA _{G+} [mg kg ⁻¹ dwt]	13.82↑ ***	0.00
PLFA _{G-} [mg kg ⁻¹ dwt]	6.27↓ **	0.29
PLFA _{Ac} [mg kg ⁻¹ dwt]	176.94↓ ***	0.58
PLFA _{Fungi} [mg kg ⁻¹ dwt]	27.64↑ ***	0.98
<i>trans/cis</i>	2.92↓ *	3.27↑ *
<i>cy/pre</i>	82.77↓ ***	7.61↑ ***

Source: Modified from Nebeská et al. (2018).

Comparison was carried out by MANOVA: F-ratio statistic and its *p*-value; * *p* < 0.1, ** *p* < 0.05, *** *p* < 0.01; ↑ indicates a significant increase or ↓ a significant decrease.

The only negative change was decreasing the concentration of nutrients: S and N_{tot} , likely due to consumption by *M. × giganteus* and storage in rhizomes; other indicators did not change significantly, in particular, activities of extracellular enzymes.

The positive effect of *M. × giganteus* on soil microorganisms can be registered by decreasing of stress indicators in rhizosphere soil in comparison to bulk soil.

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