

Chapter 2

The Potential of Rhizosphere Microorganisms to Promote the Plant Growth in Disturbed Soils

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Abstract The significance of rhizosphere microorganisms, especially mycorrhizal fungi and bacteria, in polluted soils can be enormous, since they are able to increase the tolerance of plants against abiotic stress, stimulate plant growth and contribute in this way to an accelerated remediation of disturbed soils. The majority of known higher plant species is associated with mycorrhizal fungi, which can increase the tolerance of plants against abiotic stress, e.g. by an improved nutrient supply or by detoxification of pollutants. Rhizosphere bacteria can strongly promote the growth of plants solely and in interaction with mycorrhizal fungi. They can contribute to

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the mobilization of nutrients and degradation of organic pollutants. Co-inoculation of plants with mycorrhizal fungi and rhizosphere bacteria is a very promising biotechnological approach for the promotion of plant growth and soil remediation. The application of microbial inoculum for the remediation of disturbed soils was tested with several plant species, e.g., fast growing tree species, but mostly on a small scale. Main reasons for the lack of field applications in a larger scale are the lack of suitable time- and cost-effective strategies for a site-specific selection, preparation and application of microbial inoculum and the strong restriction of information on on-site efficiency of inoculated microbial strains.

This chapter focuses on fundamental and applied aspects of soil microorganisms associated with the rhizosphere of plants at various disturbed sites. Major objectives are to present strategies for the promotion of phytoremediation of disturbed soils with the use of microbial inoculum and to indicate potentials and limitations of such microbial inoculation in the field.

Keywords Rhizosphere • Mycorrhiza • Bacteria • Polluted soil

2.1 Introduction

A fundamental knowledge on plants' physiological properties and their associated microorganisms in the undisturbed natural environments is necessary to understand the impact of microorganisms on the plant development in general. The existence of positive plant-microbial interactions also in disturbed soils is unquestionable, but the mechanisms are often scarcely known. Microorganisms contribute essentially to the protection of plants against unfavourable soil conditions. In this chapter a selection of possible unfavorable soil properties in disturbed soils will be focused to analyse the possible impact of associated microorganisms on plants growth and vitality. Applicability of microbial inoculum for an improved remediation of such disturbed soils will be presented.

2.2 The Rhizosphere—A Hot Spot of Microbial Activities

A narrow zone of soil affected by the presence of plant roots is defined as rhizosphere. The rhizosphere is known to be a hot spot of microbial activities. This is caused by an increased nutrient supply for microorganisms, since roots release a multitude of organic compounds (e.g., exudates and mucilage) derived from photosynthesis and other plant processes (Brimecombe et al. 2007). Therefore, rhizosphere is an environment with a high microbial diversity. An important consequence of the high diversity is an intense microbial activity with feedback effects on root development and plant growth in general. In general, the microbes serve as

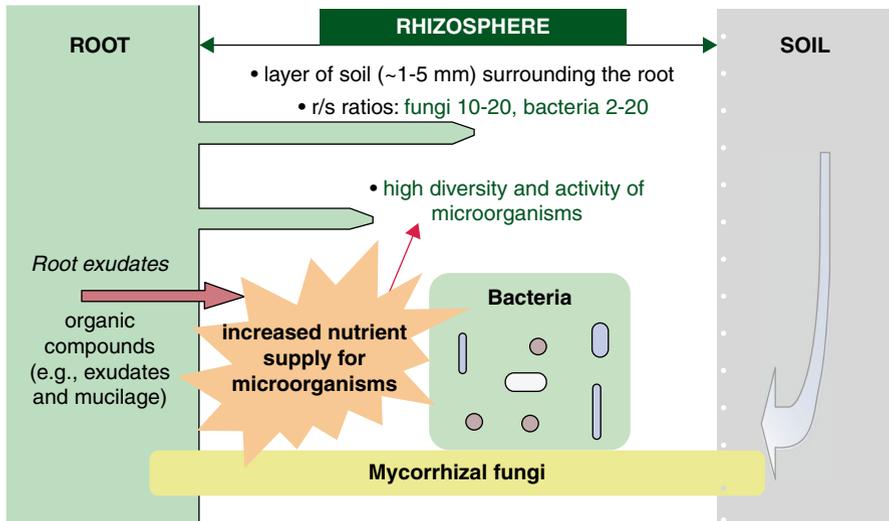


Fig. 2.1 Rhizosphere microorganisms as a critical link between plants and soil. (Adapted from Richardson et al. 2009)

intermediary between the plant (Fig. 2.1), which requires soluble mineral nutrients, and the soil, which contains the necessary nutrients but often in low concentrations and/or complex and inaccessible forms. Thus rhizosphere microorganisms provide a critical link between plants and soil (Lynch 1990).

The highest portion of microorganisms which inhabit the rhizosphere are fungi and bacteria. When considering the rhizosphere effect on their abundance, the fungal abundance is 10–20 times higher and the bacterial abundance 2–20 times higher in the rhizosphere than in the bulk soil (Morgan et al. 2005). Competition for nutrient sources in the rhizosphere is very high. Therefore, different microorganisms have developed distinct strategies, giving rise to a range of antagonistic to synergistic interactions, both among themselves and with the plant (Perotto and Bonfante 1997). A very high diversity of interactions can be assumed on the basis of the tremendous diversity of soil microorganisms and plants. The understanding of fundamentals of these interactions is critical for their use in plant growth promotion and remediation of disturbed soils.

This chapter focuses on mycorrhizal fungi and rhizosphere bacteria that are believed to play a crucial role in the proper development of plants in unfavourable soil conditions. Several examples of the role of rhizosphere microorganisms in the improvement of plant fitness in disturbed soils with unfavourable soil properties for plant growth (nutrient- and water-deficiency, soil-borne pathogens, extreme soil pH, heavy metal contamination, organic pollutants) were described. The need of site-specific selection of plant growth and soil remediation promoting rhizosphere organisms for field use was emphasized.

2.3 Role of Rhizosphere Microorganisms in the Improvement of Plant Fitness

2.3.1 *Mycorrhizal Symbiosis*

The most common mutualistic association between fungi and plant roots is the mycorrhizal symbiosis. In this association the fungal partner can provide the plant with enhanced access to water and nutrients due to the extended area for their acquisition through the extraradical hyphal network. Additionally, many fungal partners can efficiently contribute to the nutrient mobilization in the soil. They are able to produce enzymes involved in the hydrolysis of nitrogen and phosphorus compounds from the organic matter in the soil and contribute to the weathering of minerals, e.g., by the release of organic acids. Mycorrhizal fungi can alleviate abiotic (e.g., increased heavy metal concentrations) and biotic (e.g., soil-borne pathogens) stress by the increase of plant fitness through enhanced nutrient supply and in case of ectomycorrhizal fungi by covering the fine roots with a hyphal mantle. The plants, in return, provide carbohydrates for fungal growth and maintenance (Smith and Read 1997). It has been estimated that between 4 and 20% of net photosynthates could be transferred from the plant to its fungal partner (Morgan et al. 2005). The mycorrhizal symbioses usually increase the growth of the host plants in the long term, however, their effects on the plant growth might also be neutral or even parasitic if the costs for the plants exceed the advantages (Johnson et al. 1997).

The most common types of mycorrhizal associations are ectomycorrhizae (EM) and arbuscular mycorrhizae (AM).

Ectomycorrhizal fungi form associations with many woody plants ranging from shrubs to forest trees in the *Salicaceae*, *Pinaceae*, *Fagaceae*, *Betulaceae* and *Dipterocarpaceae* (Smith and Read 1997). Communities of ectomycorrhizal trees are dominating in boreal and temperate plant biomes and are also important in certain tropical and rain forests (Read 1993). There are about 5000–6000 ectomycorrhizal fungal species in basidiomycetes and ascomycetes described, but it was suggested that there might well be about 10,000 species (Brussaard et al. 1997). Mycelium of ectomycorrhizal fungi forms a mantle of varying thickness around the fine roots. The mantle increases the surface area of absorbing roots and often affects fine-root morphology, resulting partly in root bifurcation and clustering. Contiguous to the mantle, hyphal strands can extend into the soil and often aggregate to form rhizomorphs, specialized for long-distance transport of nutrients and water. Hyphae of ectomycorrhizal fungi also penetrate inwards between the cells of roots producing a netlike structure called the Hartig net, which constitutes the interface for the exchange of photoassimilates, soil water and nutrients between the host plant and its fungal partners. The internal organization of mantle structures and rhizomorphs with respect to hyphal differentiation and with respect to their physical relation can reveal some hints for their function (Agerer 1991).

A single plant root can be colonized by many different mycorrhizal fungi. These fungi partly are able to colonize a variety of different plant species. The natural

mechanisms promoting high fungal diversity have remained unclear, however it seems likely that differential preferences for soil conditions and host plants are essential (Bruns 1995).

AM occur in the majority of herbaceous and graminaceous species of temperate and semi-arid grasslands as well as in many tree species especially of tropical and subtropical forests. Arbuscular mycorrhizal fungi are obligate biotrophs and involve a very small group of fungi in the *Glomales* (Glomeromycota). In AM, an internal mycelial phase with characteristic structure is present. In this association neither the fungal cell wall nor the host cell membrane are breached. As the fungus grows, the host cell membrane envelopes the fungus, creating a new compartment where material of high molecular complexity can be deposited. This apoplastic space prevents direct contact between the plant and fungus cytoplasm and allows efficient transfer of nutrients between the symbionts. Among commonly observed structures are found frequently: vesicles, arbuscules, hyphal coils, and internal hyphae. There are problems in extrapolating from structure to function in what now appears to be structurally and possibly also functionally diverse symbiosis (van der Heijden 2001). The term AM covers a diversity of mycorrhizal structures. AM development differs, not only over time, but also between plant species, especially with respect to the extent of development of vesicles, coils and arbuscules within the cortical cells (van der Heijden 2001). The external phase is important as well, made up of branched single hyphae that ramify through the soil, forming anastomosing networks.

Although some plants can form mycorrhizae with both arbuscular mycorrhizal and ectomycorrhizal fungi, they usually prefer one of these mycorrhizal types (Lodge 1989). However, the reasons for their preferences are still unknown. Dual mycorrhiza formation with arbuscular and ectomycorrhizal fungi were observed, e.g., in the genera *Salix*, *Alnus*, *Populus*, and *Eucalyptus*. So far it is not clear whether dual mycorrhiza is a functionally mutualistic relationship. The apparent dual mycorrhizal stage of these plants might be explained by: (i) lack of resistance (decreased plant control). This means that—arbuscular mycorrhizal fungi, with supposed higher inoculum potential, colonize seedlings, however, they are rapidly replaced by ectomycorrhizal fungi which prevent colonization of newly-formed roots by arbuscular mycorrhizal fungi; (ii) niche differentiation (increased plant benefits). This means that plants with the ability to form both types of mycorrhiza might have a selective advantage in specific environmental conditions (e.g., in flood plains) (van der Heijden 2001). It was revealed that, e.g., *Salix* spp. are able to establish AM rarely and the roots of these plants are dominated mostly by ectomycorrhizal fungi (van der Heijden 2001).

The soil surrounding mycorrhizal roots supports distinct bacterial communities compared to the bulk soil. The rhizosphere combined with the hyphosphere of mycorrhizal fungi comprises the mycorrhizosphere. Mycorrhizosphere inhabitants can include intrahyphal bacteria in ectomycorrhizal fungi (Bertaux et al. 2003), and intraspore bacteria in some arbuscular mycorrhizal fungi (Bianciotto et al. 1996). It has been shown that some mycorrhizosphere bacteria can promote mycorrhiza formation. The details of mechanisms that are involved will be described in the next paragraph.

2.3.2 *Plant Growth Promoting Rhizobacteria (PGPR)*

The rhizosphere is colonized with bacteria that can individually or in cooperation with mycorrhizal fungi improve the plant fitness. In the rhizosphere bacteria continuously metabolize various organic compounds from root exudates. Therefore, their activities result in quantitative and qualitative alterations of the released root exudates. Bacteria in the rhizosphere can significantly influence the nutrient supply of plants by competing for mineral nutrients and by mediating the turnover and mineralization of organic compounds. Therefore, bacteria in the rhizosphere can be a leading control of the turnover of nutrients in the soil (Robinson et al. 1989). Rhizosphere bacteria can influence plant growth also directly by releasing a variety of compounds, e.g., phytohormones or antimicrobial compounds (Perotto and Bonfante 1997).

The diversity and structure of bacterial communities is plant-specific and varies over time (Smalla et al. 2001; Barriuso et al. 2005). Diversity of bacteria is affected by the plant age, the season and the soil conditions (Hrynkiewicz et al. 2010a). Rhizosphere bacteria can have a negative, neutral or positive effects on plant fitness. Detrimental microbes include both major plant pathogens and minor parasitic and non-parasitic deleterious rhizosphere bacteria (Barea et al. 2005). Plant growth promoting rhizobacteria (PGPR), can have biofertilizing and/or biocontrol functions (Barea et al. 2005). However, the effect of rhizosphere bacteria depends mostly on the genotype of the microorganisms and plants involved as well as on the environmental conditions (Brimecombe et al. 2007). *Pseudomonas* spp. and *Bacillus* spp. belong to the largest groups of rhizosphere bacteria (Brimecombe et al. 2007).

PGPR are usually in contact with the root surface, and improve growth of plants by several mechanisms, e.g., enhanced mineral nutrition, phytohormone production, disease suppression (Tarkka et al. 2008). Two groups of PGPR were described: one group is involved in the nutrient cycling and plant growth stimulation (biofertilizers) (Vessey 2003) and the second group is involved in the biological control of plant pathogens (biopesticides) (Whipps 2001). Biofertilizers are based on living microorganisms which (when applied to seed, plant surface or soil) colonize the rhizosphere or the interior of the plant and promote growth by increasing the supply or availability of primary nutrients to the host plant (Vessey 2003). Biopesticides promote plant growth by the control of deleterious organisms, e.g., through the production of antibiotics.

In summary, bacteria may support the plant growth by several mechanisms, e.g.,: increasing the ability of nutrients in the rhizosphere (i), inducing root growth and thereby increase of the root surface area (ii), enhancing other beneficial symbioses of the host (iii) and by combination of modes of action (v) (Vessey 2003).

PGPR can increase the availability of nutrients, e.g., by enzymatic nutrient mobilization from organic matter and production of siderophores (Anderson et al. 1993; Whiting et al. 2001; Jing et al. 2007). Bacteria producing extracellular degrading enzymes are major decomposers of organic matter. They contribute essentially to the soil aggregation and nutrient availability (Johansen and Binnerup 2002). In soils

with low phosphate, bacteria can release phosphate ions from low-soluble mineral P crystals and from organic phosphate sources. These bacteria exude organic acids that dissolve the P crystals and exude enzymes that split organophosphate (Vessey 2003; Tarkka et al. 2008). Some rhizosphere bacteria also produce siderophores which can be absorbed as the bacterial Fe^{3+} -siderophore complex by a number of plant species in the deficiency of iron (Vessey 2003). Microbial siderophores in the rhizosphere can significantly contribute to the biocontrol of soil-borne pathogens due to their competitive effects (Hiihte et al. 1994).

PGPR can also promote the root growth. This can be caused by the ability of most rhizobacteria to produce phytohormones, e.g. indole-3-acetic acid (IAA), cytokinins, gibberellins, ethylene which promote cell division and cell enlargement, extension of plant tissue and/or other morphological changes of roots (Salisbury 1994).

2.3.3 *Mycorrhization Helper Bacteria*

Mycorrhizal fungi and bacteria in the rhizosphere can interact with each other at different levels of cellular integration, ranging from apparently simple associations, through surface attachment, to intimate and obligatory symbiosis. This synergism may not only be important in promoting plant growth and health, but may also be significant to rhizosphere ecology (Perotto and Bonfante 1997).

PGPR can enhance plant growth also indirectly by stimulating the relationship between the host plant and mycorrhizal fungi. Mycorrhizae are often described as tripartite interactions, because in their natural environment, bacteria are associated with arbuscular and ectomycorrhizal fungi by colonizing the extraradical hyphae or as endobacteria living in the cytoplasm of at least some fungal taxa. For rhizobacteria that increase the ability of roots to establish symbiotic interactions with ectomycorrhizal fungi, Garbaye (1994) proposed the term “mycorrhization helper bacteria” (MHB). He suggested a number of possible mechanisms for the bacterial helper effects; for example, the production of vitamins, amino acids, phytohormones and/or cell wall hydrolytic enzymes. Some of these effects could directly influence the germination and growth rate of fungal structures, whereas others could act on root development and on root susceptibility to fungal colonization (Garbaye 1994). Several reports have demonstrated enhanced arbuscular mycorrhizal fungal colonization in roots in the presence of MHB (e.g., Artursson et al. 2006; Hildebrandt et al. 2002). Although promotion of mycorrhiza formation and plant growth by MHB have been described (e.g., Poole et al. 2001; Artursson et al. 2006), explanations of the mechanisms are often missing.

As a possible strategy for selection of fungus-associated bacterial strains by ectomycorrhizal fungi de Boer et al. (2005) suggested exudation of soluble fungal storage sugars (usually trehalose), polyols (e.g., mannitol) or organic acids (in particular oxalic acid) which can increase the number of bacteria or exudation of inhibitory chemicals which select antibiotic-resistant bacteria. It is hardly known

and a future challenge to analyze if there is a specific fungal selection for particular bacterial strains and if cooperation of these bacterial strains is restricted to given ectomycorrhizal fungi, since this would be essential to know for a successful development of joint inoculum.

The majority of MHB, which were described so far, belong to the fluorescent pseudomonads and sporulating bacilli (Garbaye and Bowen 1989; Founone et al. 2002). It seems that MHB include a variety of Gram-negative and Gram-positive species, suggesting that their activities could perhaps be found in all bacterial groups that exist in the rhizosphere (Tarkka et al. 2008). However, the beneficial effects of these bacteria are controlled by soil properties (Oliveira et al. 2005).

2.4 Effect of Rhizosphere Microorganisms on the Plant Growth in Disturbed Soils

Soils can be disturbed by a wide range of factors concerning unfavorable agricultural management or industrial activities. Fertility of various soils observed in the last decades decreased at an alarming rate due to loss of organic matter as a result of erosion, oxidation, compaction, biological impoverishment as well as wide range of pollutants. Plant growth affects the physical (e.g., formation of new soil pores) and chemical (e.g., formation of soil organic matter) quality of soils this is why plant growth at disturbed sites can increase soil fertility substantially. However, in many cases unfavourable conditions in disturbed soils may cause a lack of any vegetation or a diminished vegetation development. Rhizosphere microorganisms are especially critical for plant colonization of unfavourable soils, since they can alleviate biotic and abiotic stress of plants. In this chapter we will review, the present knowledge on plant growth promotion by rhizosphere inhabiting microorganisms in disturbed soils.

2.4.1 Nutrient- and Water-Deficiency

The world population is expanding rapidly and will likely be 10 billion by the year 2050 (Cakmak 2002). The expected increases in world population will result in a serious pressure on the existing agricultural land *via* intensification of crop production. The projected increase in food production must be accomplished on the existing cultivated areas because the expansion of new land is limited due to environmental concerns, urbanization and increasing water scarcity. In the same time, soil productivity is decreasing globally due to enhanced soil degradation in the form of erosion, nutrient depletion water scarcity, acidity, salinisation, depletion of organic matter and poor drainage (Cakmak 2002). Nearly 40% of the agricultural land on the world has been affected by soil degradation (e.g., 25% of Euro-

pean, 38% of Asian, 65% of African, 74% of Central American agricultural land) (Scherr 1999). Agricultural production must be increased on the existing land, and therefore crop production must be intensified per unit of agricultural land. Mineral nutrients are the major contributor to enhancing crop production, and in maintaining soil productivity and preventing soil degradation. Generally, improving the nutritional status of plants by maintaining soil fertility is the critical step in the doubling of food production of the world. Impaired soil fertility by continuous cropping with low supply of mineral nutrients is considered a major risk for food production and ecosystem viability (Pinstrup-Andersen et al. 1999; Tillman 1999). Reduced soil fertility and crop production results in an increased pressure to bring more land into crop production at the expense of forests and marginal lands. Such areas are generally poor in fertility and sensitive to rapid degradation when cultivated (Cakmak 2002). Since especially these habitats are often very important for rare plant and animal species, it would be much better to find solutions for the remediation and later use of disturbed soils, like former sewage fields or ash dumps, if not for food at least for biomass production. A promising strategy is the integration of plant nutrition research with development of new biotechnological strategies to promote the plant growth through applications of suitable microorganisms (biofertilization). An increased nutrient use efficiency through improved soil management become an important challenge, particularly for the elements nitrogen and phosphorus.

A group of especially promising rhizosphere organisms for applications on nutrient-deficient disturbed soils are mycorrhizal fungi. They can biotrophically colonize the root cortex and develop an extramatrical mycelium which helps the plant to acquire mineral nutrients and water from the soil. They play a key role in nutrient cycling in ecosystems and their external mycelium, in association with other soil organisms, form water-stable aggregates necessary for a good soil quality (Azcón-Aguilar and Barea 1997). Moreover, it was demonstrated that arbuscular mycorrhizal fungi produce glomalin—a glycoprotein, which has been suggested to contribute to hydrophobicity of soil particles and participate in the initiation of soil aggregates (Barea et al. 2002).

Mycorrhizal fungi are known to enhance the nutrient supply of their host plants especially in nutrient-deficient conditions, e.g., by a very efficient soil exploitation and by excretion of significant quantities of phosphatases (Tibbett et al. 1998; Tibbett and Sanders 2002). Mechanisms of ectomycorrhizal fungi for adaptation on N- and P-limitation in unfavourable soil conditions, e.g., by the utilization of seed protein N were demonstrated by Tibbett et al. (1998). Ectomycorrhizal fungal species vary in their ability to acquire specific nutrients from soil (Leake and Read 1997; Erland and Taylor 2002) and this differential efficiency can be considered as niche partitioning. They may use the same substrate but extract different components. This idea could maintain the theory of high ectomycorrhizal fungal diversity in the nutrient-deficient soils. Unfortunately with the exception of N, there is little information available on the effects of specific nutrients upon ectomycorrhizal fungal diversity (Erland and Taylor 2002).

2.4.2 Extreme Soil pH

The soil pH is correlated with various biological and other chemical soil properties. About 40% of cultivated soils globally have acidity problems leading to significant decreases in crop production despite adequate supply of mineral nutrients such as N, P and K (Herrera-Estrella 1999; von Uexküll and Mutuert 1995). In acid soils major constraints to plant growth are toxicities of hydrogen (H), aluminium (Al) and manganese (Mn) and deficiencies of P, calcium (Ca) and magnesium (Mg). Among these constraints Al toxicity is the most important yield-limiting factor (Marschner 1991). Availability of P to plant roots is limited both in acidic and alkaline soils, mainly, due to formation of sparingly soluble phosphate compounds with Al and Fe in acidic and Ca in alkaline soils (Marschner 1995). Plant species have evolved adaptive mechanisms to improve their ability to cope with soils having low levels of available P by the formation of mycorrhizal association (Marschner 1995; Dodd 2000). Mycorrhizal colonization of plants enhances their ability to explore the soil for P through the action of the fungal mycelium. This results in increased exploration of the soil for available nutrients and delivers more mineral nutrients, particularly P, to plant roots (Dodd 2000; George and Marschner 1996; Marschner 1998). It is estimated that the extent of fungal mycelium may be in the range of 10–100 m per cm root or per gram of soil under field conditions in P-poor soils (McGonigle and Miller 1999). In general, the contribution of mycorrhizal associations to the plant nutrient supply is larger in soils with poor availability of mineral nutrients than in soils rich in nutrients. In pot experiments, mycorrhizal colonization contributed to the total P uptake with between 70 and 80% and to the total Zn and Cu uptake with 50 and 60% in white clover (*Trifolium repens*) (Li et al. 1991).

Mycorrhizal fungi vary with regard to their pH optima for growth and root colonization potential (Erland and Taylor 2002). Changes in soil pH can alter the enzymatic activities of some fungi, since at least some of the enzymes produced by EM have rather narrow pH optima (Leake and Read 1997). The colonization density of the ectomycorrhizal fungal species *Cenococcum geophilum* increased on beech (*Fagus sylvatica* L.) with decreasing soil pH (Kumpfer and Heyser 1986). So far, little is known on the preferences of ectomycorrhizal fungi to alkaline soils, e.g., on fly ash deposits.

Beside mycorrhizal fungi, bacteria can essentially improve the adaptation of plants to an extreme soil pH, although their distribution itself is controlled primarily by the soil pH (Fierer and Jackson 2006). Most prokaryotes grow at relatively narrow pH ranges close to neutrality. A general adaptation to extreme pH levels is to regulate the intracellular pH and keep it close to neutral. Some enzymes found in the bacterial outer membrane tend to have low pH optima, whereas all known cytoplasmic enzymes have pH optima from pH 5–8 (Torsvik and Øvreås 2002). Also in disturbed arable and landfill soils the pH was a leading control of the density of culturable bacteria in the rhizosphere of willows (*Salix* spp.) (Hryniewicz et al. 2010a).

Re-vegetation of fly ash dumps, installed for final storage of this principal by-product of coal-fired power stations, is hampered by their unfavourable chemical

and physical properties for plant growth in general and in detail often by an unfavourable soil pH (often higher than 8.5) (Hryniewicz et al. 2009). This pH leads to a strong deficiency of essential nutrients (usually N and P), high soluble concentrations of trace elements and is often combined with the presence of compacted and cemented layers (Selvam and Mahadevan 2000). The fly ash is composed of small particles (<200 μm) and its physical composition is very uniform (Pillman and Jusaitis 1997). Beside the high soil pH, high hydrophobicity of the particle surfaces of fly ash cause water deficiency and low additionally plant growth and also microbial colonization. However, it was revealed that site-adapted rhizosphere microorganisms could significantly promote the plant establishment and growth even on fly ash (Hryniewicz et al. 2009). The promotion of autochthonous ectomycorrhizal fungi with site-adapted inoculated rhizosphere bacteria promoted the growth of willows (*Salix* spp.) in the mentioned study significantly.

2.4.3 Soil-Borne Pathogens

Soil is a reservoir for many potential plant pathogens and especially plants with a decreased vitality, like in unfavourable soil conditions, can be infected by them. Primary conditions that promote infection of roots can be poor sanitation, inadequate drainage and improper irrigation. Moreover, intensified production in agriculture, connected with increased use of agrochemicals may cause several negative effects e.g., development of pathogen resistance to the applied agents and their unforeseen impacts on the environment (Compant et al. 2005). Decreasing the vegetation diversity leads to pauperization of soil inhabitants, decreasing of interconnectedness and functional interchangeability (van Bruggen et al. 2006). An extremely simplified vegetation, such as a monoculture, selects a specific microbial community, including plant pathogenic microorganisms and sometimes also their parasites or antagonists (Bruggen et al. 2006). Population levels of soil-borne pathogens, include bacteria, fungi and some viruses.

Some root associated micororganisms, like mycorrhizal fungi can significantly increase the resistance of plants to soil-borne pathogens. Most of soil-borne plant diseases of roots (e.g., root rot or wilting) are caused by fungi such as *Rhizoctonia*, *Fusarium*, or *Verticillium* spp. or by oomycetes (e.g., root rot) including *Phytophthora*, *Pythium*, and *Aphanomyces* spp. (Whipps 2004). Alleviation of deleterious effects by mycorrhizal fungi were also observed in case of parasitic nematodes (de la Peña et al. 2006) and phytophagous insects (Gange 2006). Mycorrhizal effects on aboveground diseases largely rely on the lifestyle and challenge strategy of the attacker (Pozo and Azcón-Aguilar 2007). However, the ability to enhance resistance/tolerance differs among mycorrhizal isolates (i), the protection is not effective for all pathogens (ii), and the protection is modulated by environmental conditions (iii) (Pozo and Azcón-Aguilar 2007). Different mechanisms can participate in plant protection from root pathogens by mycorrhizal fungi: improved nutrient status of the host plant (i), competitive interactions with pathogenic fungi (ii), anatomical or ar-

chitectural changes in the root system (iii), microbial community changes in the rhizosphere (iv) and activation of plant defence mechanisms (v) (Wehner et al. 2010).

Root pathogens can cause a considerable loss of tree seedlings in nurseries and are generally difficult to control using conventional methods. It was already well documented that inoculation of tree seedlings in nurseries with EM fungi may provide some suppression of pathogens (Duchesne 1994). Ectomycorrhizal fungi have additionally a mechanical barrier effect against infection of roots with pathogens provided by their hyphal mantle (Duchesne et al. 1987), can produce antibiotics (Duchesne 1994; Schelkle and Peterson 1996) or acidify alkaline soils (Rasanayagam and Jeffries 1992).

Also plant associated bacteria can be used successfully for the biocontrol of soil-borne pathogens (e.g., Sturz et al. 2000; Compant et al. 2005). Biocontrol mechanisms mediated by bacteria are: competition for an ecological niche or substrate (i), production of inhibitory allelochemicals (ii), and induction of systemic resistance in host plants to a broad spectrum of pathogens and/or abiotic stress (iii) (Compant et al. 2005).

Biocontrol effects of bacteria and mycorrhizal fungi can be combined successfully. For example, *Bacillus subtilis* inhibited the growth of root pathogens like *Fusarium* and *Cylindrocarpon* spp. in co-inoculation with ectomycorrhizal fungi (*Laccaria proxima*, *Suillus granulatus*) (Schelkle and Peterson 1996). Suppression of pathogenic fungi by helper bacteria may be direct by production of antibiotics (Malajczuk 1988) or indirect by stimulation of mycorrhizae formation on the plant roots. Both mycorrhizal fungi and bacteria may synthesise siderophores (Hryniewicz et al. 2010a, b) which are involved in the inhibition of pathogenic fungi (Neidhardt et al. 1990).

2.4.4 Heavy Metal Contamination

Especially ectomycorrhizal fungi can promote the establishment of plant species at heavy metal contaminated sites by immobilizing heavy metals in the soil, thereby reducing the availability of metals to plants (Chanmugathas and Bollag 1987; Fomina et al. 2005). As a result, plants colonized with these fungi show a higher tolerance to toxic metal concentrations (Brown and Wilkins 1985). Mechanisms of ectomycorrhizal fungi for amelioration of heavy metal stress are (i) sorption of metals in the hyphal sheath, (ii) reduction of their apoplastic mobility as a result of hydrophobicity of the fungal sheath, (iii) exudation of chelating substances or (iv) sorption of metals on the external mycelium (Jentschke and Godbold 2000; Turnau et al. 1996). Chelating substances of fungal origin which are able to bind metals are for example organic acids or slimes at the surface of mycelia (Jentschke and Godbold 2000). The efficiency of plant protection by ectomycorrhizal fungi differs between distinct isolates and different toxic metals (Meharg and Cairney 2000). A high intra-specific heterogeneity in metal tolerance was found in an *in vitro* screening with 49 strains of 5 species of ectomycorrhizal fungi from polluted and non-polluted sites

with increased Cd, Cu, Ni and Zn contents (Blaudez et al. 2000). There can be also strong differences in the metal tolerance even between ectomycorrhizal plants of the same family. The reasons for particularly successful protection of host plants by distinct communities of ectomycorrhizal fungi are still unknown (Abler 2004). Toxic metals are believed to affect fungal populations by reducing the abundance, species diversity and selection for a tolerant population (Duxbury 1985). It has been hypothesized that tolerant EM forming plants are protected by well-adapted ectomycorrhizal fungi and that such fungi might be advantageous to remediate polluted sites more effectively by a general plant growth promotion.

It was shown, that mycorrhizal fungi, in spite of their possible metal restraining, can increase the total heavy metal uptake of their host plants through an increased plant growth (Jentschke and Godbold 2000; Schützendübel and Polle 2002). Mycorrhizal fungi are especially effective in plant protection against abiotic stress in increased heavy metal concentrations (Meharg and Cairney 2000; Schützendübel and Polle 2002). Phytoremediation, the remediation of contaminated soils and water with plants, is a promising and relatively cheap clean-up strategy and suitable in case of moderate and low contaminations (Pilon-Smits 2005). Enhanced phytoremediation can be achieved by inoculation of the plant rhizosphere with selected microorganisms (Siciliano and Germida 1999). Beside mycorrhizal fungi, rhizobacteria can contribute to increase the plant growth and metal uptake of plants on polluted soils substantially, however less is known on their mechanisms of metal protection of plants.

2.4.5 Organic Pollutants

Organic pollutants can be degraded by plants through biochemical reactions taking place within the plants and in the rhizosphere. The remediation of soils containing diverse organic pollutants, including organic solvents, pesticides, explosives and petroleum is possible with the use of plants and their rhizosphere processes (phytodegradation) (Mirsal 2004). Phytodegradation of organic pollutants may be enhanced by bacterial activities. In this process, plants interact with soil microorganisms by providing nutrients in the rhizosphere which leads to an increased microbial activity and degradation of toxic pollutants (Mirsal 2004).

Mycorrhizal fungi and rhizobacteria were demonstrated to promote plant growth and degradation of pollutants in soils with increased pollutant concentrations. For example, EM associations can display considerable resistance against toxic organic compounds such as m-toluate (Sarand et al. 1999), petroleum (Sarand et al. 1998), or polycyclic aromatic hydrocarbons (Leyval and Binet 1998; Wenzel 2009). Densely packed mycorrhizal sheaths and phenolic inter-hyphal material can protect plant roots from direct contact with the pollutant (Ashford et al. 1988).

Degradation of organic pollutants was also revealed by rhizosphere (Rentz et al. 2005) and endophytic bacteria (Wang and Dai 2011).

In summary, very specific adaptations of microorganisms on different unfavourable soil conditions are required and the adaptation is even more difficult through the fact that several unfavourable soil conditions are often combined, e.g. low soil pH with high metal mobility and low P availability. Thus, in soils with long-term stress a selection according to the site-specific needs can be supposed. The investigation of site-adapted cultivable microorganisms in unfavourable soils will contribute to identify leading controls of site-specific populations and to provide fundamental knowledge and strain collections for subsequent selections and applications of plant growth and site remediation promoting microbial strains (Hrynkiewicz et al. 2010b).

2.5 Selection and Use of Microorganisms for the Promotion of Plant Growth and Soil Remediation

Positive effects of mycorrhizae and/or rhizobacteria on plant growth and health as biostimulators, biofertilizers and/or bioprotectors in sustainable agriculture and horticulture were described by many authors (e.g., Azcón-Aguilar and Barea 1997; Barea et al. 2002, 2005; Compant et al. 2005; Ryan et al. 2009). A rising portion of disturbed soils worldwide leads to an urgent need of successful remediation strategies. It is correlated with an intense search for microorganisms, which are site-adapted and able to promote the plant growth on disturbed soils and in this way the phytoremediation of such sites.

Mycorrhizal fungi and bacteria can be well adapted to harsh soil conditions and promote the remediation of disturbed soils directly and by plant growth promotion (Schützendübel and Polle 2002; Fomina et al. 2005; Baum et al. 2006; Zimmer et al. 2009; Wenzel 2009). However, their field application is still very limited caused e.g., by the lack of the knowledge how to calculate the biological and economical efficiency and by the lack of fast and effective site-specific selection procedures. Maximum on-site benefits will only be obtained from inoculation with efficient fungi and/or bacteria in compatible host/microorganism/site combinations. Compatible highly-effective microorganisms can contribute significantly to the biological degradation (organic pollutants) or removal (heavy metals) of contaminants. This is why the selection of microbial inoculum is a main support of successful biotechnological application in the field.

2.5.1 Selection Criteria of Microorganisms for Inoculation of Unfavourable Soils

Applications of inoculation with microorganisms provide a great challenge in the future to increase crop production, cure problems with nutrient uptake, control plant

pathogens (Bashan 1998) and remediate disturbed soils. However, several obstacles must be overcome to achieve the successful commercialization of such treatments.

On the one hand, microbial inoculum must be economically mass-produced, formulated into a cost-effective and readily applicable product to be commercially successful (Bashan 1998). Microbial inoculum should be relatively universal for various plants and soils and its effectiveness should be relatively easy to evaluate on a standard scale. One serious problem is, that many experiments point to plant- and soil-specificity instead of being universal (Vessey 2003). Most relevant and valuable for the investigation of microorganisms for subsequent applications in remediation of polluted soils are experiments and observations made in natural conditions. However, only detailed investigations (e.g., physiological and molecular characterization) on individual microorganisms with high precision and in controlled environmental conditions can explain basic causal mechanisms of their effects on plants and soil. Therefore, all levels of methodological hierarchy are important for detection, explanation and subsequent controlled use of interactions between plants and associated soil microorganisms (Read 2002).

2.5.1.1 Selection of Microorganisms Naturally Adapted to Unfavourable Soil Conditions

Information on the diversity of microorganisms at polluted sites is supposed to be especially valuable for a future selection of microbial inoculum for such sites (e.g., Derry et al. 1998; Liu et al. 2000; Hryniewicz et al. 2008). Usually, at such sites a decline in the number, diversity and activity of microorganisms was observed (Schloter et al. 2003; Maila et al. 2006; Labud et al. 2007). The relationships between microbial diversity and ecosystem sustainability are still poorly understood. Information on microbial diversity and activity may provide evidence of ecosystem degradation, but might be also a valuable source of information on site-adapted microorganisms for future application as microbial inoculum. Molecular techniques, e.g. denaturing gradient gel electrophoresis (DGGE), terminal restriction fragment length polymorphism (T-RFLP) or PCR-single-strand conformation polymorphism (PCR-SSCP), have provided detailed information on the taxonomic and phylogenetic relationships within the major groups of mycorrhizal fungi and bacteria. They can contribute to describe the host-specificity and co-evolution between plants and mycorrhizal fungi and describe the mycorrhizal community structure in the field (Read 2002). Progress towards a fundamental understanding how mycorrhizae and associated bacteria influence the vegetation development and effects at polluted sites is still a big challenge.

2.5.1.2 Properties of Successful Microbial Inoculum

The majority of soil microorganisms (95–99%) is known to be at least so far non-culturable (Torsvik and Øvreås 2002). However, the basic criterium for subsequent

selection and later application of microbial inoculum useful for plant-growth promotion is cultivability and fast multiplication of microorganisms. Information of critical factors influencing plant-microbe-pollutant interactions in soils could lead to an improved selection of microbial inoculum for a microbial-assisted bioremediation. A fundamental condition for subsequent on-site applications of selected microorganisms is their safety for the environment and for humans. Therefore, before field applications, all selected microorganisms have to be precisely identified and toxicologically assessed.

Very few different microbial taxa have been tested so far for their capability to promote plant growth at disturbed and polluted soils and little is known on the microbial spectrum which might be especially relevant to promote plant species in disturbed soils. In general, numerous species of mycorrhizal fungi and soil bacteria which inhabit the rhizosphere can promote plant growth (Vessey 2003; Compant et al. 2005), e.g., by enzymatic nutrient mobilisation from organic matter (mostly P and N) and production of siderophores (Whiting et al. 2001; Jing et al. 2007) and might be promising also for disturbed or polluted soils. They can contribute essentially to soil aggregation and nutrient availability (Johansen and Binnerup 2002), which is often especially important for disturbed soils.

Therefore, enzyme activities can be suitable selection criteria for microbial inoculum for plant growth promotion in disturbed soils. Microbial enzyme activities in the soil were predominantly measured as total potential activities rather than at the level of isolates within a community (e.g., Khan et al. 2007). However, investigations of single strains are necessary for the selection of potential inoculum (Hryniewicz et al. 2010b).

Acid phosphatases contribute to the P mobilisation from organic matter. *In vitro* synthesis of extracellular phosphatases by ectomycorrhizal fungi was investigated by Colpaert and Van Laere (1996). These enzymes cause the release of phosphate from a range of substrates as inositol phosphate, polyphosphates, phosphorylated sugars into the soil solution (Tibbett et al. 1998). The production of these enzymes is species- and strain-dependent and often stimulated by deficiency of mineral phosphate (Dighton 1991). It was revealed that a strain of the ectomycorrhizal fungus *Paxillus involutus*, which synthesized significantly higher amounts of acid phosphatases than another tested strain of this species, promoted the mycorrhiza formation and biomass production of willows (*Salix* spp.) also more successfully (Hryniewicz et al. 2010b).

In the present case, the strain-specific phosphatase activity *in vitro* was a suitable criterion for the selection of plant growth promoting candidates. However the relevance of single enzymes for selection might differ site-specific, since the growth limiting elements might be different.

Beside the phosphatase activity, cellulolytic and pectolytic activities have been used for selection of microorganisms for promotion of plant growth and mycorrhiza formation. High cellulolytic and pectolytic activities of mycorrhizal fungi and rhizosphere bacteria allow the disintegration of living and dead plant tissue (Wood 1960; Bateman and Miller 1966) and, consequently, can enable microorganisms to enter roots. High cellulolytic and pectolytic activities were detected among mycor-

rhizal fungi (Garbaye 1994) and their helper bacteria (Duponnois and Plenchette 2003). Therefore, also cellulolytic and pectolytic activities might be suitable selection criteria.

Furthermore, lipolytic activities might be relevant for the selection of microorganisms especially for biodegradation, since they can improve not only the N supply of plants but also promote the biodegradation of organic pollutants (e.g., petroleum-derived wastes) in soils (Chaturvedi et al. 2006).

A further suitable selection criterion for plant growth promoting microorganisms for disturbed soils is the ability to produce siderophores (Burd et al. 1998; Kuffner et al. 2008). Siderophores are complexing compounds released to improve iron acquisition, which is an essential nutrient of plants, but relatively insoluble in soil solution (Hu and Boyer 1996; Hryniewicz et al. 2010a, b). In rhizosphere microbial communities siderophore synthesis might be especially important for successful competition of rhizosphere microorganisms in disturbed soils with extremely low nutrient concentrations. Beside their direct effects on the iron supply of plants, siderophores can contribute additionally to the suppression of pathogens in the rhizosphere through their withhold from iron supply (Buyer and Leong 1986).

Furthermore, auxins are recognized as highly active plant growth stimulators, and indole-3-acetic acid (IAA) is a key substance (Woodward and Bartel 2005). Indole-3-acetic acid (IAA) production is widespread among soil microorganism, mostly ectomycorrhizal fungi (e.g., Rudawska and Kieliszewska-Rokicka 1997; Niemi et al. 2004; Niemi and Scagel 2007; Hryniewicz et al. 2010a). Several authors revealed that fungal strains with high IAA-synthesizing activity induce stronger growth of fine roots and significantly higher numbers of mycorrhizae compared to strains with low activity of IAA (Normand et al. 1996; Rudawska and Kieliszewska-Rokicka 1997; Karabaghli et al. 1998).

In summary, enzyme activities, production of siderophores and auxins can be used successfully for the selection of highly active microbial strains for the promotion of plant growth in disturbed soils. However, beside these criteria, the selection of suitable combinations of host plants and microbial inoculum is necessary.

Specificity of combinations of mycorrhizal fungal and bacterial strains as well as host plants for the remediation of disturbed soils is rarely known. It is still in discussion if a specific fungal selection of particular bacterial strains exists and whether cooperation of these bacterial strains is restricted to given ectomycorrhizal fungi. In several previous published works (e.g., Baum et al. 2006; Hryniewicz et al. 2009; Zimmer et al. 2009) it was demonstrated that interactions of mycorrhizal fungi and bacteria can be significantly growth promoting even in situations when the microorganisms used as inoculum does not originate from the same host plant and site. Also several previous studies (e.g., Bianciotto et al. 1996; Jana et al. 2000; Xavier and Germida 2003) revealed a low specialization of bacterial strains to mycorrhizal fungi and their host plants. This feature of inoculum might assure a broader spectrum for practical applications of microbial inoculum. As a possible mechanism for selection of fungus-associated bacterial strains by ectomycorrhizal fungi de Boer et al. (2005) suggested exudation of soluble fungal storage sugars (usually treha-

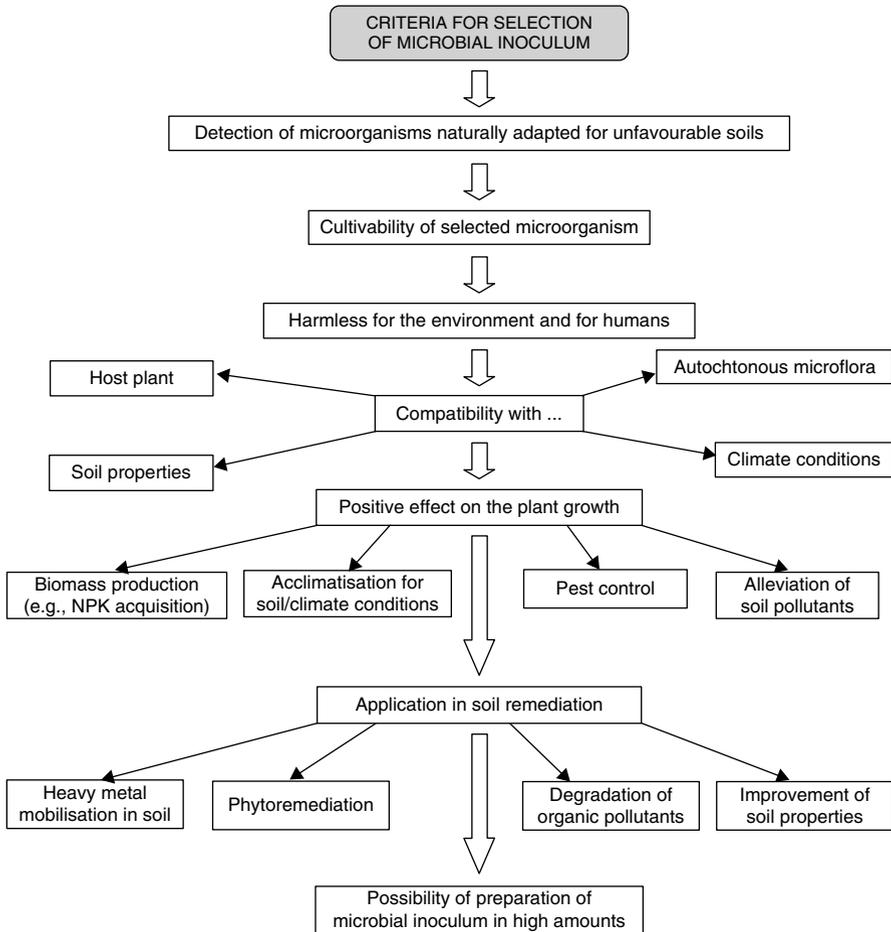


Fig. 2.2 Selection criteria of microorganisms for inoculation of unfavourable soils

lose), polyols (e.g., mannitol) or organic acids (in particular oxalic acid) which can increase the number of bacteria or exudation of inhibitory chemicals which select antibiotic-resistant bacteria (Fig. 2.2).

2.5.2 Chances and Risks of In Vitro Selection for Field Applications

Special attention should be paid to the complexity of interactions in plant-microbe-soil-pollutant systems in natural conditions. Emphasis should be laid on the evaluation of results obtained from *in vitro* and pot experiments in comparison

to the results from heterogeneous, varied polluted field sites and the functioning of phyto-/rhizoremediation systems under various ecological conditions (Wenzel 2009). Moreover, some isolated microorganisms can effectively degrade single pollutants *in vitro*, but when introduced into actual field conditions with varied combinations of pollutants, they cease to function as anticipated (Quan et al. 2003; Singer et al. 2005).

In addition, introduced strains may not compete well with the indigenous microorganisms in the soil to remain dominant or viable (Bouchez et al. 2000; Das and Mukherjee 2007; Mohanty and Mukherji 2008; Supaphol et al. 2006). Bioremediation efficiency is thus a function of the ability of the inoculated microbial degraders to remain active in the natural environment (Alexander 1999).

The experimental scale and the bioavailability of the pollutants on the sites have to be considered, since some microbial treatments which were successful *in vitro* and in pot experiments failed in long-term contaminated soils in the field (Wenzel 2009). However, the scaling up of processes in the plant-soil-microbe system (as for example the bioremediation of industrially contaminated sites) represents one of the greatest challenges facing environmental scientists and yet is essential for sustainable land management worldwide (Standing et al. 2007). In this connection, investigations also on the microscale will be essential furthermore, since they provide basic information for subsequent tests in the macroscale. Enhanced degradation capabilities of inoculated microorganisms may be obtained by the selection, breeding and engineering of plants that exude specific carbon substrates (e.g., opines, flavonoides) that can be preferentially used by the microbial degrader strains/populations present in the polluted soil (Wenzel 2009). Additionally, e.g., root exudate compounds (phenylpropanoids) were identified, which created a nutritional bias in favor of enhanced polychlorinated biphenyl (PCB) degradation (Narasimhan et al. 2003). Furthermore, several experiments were carried out with genetically modified rhizosphere bacteria which were able to enhance the rhizodegradation of organic pollutants, e.g., *Pseudomonas fluorescens* expressing enzymes for toluene degradation (Yee et al. 1998), *Rhizobium tropici* expressing enzymes for degradation of dioxine-like substances (Saiki et al. 2003). Bacterial biosensors, which were designed for the detection of chemical, physical or biological signals via the production of a suitable reporter protein (e.g., green fluorescent protein, GFP), can be used successfully for fundamental research on bioremediation of polluted soils. However, such experiments so far are restricted to the lab scale, since ecological and public consequences have to be tested before their application in the field might be permitted (Wenzel et al. 2009).

2.5.3 Status and Perspectives of Commercialisation of Microbial Inoculum

Use of microbial inoculum instead of indigenous microbial populations might be preferable or even necessary to diminish plant stress or increase the biomass

production at disturbed sites, with partly low or functionally-disturbed diversity of microorganisms in the soil. Applications of microbial inocula might provide a great challenge to improve the nutrient supply of plants and to control plant pathogens (Bashan 1998) or to alleviate drought stress of plants (Boomsma and Vyn 2008). However, before microbial inoculation becomes a viable technology several obstacles must be overcome. Microbial inoculum to be commercially successful must be economically mass-produced, formulated into a cost-effective and readily applicable product (Bashan 1998). Mycorrhizal and/or bacterial inoculum should be relatively universal for various plants and soils and its effectiveness should be relatively easy to evaluate on a standard scale (Vessey 2003). Solution of these and similar problems is challenging, since research of these problems is rather limited to relatively few microbial and plant taxa (Table 2.1).

2.6 Concluding Remarks and Outlook

Microbial activity in the rhizosphere contributes significantly to the sustainability of agriculture and forestry as well as to the remediation of disturbed soils. Selective promotion of desirable rhizosphere processes requires a fundamental understanding of the complex microbial interactions in the rhizosphere. Especially, mycorrhizal fungi and rhizobacteria belong to the microorganisms in the rhizosphere, which contribute essentially to increase the soil fertility and remediate physically and chemically disturbed soils.

Inoculation of soils with selected plant growth and soil remediation promoting microorganisms has the capacity to improve the plant fitness in unfavourable conditions of polluted soils and increase the plant uptake of heavy metals and the degradation of organic pollutants. The great challenge is the successful use of such inoculum in the field with natural environmental conditions and competition by autochthonous microorganisms. Complex and integrated approaches for the rhizosphere management are required, since disturbed soils are usually characterised by a high complexity and heterogeneity. An improved fundamental knowledge of physiological traits of rhizosphere microorganisms and their impact on rhizosphere processes, which are especially relevant for the remediation of disturbed soils will be essential to allow an increased and successful use of microbial inoculum in the field. The development of microbial inoculum for an improved remediation of disturbed soils should focus on such sites, where less complicated alternatives for growth promotion, like e.g. crop-selection or fertilization, failed and the lack of valuable autochthonous microorganisms was assumed. At present it seems necessary to use always site-specific selections of inoculum, since a general suitability of inoculum for diverse site conditions seems rather unlikely.

Table 2.1 Microbial inoculum with the criteria of selection and suggested mechanisms of action

Group of microorganisms	Criteria of selection	Suggested mechanisms of action (activity) and effect	References
EM fungi and/or PGPR bacteria	<ul style="list-style-type: none"> - Improvement of plant fitness in unfavourable soil conditions (e.g., with high heavy metal concentrations): <ul style="list-style-type: none"> - increased biomass production (shoot and root); - increased shoot lengths - Morphological features of EM: <ul style="list-style-type: none"> - emanating hyphae and rhizomorphs, - thick and densely packed mycorrhizal sheaths with - phenolic inter-hyphal compounds 	<ul style="list-style-type: none"> - Mutualistic benefit from mycorrhiza formation; - Physical protection of plant roots (fungal mantle) from direct contact with pollutants 	Baum et al. (2006), Wu et al. (2006), Zaidi et al. (2006), Zimmer et al. (2009) and Hryniewicz et al. (2009, 2010a)
EM fungi	<ul style="list-style-type: none"> - Physical protection of plant roots (fungal mantle) from direct contact with the pollutant and impeded pollutant transport through increased soil hydrophobicity - Large surface increase efficiency in nutrient and water availability by plants; - Large cation exchange capacity of extramatrical hyphae reduce bioavailable concentrations of pollutants, through their substantial adsorption capacities 	<ul style="list-style-type: none"> - Physical protection of plant roots (fungal mantle) from direct contact with the pollutant and impeded pollutant transport through increased soil hydrophobicity - Large surface increase efficiency in nutrient and water availability by plants; - Large cation exchange capacity of extramatrical hyphae reduce bioavailable concentrations of pollutants, through their substantial adsorption capacities 	Ashford et al. (1988), Colpaert and Asche (1993), Hartley et al. (1997), Marschner (1998), Meharg and Cairney (2000) and Agerer (2001)
AM fungi	Increase, no effect or decrease of the uptake of metals by plants	Mechanisms not specified caused by the high diversity of effects	Wenzel et al. (2009)
EM fungi and bacteria	Broad spectrum of enzymatic activity	<ul style="list-style-type: none"> - Increased in plant nutrient supply (NPK); - Utilization of rhizodeposition-specific C sources 	Baum et al. (2006) and Hryniewicz et al. (2010a, b)
Bacteria	<ul style="list-style-type: none"> - N₂-fixing (e.g. <i>Azotobacter chroococcum</i>); - P-solubilising (e.g., <i>Bacillus megaterium</i>); - K-solubilising (e.g., <i>Bacillus mucilaginosus</i>) 	<ul style="list-style-type: none"> - Increased metal uptake by the plants - Increased plant nutrient supply - Accelerated phytoremediation of contaminated soils 	Wu et al. (2006)

Table 2.1 (continued)

Group of microorganisms	Criteria of selection	Suggested mechanisms of action (activity) and effect	References
EM fungi and bacteria	Synthesis of chelators: – metallothioneins, – siderophores, – organic acids	Detoxification of pollutants by the following strategies: – increased solubility and changes in speciation of metals/ metalloids through the production of organic ligands via microbial decomposition of soil organic matter; – exudation of metabolites (e.g., organic acids) and siderophores that can complex cationic metals or desorb anionic species (e.g., arsenate) by ligand exchange; – immobilization of cationic metals (e.g., Cd, Cu, Zn) by microbial siderophores	Mehra and Winge (1991), Neubauer et al. (2002), Gadd (2004), Hryniewicz et al. (2010a, b) and Wenzel (2009)
Bacteria	Synthesis of biosurfactants (e.g., rhamnolipids used in remediation of crude oil from the soil)	Mobilization of hydrophobic pollutants from soil particle surfaces, enabling their transport to sites of high degradation activity	Urum et al. (2004)
Ericoid and EM fungi, bacteria	Changes in the pH (reduction and oxidation processes) of the rhizosphere	Modification of the solubility of metals and metalloids in the soil	Martino et al. (2003), Fomina et al. (2005) and Gadd (2004)
EM fungi and bacteria	Synthesis of secondary compounds: – auxin-like substances – vitamins	– Plant growth promotion in polluted soils, – accelerated phytoremediation of polluted soils	Hryniewicz et al. (2010a, b) and Zaidi et al. (2006)
Bacteria	Synthesis of ACC (1-aminocyclopropane-1-carboxylate) deaminase	Increased tolerance of plants to high heavy metal concentrations in the soil: – high ethylene concentrations produced by plant roots in response to abiotic stress; – Regulation of ethylene concentrations in plants by ACC deaminase via metabolisation of the ethylene precursor ACC into α -ketobutyric acid and ammonia	Burd et al. (1998), Belimov et al. (2001), Glick (2005), Idris et al. (2004) and Arshad and Frankenberg (2002)

Table 2.1 (continued)

Group of microorganisms	Criteria of selection	Suggested mechanisms of action (activity) and effect	References
EM fungi and bacteria	Degradation of soil pollutants (e.g., hydrocarbons)	– Decrease of the concentrations of pollutants and alleviation of abiotic stress for plants	Meharg and Cairney (2000) and Chaineau et al. (2005)
EM fungi	Accumulation of heavy metals in the fungal biomass	Alleviation of abiotic stress for plants	Berthelsen et al. (2000), Blaudez et al. (2000), Leyval and Joner (2000) and He et al. (2000)
EM fungi	Presence of antioxidative systems (e.g., increased activity of Mn-SOD in Cd treated fungi)	Alleviation of abiotic stress for plants	Jacob et al. (2001)
EM fungi and bacteria	Tolerance to high concentrations of diverse pollutants (e.g., heavy metals, organic compounds)	High microbial ability to tolerate abiotic stress	Wenzel (2009)

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