Chapter 10
The Rhizosphere Microbiome: Microbial Communities and Plant Health

Sandeep Jain, Jyoti Jain, and Jayesh Singh

Abstract Exploration of rhizosphere and rhizosphere microbiome has been the research focus for last many decades. The rhizosphere is a junction for intercommunication among plants, insects, and microorganisms. It serves as diverse habitat with a nutrient-rich niche by providing a platform interaction among plants-soil-microorganism trio along with energy and matter trade-off. The rhizosphere microbiome also influences plant vigour, health, and defence against stresses by interfering with nutrient uptake, chemical signalling, and enzyme activity. Interaction among the microbiome, the environment, and the genetic makeup of host is well-known to contribute towards host health. The present chapter summarises the major effects of microbial communities present in rhizosphere on plant health and diseases.

10.1 Introduction

10.1.1 Rhizosphere: Hotspot of Root–Microbe Interaction

Rhizosphere acts as hotspot of root–microbe interaction. The etymology of rhizosphere can be expressed as rhiza (Greek), meaning root, and "sphere," meaning region influenced by roots. Lorenz Hiltner in the year 1904 was the first to use this term to describe the effects of root exudates on the proliferation of advantageous and deleterious microbes around roots (Hartmann et al. 2008). Rhizosphere is regarded as one of the most diverse ecosystems in the universe with huge energy flow (Barriuso et al. 2008). It is the region where intense biogeochemical activities take place depending on root architecture, exudates, and mucilage which influence the

---

S. Jain (✉)
Department of Plant Pathology, Punjab Agricultural University, Ludhiana, India
e-mail: sandeepjain@pau.edu

J. Jain · J. Singh
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India
e-mail: jyotijain-pbg@pau.edu

A. Varma et al. (eds.), *Plant Microbiome Paradigm*,
https://doi.org/10.1007/978-3-030-50395-6_10

microorganisms feeding on these compounds within the soil matrix. Besides this, the pH and redox gradients of the rhizosphere are also assumed to influence rhizospheric microbial communities (Schmidt et al. 2011; Shrivastava et al. 2014; Prasad et al. 2015, 2020). The roots exudation effectively widens the functional boundary of the belowground plant–microbe interface as it may control the soil microbial community in their locale, prevent or defend against herbivores, invigorate beneficial symbioses, alter the physiochemical properties of the soil, or slow down the growth of competing plant species resulting in entirely different environment at the root interface compared to bulk soil (Bais et al. 2004, 2006; Hinsinger et al. 2005). This narrow region bordering and affected by plant roots is a junction for microbial colonisation and activity, termed as rhizodeposition. During rhizodeposition, various major processes take place like depletion of border cells and root cap, soluble root exudates, insoluble mucilage, organic carbon, carbon flow to rhizosphere symbionts, and lysis of root cells (Jones et al. 2009).

Rhizosphere is categorised into three zones based on microorganisms existing in close proximity to roots, and the influence of root exudates on them as endorhizosphere, rhizoplane, and ectorhizosphere. Endorhizosphere is made up root endodermis and cortex. Rhizoplane refers to the root facet where soil particles and microorganisms cohere and involves epidermis, cortical layers, and mucilaginous polysaccharides. The third zone is ectorhizosphere consisting of soil immediately adjoining the root (Prashar et al. 2013).

10.2 Rhizosphere Microbiome: Diversity of Microbial Communities

The complex soil communities of microorganisms associated with plant roots are regarded as the plant microbiome which is also considered as the plants' other genome. The root microbiome is dynamic and plays a key role in various nutrient cycling like nitrogen and phosphorus in addition to provide protection against various biotic and abiotic stresses, thus contributing towards plant health and increased productivity (Bender et al. 2016; Lladó et al. 2017; Berendsen et al. 2012; Kumar et al. 2020; Nath et al. 2018). Root–microbe interactions may be beneficial to the plant or to the microbes or to neither of them. Both plants and microbes can be benefitted directly through mutualistic relationship or indirectly via decomposition, nutrient cycling and solubilisation (Glick 1995), emanation of growth hormones (Narula et al. 2006), induction of the resistance (Pieterse et al. 2001), and antagonism of pathogens (Kloepper et al. 2004). According to two contrary schools of thoughts, the root exudation is an "active" or "passive" process. Cook et al. (1995) hypothesised that plants may actively moderate the root microbiome for their welfare by specifically influencing microbe in a targeted manner. Other school of thought is that root exudation is a passive process releasing waste products (Jones et al. 2009; Dennis et al. 2010).

By releasing nearly one half of their total photosynthetic fixed carbon, rhizosphere microbiome provides unique locale for a diverse conglomeration of microorganisms which are an important part of food chain that consumes the bulk of nutrients exuded by plant roots (Lynch and Whipps 1990; Bonkowski et al. 2009). It has been estimated that rhizosphere microbiome can harbour approximately hundred billion microbial cells per gram of root (Egamberdieva et al. 2008) which is many times more than (10^8) in bulk soil (Foster 1988). The rhizospheric microbial communities are different from those present within the root and are reduced in diversity compared with the microbial communities of bulk soil. Organisms like nitrogen-fixing bacteria, arbuscular mycorrhizae, plant growth-promoting rhizobacteria (PGPR), biological control agents, and mycoparasitic saprobes have been well documented for their beneficial impact on plant vigour (Singh et al. 2019). Rhizospheric microorganisms which are detrimental to plant health are various plant pathogens particularly oomycetes fungi, bacteria, and nematodes. Apart from these, rhizosphere also serves as a stockpile for certain human pathogens such as *Pseudomonas*, *Staphylococcus*, and *Stenotrophomonas* (Berg et al. 2005).

10.3 Rhizosphere Microbiome: Vigour and Well-Being

The diverse rhizospheric microbial population plays a key role towards plant vigour and yield as it protects against pathogens and produce phytohormones (Lu et al. 2018; Singh et al. 2019). Approximately nearly 5–20% of total carbon fixed through photosynthesis is exuded as root exudates and functions either as substrate, chemoattractant, or signalling molecules (Mendes et al. 2013). These chemicals allure advantageous microbes that elicit pest resistance, water holding, and the synthesis phytohormones like auxins and may influence plant phenotype. Interactions among microbes-root exudates-plant physiology aggressively influence rhizospheric microbial population and alters the plants phenotypic traits. At molecular level, cross-talk differs depending upon propinquity to other microbes and management practices, etc.

Naturally occurring plant communities are influenced by rhizosphere microorganisms either directly or indirectly (van der Heijden et al. 1998, 2006, 2008; Schnitzer et al. 2011). Microbial species diversity below ground has been found to be an indicator of aboveground plant diversity and productivity (Hooper et al. 2005; Lau and Lennon 2011). The underground microbial richness ensures plant productivity under diverse climatic conditions (Wagg et al. 2011). Thus, microorganisms present both in rhizosphere and bulk soil may be utilised as a bench mark of soil quality. The plant beneficial and plant pathogenic microorganisms are discussed below:

10.3.1 The Beneficial Rhizo-Microorganisms

The plant growth-promoting microbes present in rhizosphere including bacteria, fungi, actinomycetes, protozoa, and algae act through a variety of important mechanisms like biofertilisation, root growth stimulation, rhizoremediation, abiotic stress control, and direct disease control. The beneficial effects of different rhizosphere microorganisms like *Proteobacteria* (*Pseudomonas* and *Burkholderia*) and *Firmicutes* (*Bacillus* sp.) and for fungi imperfecti (deuteromycetes) genera like *Trichoderma*, *Gliocladium*, and *Piriformospora indica* along with non-pathogenic *Fusarium oxysporum* are well documented (Kogel et al. 2006; Prasad 2008; Qiang et al. 2012; Deshmukh and Shinde 2016; Prasad et al. 2020). Among these rhizosphere microbial communities, bacteria are the most abundant (Kaymak 2010). Recently, much more information has been generated pertaining to diverse rhizospheric communities like in case of *Planctomycetes* (Hol et al. 2010; Jogler et al. 2012). The increased plant vigour by the incorporation of these microorganisms as biological control agents is well documented (Saharan and Nehra 2011; Bhattacharyya and Jha 2012). Microorganisms associated with plant microbiome can benefit the plants either by increasing the nutrient use efficiency, acting as biocontrol agents against various pathogens, or promoting plant growth by production of auxins (Singh et al. 2019).

10.3.1.1 Enhancement of Nutrient Recovery

Different nutrients like N, P, and S are present in most of the soils but are not readily available for plant uptake. Microorganisms convert these organic nutrients into available forms via different processes like production of extracellular enzymes which solubilises and fixes nutrients into available forms.

They also enhance the solubility of certain nutrients such as Fe due to various oxidation and reduction reactions. They are also reported to release organic acids which are responsible for releasing nutrients from minerals and increased rate of weathering (Coyne and Mikkelson 2015).

The most classical example is the symbiotic relationship between arbuscular mycorrhizal and roots of higher plants thereby increasing the supply of various nutrients such as copper, iron, nitrogen, phosphorus, and zinc (Prasad et al. 2017). Arbuscular mycorrhizal fungi are also reported to produce many enzymes responsible for solubilising organic P and, thus, can absorb soluble P from the soil at very low concentrations compared to plant roots alone.

Microorganisms play a vital role in nitrogen cycle as they can convert atmospheric nitrogen into fixed nitrogen. Above 90% nitrogen is fixed by nitrogen-fixing bacteria which fulfils up to 1/5th of the N required by cultivated crops. Nitrogen-fixing bacteria are either free-living/nonsymbiotic (*Azotobacter*, *Cyanobacteria*, *Beijerinckia*, *Clostridium*, and *Anabaena* species) or mutualistic/symbiotic (*Azospirillum*, *Frankia*, and *Rhizobium* species).

Azospirillum is an example of free-living nitrogen-fixing bacteria and is known to enhance rice yields (Tejera et al. 2005). Mutually beneficial relationship between bacteria and plant roots is popularly called as symbiotic. Such mutual relationship starts with the entry of bacteria into root hair followed by multiplication and formation of nodules on the host roots and enlargement of both plant and bacterial cells in association with each other. *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, and *Mesorhizobium* comprise of large group of rhizobacteria known to establish symbiotic relationship by formation of nodules on roots of leguminous plants, thus fixing nitrogen to ammonia and solubilising it into available form. *Frankia* has been reported to be associated with non-leguminous host plants (Bhattacharyya and Jha 2012).

Besides N fixation, the ability of rhizosphere microorganisms for P solubilisation is another important trait associated with plant phosphate nutrition. Phosphorus (P) is one of the major macronutrients required by plants. It is applied to soil as chemical phosphatic fertilisers. However, a major part of this phosphatic fertiliser applied to soil gets immobilised, precipitates as orthophosphate and gets adsorbed by Fe and Al oxides via legend exchange and becomes unavailable to plants.

Growth-promoting phosphate solubilising bacterial strains employ following strategies to convert phosphorus into soluble form:

(a) Lowering of soil pH by producing low molecular weight mineral-dissolving compounds such as organic acids (mainly gluconic and keto-gluconic acids), O_2/CO_2 exchange, protons, and hydroxyl ions through which their hydroxyl and carboxyl groups chelate the Fe, Al, and Ca ions bound to phosphate, thereby competing for adsorption sites with phosphate. Inorganic acids are less effective compared to organic acids for phosphate solubilisation at same pH level (Kim et al. 1997). Many times, phosphate starvation may enhance phosphate solubilisation (Gyaneshwar et al. 1999).

(b) Release of extracellular enzymes (biochemical phosphate mineralisation). Key mode of action for mineralisation of organic P in soil is the release of nonspecific acid phosphatases (NSAPs) or alkaline phosphomonoesterases (Jorquera et al. 2008) which is responsible for dephosphorylation of phosphoester or phosphoanhydride bonds of organic matter; phytases causing phytate degradation; phosphonatases; and C–P lyases to split the C–P bond of organophosphonates. These enzymes hydrolyse the organic P into the soil.

(c) Substrate degradation leading to liberation of phosphate and mineralisation (McGill and Cole 1981).

Microorganisms engaged in phosphorus solubilisation are primarily arbuscular mycorrhizae and phosphorus-solubilising bacteria (Fankem et al. 2006). Out of the total microbiota prevalent in the soil, phosphorus-solubilising bacteria (PSB) account for 1–50%, while phosphorus-solubilising fungi (PSF) are meagre (0.1–0.5%) for P solubilisation capability. Among bacteria, ectorhizospheric types (*Pseudomonas striata*, *Bacillus megaterium*, *B. circulans*, *B. subtilis*, *B. polymyxa*, *Bacillus sircalmous*, and *Enterobacter*) and endosymbiotic *Rhizobia* have been reported as most efficient phosphate solubilisers (Igual et al. 2001; Subbarao 1988; Kucey et al. 1989). Besides bacteria, fungi (*Penicillium* and *Aspergillus*), actinomycetes, algae (*Cyanobacteria*), mycorrhiza, and a nematophagous fungus *Arthrobotrys oligospora* are well documented for their P solubilisation activity (Whitelaw 2000; Duponnois et al. 2006). Phosphate-solubilising bacteria belong to genera *Arthrobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium*, *Rhodococcus*, and *Serratia* (Ahmad et al. 2008). *Kocuria turfanensis* strain 2M4 acts as phosphate solubiliser which is also reported to produce IAA and siderophores (Goswami et al. 2014).

Iron (Fe) holds fourth rank among the most abundant nutrient on the earth; still Fe deficiency is a widespread problem particularly in arid and semi-arid regions. This is because Fe is not readily assimilated due to presence of rarely soluble ferric ion (Fe^{+3}). Hence, the amount of iron available for assimilation is very low (Aloni et al. 2006). Rhizospheric microorganisms play a key role to overcome Fe deficiencies and greatly influence the Fe uptake by production siderophores, which form Fe^{3+} chelates and are transported through plasma membrane (Awad et al. 1994; Sabry et al. 1997; De Felipe and Fijación 2006). They are mostly produced by microorganisms growing under low stress of iron. Most of the siderophores produced by bacterial genera such as *Streptomyces* and *Pseudomonas* are catecholates, whereas siderophores produced by fungi are hydroxamates (Das et al. 2007).

Siderophores have been associated with improved plant vigour, e.g. PGPR (*Aeromonas*, *Azadirachta*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, *Serratia*, and *Streptomyces* sp.) increased chlorophyll level as in comparison with uninoculated plants (Berg et al. 1980).

10.3.1.2 Plant Growth Regulators

A huge and diverse variety of rhizosphere microbiome is capable of producing growth hormones such as auxins, cytokinins, gibberellins, and ethylene. Plant growth-promoting rhizobacteria (PGPR) produce organic substances also known as exogenous hormones (phytohormones) in extremely low amounts which can control different morphological and physiochemical processes of the plants. PGPR are well documented for production of phytohormones influencing root system architecture (RSA) with an increasing rate of nutrient and water uptake. The most common effect is a reduction of growth rate of primary root and increased number of lateral roots and root hairs. Further, PGPR can also modify chemical makeup and structure of cell wall of root (Zhang et al. 2007). PGPR are also known to produce growth hormones along with secondary metabolites which interfere with the plant auxin pathway (Prasad et al. 2005). Exogenous production of IAA influences a vast range of plant processes. For example, low concentrations of IAA can encourage elongation of primary root, whereas high concentration of IAA encourages lateral roots formation, decreased root length, and increased number of root hairs (Remans et al. 2008). The PGPR (*Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Enterobacter*, and *Klebsiella*) produce IAA in plants majorly through indole-3-pyruvic acid and indole-2-acetic aldehyde pathways (Joo et al. 2005). Root growth promotion by the free-living rhizobacteria like *Enterobacter cloacae*, *Alcaligenes faecalis*, *Acetobacter diazotrophicus*, *Azospirillum* sp., *Pseudomonas* sp., and *Xanthomonas* sp. is reported to be associated with IAA secretion. Auxins like 2,4-diacetylphloroglucinol (DAPG) produced by biocontrol fluorescent pseudomonads induce systemic resistance in plants (Bakker et al. 2007), enhance exudation by roots (Phillips et al. 2004), and stimulate branching of roots (Walker et al. 2011).

PGPR such as *Arthrobacter giacomelloi*, *Azospirillum brasilense*, *Bradyrhizobium japonicum*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, and *Paenibacillus polymyxa* are well documented to produce cytokinins. Cytokinins play a vital role in enhancing cell division, differentiation of root meristem, and root hair proliferation. Besides they also prevent formation of lateral roots and elongation of primary root (Riefler et al. 2006). Several PGPR are known to produce both cytokinins and gibberellins, e.g. *Pseudomonas* and *Bacillus* sp. (Han and Lee 2005). Thus, plant organogenesis and root architecture are regulated by ratio of auxins and cytokinins (Aloni et al. 2006).

Another key phytohormone is ethylene which is produced in small quantities but is responsible for inhibiting elongation of roots, promoting senescence and abscission of different plant organs, and ripening of fruits (Perrig et al. 2007). Higher concentration of ethylene leads to inhibited plant growth by inducing premature senescence, thus leading to poor plant growth and yield (Li et al. 2005). Various biotic and abiotic stresses induce plants to synthesise 1-aminocyclopropane-1-carboxylate (ACC). The increased level of ethylene in response to stress conditions causes termination of important cellular mechanisms such as elongation of roots and bacterial nitrogen fixation in leguminous crop plants thereby causing premature senescence (Jackson 1991; Glick 2012; Ahmad et al. 2013).

PGPR are also capable to produce phytohormones like abscisic acid or gibberellic acid (Dodd et al. 2010). ABA is responsible for causing stomatal closure thereby reducing rate of transpiration and plays a key role under drought stress conditions (Bauer et al. 2013). Besides this it is known for its key role in root development particularly the lateral roots (De Smet et al. 2006). Whereas gibberellins encourage both elongation of primary root and extension of lateral roots (Yaxley et al. 2001). A number of PGPR, viz. *Achromobacter xylosoxidans*, *Acinetobacter calcoaceticus*, *Azospirillum* spp., *Azotobacter* spp., *Bacillus* spp., *Herbaspirillum seropedicae*, *Gluconacetobacter diazotrophicus*, and *Rhizobium*, have been well documented for gibberellins production (Bottini et al. 2004; Dodd et al. 2010). Additionally, both of these phytohormones also induce resistance in plants. Thus, PGPR produced phytohormones and can regulate jasmonate and salicylic acid pathways involved in plant resistance.

In spite the fact that production of phytohormones by PGPR has been well studied, the genetic factors responsible for biosynthesis are still not, and the knowledge about role of bacterial mutants in phytohormones production is scanty. Thus, the role of bacterial synthesised towards plant hormonal balance is not well studied.

Within the rhizosphere, both living (like root exudates) and non-living (like pH, oxygen, type of soil, metals, etc.) factors may influence the effect of PGPR's favourable traits that can lead to distinct expression patterns with different effects on host plant (Drogue et al. 2013). Root exudation by plants may influence the expression of PGPR genes particularly those encoding for plant favouring traits. The expression of phlA gene of *Pseudomonas protegens* was enhanced four times near the roots of maize and wheat compared to those of legumes and cucumber. Sugar content in the root exudates largely influenced synthesis of antimicrobial compounds by fluorescent pseudomonas like DAPG, pyoluteorin, and pyrrolnitrin (Duffy and Défago 1999). Root exudates play a key role in tryptophan biosynthesis pathways (Spaepen et al. 2007). In the absence of exogenous tryptophan supply, bacterial IAA biosynthesis is insignificant. In addition, root exudates also contain vitamins and organic acids which can significantly increase IAA biosynthesis in PGPR (Shukla et al. 2011; Zakharova et al. 2000; Somers et al. 2004). Thus, the composition of root exudates can precisely modify genes encoding for plant favouring traits.

In conclusion, rhizosphere microbiota may lessen impact of various living and non-living stresses on plants. But performance of microorganisms is affected by numerous factors such as not consistent efficiency under geographically different climatic conditions and narrow shelf life. More basic knowledge needs to be generated pertaining to beneficial interactions among microorganisms and plant roots both at cellular and molecular level, as well as the effect of beneficial microbes on virulence spectrum of phytopathogens.

10.3.2 The Deleterious Rhizo-Microorganisms

The rhizosphere in addition to beneficial microorganisms also attracts soil-borne pathogens which are deleterious for plant vigour and well-being. It provides a battlefield where the complex rhizosphere microbiome interacts with soil-borne pathogens and influences the phytopathogens and impacts their pathogenicity causing major yield reductions of food, feed, and fibre crops. Predominant soil-borne plant pathogens include nematodes (*Meloidogyne*, *Heterodera*, *Longidorus*, *Paratrichodorus*, etc.), true fungi, bacteria, and viruses. Among these, viruses need vectors (nematodes, insects, and fungi) to invade plant roots (Campbell 1996).

Plants show a variety of symptoms in response to infection with fungal soil-borne pathogens such as pre- and post-emergence damping off of seedlings (*Pythium* sp.), root rots (*Rhizoctonia* sp.), wilts (*Fusarium* sp.) etc. In response to infection by root rot causing phytopathogens, there is increased mortality of root tips causing reduced root growth leading to poor absorption of water and nutrients. This could be due to destruction of root hairs. As a result, plant shows retarded growth and may exhibit nutritional deficiency.

Two important phenomena, viz. fungistasis and rhizodeposition, that occur in the rhizosphere determine the fate of the pathogen and its ability to initiate infection. Fungistasis refers to reduced rate of germination due to exogenously induced dormancy (Dobbs and Hinson 1953; Lockwood 1977). The fungistatic mechanisms facilitated by soil microorganisms include the presence of volatile or soluble inhibitory substances or lack of essential nutrients for spore germination (Ko and Lockwood 1967; Liebman and Epstein 1992).

Soil-borne fungal plant pathogens, viz. *Rhizoctonia*, *Fusarium*, *Sclerotium*, *Pythium*, and *Phytophthora*, perpetuate in the soil as chlamydospores, oopsores, sclerotia, or hyphae or survive on plant debris (Bruehl 1987). The root exudates stimulate these resting propagules to germinate and invade roots of susceptible plants. This stimulus is particularly important for less virulent phytopathogens which remain in dormant phase in the absence of either nutrients or fungistasis. The microorganisms prevalent in rhizosphere are governed by the resistance or susceptibility level of the crop varieties grown.

For the successful establishment of the pathogen in the rhizosphere, host signals play a vital role. The life cycle of fungi like formation of surviving structures (oospores, sclerotia, etc.) is influenced by various parameters such as pH level of soil, soil type, and root exudates. At low concentrations, phenolic compounds present in root exudates like p-hydroxybenzoic, Gallic, coumaric, cinnamic, ferulic, salicylic, cinnamic acids, etc. stimulate germination of spores of pathogenic fungi; however, presence of these compounds at higher concentrations causes inhibition of spore germination (Wu et al. 2008). This has been demonstrated in *Veratrum taliense* (Liliaceae), *Phytophthora capsici*, and *Rhizoctonia cerealis* combination (Zhou et al. 2003). Both soil physical characteristics and microbes diversity influence the alkaloid makeup (retrorsine and retrorsine N-oxide) in roots and shoots of *Jacobaea vulgaris* (Joosten et al. 2009). These compounds prevent hyphal growth of various phytopathogenic fungi, for example, *Fusarium* and *Trichoderma* sp. (Hol and Veen 2002). Saponins among diverse group of glycosides also adversely affect plant pathogenic fungi by interfering with membrane integrity (González-Lamothe et al. 2009; Osbourn et al. 2011). Evidence of role of saponins (avenacin) in plants defence against root rot fungi *Gaeumannomyces graminis* var. *avenae* has been well presented (Bednarek and Osbourn 2009; González-Lamothe et al. 2009; Osbourn et al. 2011). Avenacin is also responsible for eliciting other processes in the plant such as callose deposition (Bednarek and Osbourn 2009) thereby inducing resistance.

Oomycete pathogens reproduce asexually by production of motile biflagellate zoospores which invade plant roots and cause infection. The composition of root exudates influence chemotactic attraction of zoospores of *Phytophthora* sp. van West et al. (2002) demonstrated that the zoospores that get attracted towards roots is also due to electrotaxis, whereby roots produce electric currents in response to ion exchange at growing ends. Thus, electrotaxis play a critical role in colonisation of roots by zoosporic pathogens.

10.3.2.1 Nematodes

Plant pathogenic nematodes are either free living, ectoparasitic, or endoparasitic. Nematodes move towards roots of plants in response to root exudates (Bird 1959; Young et al. 1996). Perry (2005) and Curtis et al. (2009) have designated these attractants as long distance (attract nematodes to the general root area), short distance (attract nematodes to the roots themselves), and local attractants (orient the nematodes to the preferred penetration site). In the complex rhizosphere, both volatile (long-distance chemotaxis) and water-soluble compounds (short-distance chemotaxis) act as important signals for nematode scavenging (Rasmann et al. 2012).

Carbon dioxide act as major signal released by plant roots to attract nematodes (Jogler et al. 2012). Besides carbon dioxide, many other compounds like naturally occurring hydroxamic acid (DIMBOA), glutamic, and ascorbic acid can induce chemotaxis in nematodes. On the basis of chemotactic property of root attractants, trap crops have been exploited to attract the nematodes to non-host plants (Franco et al. 1999). For example, *Asparagus officinalis* and *Tagetes* species attract a vast variety of nematodes by releasing glycosides (Bilgrami 1997).

10.4 Role of Root–Microbe Communication in Shaping Rhizo-Microbiome

Being a dynamically active habitat for microorganisms, microbiome not only influences plant growth but also affects human or animal health. Efforts are being made to redesign rhizosphere microbiome favouring plant growth-promoting microorganisms and inhibiting phytopathogens. Several studies conducted in the last 20 years evidently showed that the plant genetic makeup and soil properties are two major factors that outline microbial communities in rhizosphere (Berg and Smalla 2009; Bakker et al. 2012).

The information on rhizodeposition and its role in activating and attracting soil-borne plant pathogens are limited and patchy. The inadequate understanding of the cross-talk between plants and soil-borne phytopathogens is mainly due to a scanty knowledge of the complex physiochemical conditions in vicinity of rhizosphere (Weston et al. 2012). The chemical composition and spatiotemporal production of root exudates also called as “ecometabolomics” needs to be elucidated to understand these complex interactions. The comparatively young researchable area of ecometabolomics is the utilisation of metabolomics techniques to biology with the target to characterise biochemical communications among organisms across various spatiotemporal patterns.

References

Ahmad F, Ahmad I, Khan MS (2008) Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. Microbiol Res 163:173–181

Ahmad M, Zahir ZA, Khalid M (2013) Efficacy of rhizobium and pseudomonas strains to improve physiology, ionic balance and quality of mung bean under salt-affected conditions on farmer's fields. Plant Physiol Biochem 63:170–176

Aloni R, Aloni E, Langhans M (2006) Role of cytokinin and auxin in shaping root architecture: regulating vascular differentiation, lateral root initiation, root apical dominance and root gravitropism. Ann Bot 97:883–893

Awad E, Romheld V, Marschner (1994) Effect of root exudates on mobilization in the rhizosphere and uptake of iron by wheat plants. Plant Soil 165:213–218

Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM (2004) How plants communicate using the underground information superhighway. Trends Plant Sci 9:26–32

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266

Bakker PA, Pieterse CM, van Loon LC (2007) Induced systemic resistance by fluorescent Pseudomonas spp. Phytopathology 97:239–243. https://doi.org/10.1094/PHYTO-97-2-0239

Bakker MG, Manter DK, Sheflin AM, Weir TL, Vivanco JM (2012) Harnessing the rhizosphere microbiome through plant breeding and agricultural management. Plant Soil 360:1–13

Barriuso J, Solano BR, Lucas JA, Lobo AP, Villaraco AG, Manero FJG (2008) Ecology, genetic diversity and screening strategies of plant growth promoting rhizobacteria (PGPR). In: Ahmad I, Pichtel J, Hayat S (eds) Plant–bacteria interactions: strategies and techniques to promote plant growth. Wiley, Weinheim, pp 1–17

Bauer H, Ache P, Lautner S, Fromm J, Hartung W, Al-Rasheid Khaled AS (2013) The stomatal response to reduced relative humidity requires guard cell-autonomous ABA synthesis. Curr Biol 1:53–57. https://doi.org/10.1016/j.cub.2012.11.022

Bednarek P, Osbourn A (2009) Plant-microbe interactions: chemical diversity in plant defense. Science 324(5928):746–748. https://doi.org/10.1126/science.1171661

Bender SF, Wagg C, van der Heijden MGA (2016) An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends Ecol Evol 31:440–452. https://doi.org/10.1016/j.tree.2016.02.016

Berendsen RL, Pieterse CM, Bakker PA (2012) The rhizosphere microbiome and plant health. Trends Plant Sci 17(8):478–486. https://doi.org/10.1016/j.tplants.2012.04.001

Berg G, Smalla K (2009) Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol Ecol 68:1–13

Berg RH, Tyler ME, Novick NJ (1980) Biology of azospirillum-sugarcane association: enhancement of nitrogenase activity. Appl Environ Microbiol 39:642–649

Berg G, Eberl L, Hartmann A (2005) The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. Environ Microbiol 7(11):1673–1685. https://doi.org/10.1111/j.1462-2920.2005.00891.x

Bhattacharyya PN, Jha DK (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. Wood J Microb Biotechnol 28:1327–1350

Bilgrami AL (1997) Nematode biopesticides. Aligarh Muslim University, Aligarh, 262 pp

Bird AF (1959) The attractiveness of roots to the plant-parasitic nematodes *Meloidogyne javanica* and *M. hapla*. Nematologica 4:322–335. https://doi.org/10.1163/187529259X00534

Bonkowski M, Villenave C, Griffiths B (2009) Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots. Plant Soil 321(1–2):213–233

Bottini R, Cassán F, Piccoli P (2004) Gibberellin production by bacteria and its involvement in plant growth promotion and yield increase. Appl Microbiol Biotechnol 65:497–503. https://doi.org/10.1007/s00253-004-1696-1

Bruehl GW (1987) Soilborne plant pathogens. Macmillan, New York

Campbell RN (1996) Fungal transmission of plant viruses. Annu Rev Phytopathol 34:87–108

Cook RJ, Thomashow LS, Weller DM, Fujimoto D, Mazzola M, Bangera G, Kim DS (1995) Molecular mechanisms of defense by rhizobacteria against root diseases. Proc Natl Acad Sci USA 4197

Coyne BMS, Mikkelson R (2015) Soil microorganisms contribute to plant nutrition and root health. Better Crops 99(1):18–20

Curtis RHC, Forest R, Perry R (2009) Hatch and host location. In: Perry R, Moens M, Starr J (eds) Root-knot nematodes. CABI, Wallingford, pp 139–162

Das A, Prasad R, Srivastava A, Giang PH, Bhatnagar K, Varma A (2007) Fungal siderophores: structure, functions and regulation. In: Microbial siderophores, vol 12. Springer, Berlin, pp 1–42

De Felipe, Fijación MR (2006) Biológica de dinitrógeno atmosférico en vida libre. In: Bedmar E, Gonzálo J, Lluch C (eds) Fijación de Nitrógeno: Fundamentos y Aplicaciones. Granada: Sociedad Española de Microbiología. Sociedad Española de Fijación de Nitrógeno, Granada, pp 9–16

De Smet I, Zhang H, Inzé D, Beeckman T (2006) A novel role for abscisic acid emerges from underground. Trends Plant Sci 11:434–439. https://doi.org/10.1016/j.tplants.2006.07.003

Dennis PG, Miller AJ, Hirsch PR (2010) Are root exudates more important than other sources of rhizo deposits in structuring rhizosphere bacterial communities? Microbiol Ecol 72(3):313–327. https://doi.org/10.1111/j.1574-6941.2010.00860.x

Deshmukh P, Shinde S (2016) Beneficial role of rhizosphere mycoflora in the field of agriculture: an overview. Int J Sci Res 5(8):529–533

Dobbs CG, Hinson WH (1953) A widespread fungistatis in soils. Nature 172:197–199

Dodd IC, Zinovkina NY, Safronova VI, Belimov AA (2010) Rhizobacterial mediation of plant hormone status. Ann Appl Biol 157:361–379. https://doi.org/10.1111/j.1744-7348.2010.00439.x

Drogue B, Combes-Meynet E, Moënne-Loccoz Y, Wisniewski-Dyé F, Prigent-Combaret C (2013) Control of the cooperation between plant growth-promoting rhizobacteria and crops by rhizosphere signals. In: de Bruijn FJ (ed) Molecular microbial ecology of the rhizosphere, vol 1 and 2. Wiley, Hoboken, pp 281–294. https://doi.org/10.1002/9781118297674.ch27

Duffy BK, Défago G (1999) Environmental factors modulating antibiotic and siderophore biosynthesis by *Pseudomonas fluorescens* biocontrol strains. Appl Environ Microbiol 65:2429–2438

Duponnois R, Kisa M, Plenchette C (2006) Phosphate solubilizing potential of the nematofungus *Arthrobotrys oligospora*. J Plant Nutr Soil Sci 169:280–282

Egamberdieva D, Kamilova F, Validov S, Gafurova L, Kucharova Z, Lugtenberg B (2008) High incidence of plant growth stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ Microbiol 10:1–9

Fankem HD, Nwaga AD, Dieng L, Merbach W, Etoa FX (2006) Occurrence and functioning of phosphate solubilizing microorganisms from oil palm tree (*Elaeis guineensis*) rhizosphere in Cameroon. Afr J Biotech 5:2450–2460

Foster RC (1988) Microenvironments of soil microorganisms. Biol Fertil Soils 6:189–203

Franco J, Main G, Oros R (1999) Trap crops as a component for the integrated management of Globodera spp. (potato cyst nematodes) in Bolivia. Nematropica 29:51–60

Glick BR (1995) The enhancement of plant growth by free-living bacteria. Can J Microbiol 41:109–117

Glick BR (2012) Plant growth promoting bacteria: mechanisms and applications. Scientifica 2012:1–15. https://doi.org/10.6064/2012/963401

González-Lamothe R, Mitchell G, Gattuso M, Diarra MS, Malouin F, Bouarab K (2009) Plant antimicrobial agents and their effects on plant and human pathogens. Int J Mol Sci 10 (8):3400–3419. https://doi.org/10.3390/ijms10083400

Goswami D, Pithwa S, Dhandhukia P, Thakker JN (2014) Delineating *Kocuria turfanensis* 2M4 as a credible PGPR: a novel IAA-producing bacteria isolated from saline desert. J Plant Interact 9 (1):566–576. https://doi.org/10.1080/17429145.2013.871650

Gyaneshwar P, Parekh LJ, Archana GP, Podle S, Collins MD, Hutson RA, Naresh KG (1999) Involvement of a phosphate starvation inducible glucose dehydrogenase in soil phosphate solubilization by *Enterobacter asburiae*. FEMS Microbiol Lett 171:223–229

Han HS, Lee KD (2005) Phosphate and potassium solubilizing bacteria effect on mineral uptake, soil availability and growth of eggplant. Res J Agric Biol Sci 1:176–180

Hartmann A, Rothballer M, Schmid M (2008) Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 312(1):7–14. https://doi.org/10.1007/s11104-007-9514-z

Hinsinger P, Gobran GR, Gregory PJ, Wenzel WW (2005) Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytologist 168 (2):293–303. https://doi.org/10.1111/j.1469-8137.2005.01512.x

Hol WHG, Veen JA (2002) Pyrrolizidine alkaloids from *Senecio jacobaea* affect fungal growth. J Chem Ecol 28:1763–1772. https://doi.org/10.1023/A:1020557000707

Hol WHG, de Boer W, de Hollander M, Kuramae EE, Meisner A, van der Putten WH (2010) Context dependency and saturating effects of loss of rare soil microbes on plant productivity. Front Plant Sci 6:485. https://doi.org/10.3389/fpls.2015.00485

Hooper DU, Hapin FS, Ewel J, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge M, Loreau M, Aeem S, Schmid B, Setala H, Symstad AJ, Andermeer JV, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75 (1):3–35

Igual JM, Valverde A, Cervantes E, Velázquez E (2001) Phosphate-solubilizing bacteria as inoculants for agriculture: use of updated molecular techniques in their study. Agronomie 21:561–568

Jackson MB (1991) Ethylene in root growth and development. In: Matoo AK, Suttle JC (eds) The plant hormone ethylene. CRC, Boca Raton, pp 159–181

Jogler C, Waldmann J, Huang X, Jogler M, Glockner FO (2012) Identification of proteins likely to be involved in morphogenesis, cell division and signal transduction in Planctomycetes by comparative genomics. J Bacteriol 194(23):6419–6430

Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil-root interface. Plant Soil 321:5–33. https://doi.org/10.1007/s11104-009-9925-0

Joo GJ, Kim YM, Kim JT (2005) Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. J Microbiol 43:510–515

Joosten L, Mulder PPJ, Klinkhamer PGL, Veen JA (2009) Soil-borne microorganisms and soil-type affect pyrrolizidine alkaloids in *Jacobaea vulgaris*. Plant Soil 325:133–143. https://doi.org/10.1007/s11104-009-9963-7

Jorquera MA, Hernandez MT, Rengel Z, Marschner P, Mora MD (2008) Isolation of culturable phosphor bacteria with both phytate-mineralization and phosphate-solubilization activity from the rhizosphere of plants grown in a volcanic soil. Biol Fertil Soils 44:1025–1034. https://doi.org/10.1007/s00374-008-0288-0

Kaymak DC (2010) Potential of PGPR in agricultural innovations. In: Maheshwari DK (ed) Plant growth and health promoting bacteria. Springer, Berlin

Kim KY, Jordan D, McDonald GA (1997) Solubilization of hydroxyapatite by *Enterobacter agglomerans* and cloned *Escherichia coli* in culture medium. Biol Fert Soils 24:347–352

Kloepper JW, Ryu CM, Zhang S (2004) Induced systemic resistance and promotion of plant growth by Bacillus spp. Phytopathology 94:1259–1266

Ko WH, Lockwood JL (1967) Soil fungistasis: relation to fungal spore nutrition. Phytopathology 57:894–901

Kogel KH, Franken P, Heuckelhoven R (2006) Endophyte or parasite-what decides*?* Curr Opin Plant Biol 9:358–363. https://doi.org/10.1016/j.pbi.2006.05.001

Kucey RMN, Janzen HH, Legget ME (1989) Microbial mediated increases in plant available phosphorus. Adv Agron 42:199–228

Kumar M, Kumar V, Prasad R (2020) Phyto-microbiome in stress regulation. Springer, Singapore. ISBN 978-981-15-2576-6. https://www.springer.com/gp/book/9789811525759

Lau JA, Lennon JT (2011) Rapid responses of soil microorganisms improve plant fitness in novel environments. Proc Natl Acad Sci USA 109(35):14058–14062. https://doi.org/10.1073/pnas.1202319109

Li Q, Saleh-Lakha S, Glick BR (2005) The effect of native and ACC deaminase containing *Azospirillum brasilense* Cdl843 on the rooting of carnation cuttings. Can J Microbiol 51:511–514

Liebman JA, Epstein L (1992) Activity of fungistatic compounds from soil. Phytopathology 82:147–153

Lladó S, López-Mondéjar R, Baldrian P (2017) Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. Microbiol Mol Biol Rev 81:e00063–e00016. https://doi.org/10.1128/MMBR.00063-16

Lockwood JL (1977) Fungistatis in soils. Biol Rev 2(1):1–43. https://doi.org/10.1111/j.1469-185X.1977.tb01344.x

Lu T, Ke MJ, Peijnenburg WJGM, Zhu YC, Zhang M, Sun LW (2018) Investigation of rhizospheric microbial communities in wheat, barley, and two rice varieties at the seedling stage. J Agric Food Chem 66:2645–2653

Lynch JM, Whipps JM (1990) Substrate flow in the rhizosphere. Plant Soil 129(1):1–10

McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26(4):267–286. https://doi.org/10.1016/0016-7061(81)90024-0

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663. https://doi.org/10.1111/1574-6976.12028

Narula N, Deubel A, Gans W, Behl RK, Merbach W (2006) Paranodules and colonization of wheat roots by phytohormone producing bacteria in soil. Plant Soil Environ 52:119–129

Nath M, Bhatt D, Bhatt MD, Prasad R, Tuteja N (2018) Microbe-mediated enhancement of nitrogen and phosphorus content for crop improvement. In: Prasad R, Gill SS, Tuteja N (eds) Crop improvement through microbial biotechnology. Elsevier, Amsterdam, pp 291–301

Osbourn A, Goss RJ, Field RA (2011) The saponins: polar isoprenoids with important and diverse biological activities. Nat Prod Rep 28:1261–1268. https://doi.org/10.1039/c1np00015b

Perrig D, Boiero ML, Masciarelli OA, Penna C, Ruiz OA, Cassán FD (2007) Plant-growth-promoting compounds produced by two agronomically important strains of *Azospirillum brasilense*, and implications for inoculant formulation. Appl Microbiol Biotechnol 75:1143–1150. https://doi.org/10.1007/s00253-007-0909-9

Perry RN (2005) An evaluation of types of attractants enabling plant-parasitic nematodes to locate plant roots. Russ J Nematol 13:83–88

Phillips DA, Fox TC, King MD, Bhuvaneswari TV, Teuber LR (2004) Microbial products trigger amino acid exudation from plant roots. Plant Physiol 136:2887–2894. https://doi.org/10.1104/pp.104.044222

Pieterse CMJ, Van Pelt JA, Van Wees SCM, Ton J, Léon-Kloosterziel KM, Keurentjes JJB, Verhagen BWM, Knoester M, Van der Sluis I, Bakker PAHM (2001) Rhizobacteria-mediated induced systemic resistance: triggering, signalling and expression. Eur J Plant Pathol 107:51–61

Prasad R (2008) Studies on interaction between a symbiotic fungus (*Piriformospora indica*), rhizobacteria and selected plants. Ph. D. thesis. CCS University, Meerut

Prasad R, Garg AP, Varma A (2005) Interaction of medicinal plants with plant growth promoting rhizobacteria and symbiotic fungi. In: Podila GK, Varma A (eds) Basic research and applications of Mycorrhizae, vol 1. IK International, Delhi, pp 363–407

Prasad R, Kumar M, Varma A (2015) Role of PGPR in soil fertility and plant health. In: Egamberdieva D, Shrivastava S, Varma A (eds) Plant growth-promoting rhizobacteria (PGPR) and medicinal plants. Springer International, Cham, pp 247–260

Prasad R, Bhola D, Akdi K, Cruz C, Sairam KVSS, Tuteja N, Varma A (2017) Introduction to mycorrhiza: historical development. In: Varma A, Prasad R, Tuteja N (eds) Mycorrhiza. Springer International, Cham, pp 1–7

Prasad R, Chhabra S, Gill SS, Singh PK, Tuteja N (2020) The microbial symbionts: potential for the crop improvement in changing environments. In: Tuteja N, Tuteja R, Passricha N, Saifi SK (eds) Advancement in crop improvement techniques. Elsevier, Amsterdam, Netherlands, pp 233–240

Prashar P, Kapoor N, Sachdeva S (2013) Rhizosphere: its structure, bacterial diversity and significance. Rev Environ Sci Biotechnol 13:63. https://doi.org/10.1007/s11157-013-9317-z

Qiang X, Weiss M, Kogel KH, Schafer P (2012) Piriformospora indica a mutualistic basidiomycete with an exceptionally large plant host range. Mol Plant Pathol 113:508–518

Rasmann S, Ali JG, Helder J, van der Putten WH (2012) Ecology and evolution of soil nematode chemotaxis. J Chem Ecol 38:615–628

Remans R, Beebe S, Blair M, Manrique G, Tovar E, Rao IM (2008) Physiological and genetic analysis of root responsiveness to auxin-producing plant growth-promoting bacteria in common bean (*Phaseolus vulgaris* L.). Plant Soil 302:149–161. https://doi.org/10.1007/s11104-007-9462-7

Riefler M, Novak O, Strnad M, Schmülling T (2006) *Arabidopsis* cytokinin receptor mutants reveal functions in shoot growth, leaf senescence, seed size, germination, root development and cytokinin metabolism. Plant Cell 18:40–54. https://doi.org/10.1105/tpc.105.037796

Sabry SRS, Saleh SA, Batchelor CA (1997) Endophytic establishment of *Azorhizobium caulinodans* in wheat. Proc Biol Sci 264:341–346

Saharan BS, Nehra V (2011) Plant growth promoting rhizobacteria: a critical review. Life Sci Med Res 21:1–30

Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56. https://doi.org/10.1038/nature10386

Schnitzer SA, Klironomos JN, HilleRis LJ, Kinkel LL, Reich PB, Xiao K, Rillig MC, Sikes BA, Callaway RM, Mangan SA, van Nes EH, Scheffer M (2011) Soil microbes drive the classic plant diversity-productivity pattern. Ecology 92:305

Shrivastava S, Prasad R, Varma A (2014) Anatomy of root from eyes of a microbiologist. In: Morte A, Varma A (eds) Root engineering, vol 40. Springer, Berlin, pp 3–22

Shukla KP, Sharma S, Singh NK, Singh V, Tiwari K, Singh S (2011) Nature and role of root exudates: efficacy in bioremediation. Afr J Biotechnol 10:9717–9724

Singh D, Raina TK, Kumar A, Singh J, Prasad R (2019) Plant microbiome: a reservoir of novel genes and metabolites. Plant Gene. https://doi.org/10.1016/j.plgene.2019.100177

Somers E, Vanderleyden J, Srinivasan M (2004) Rhizosphere bacterial signalling: a love parade beneath our feet. Crit Rev Microbiol 30:205–240

Spaepen S, Vanderleyden J, Remans R (2007) Indole-3-acetic acid in microbial and microorganism-plant signaling. FEMS Microbiol Rev 31:425–448. https://doi.org/10.1111/j.1574-6976.2007.00072.x

Subbarao NS (1988) Phosphate solubilizing micro-organism. In: Biofertilizer in agriculture and forestry. Regional Biofert. Dev. Centre, Hisar, pp 133–142

Tejera N, Lluch C, Martínez-Toledo MV (2005) Isolation and characterization of *Azotobacter* and *Azospirillum* strains from the sugarcane rhizosphere. Plant Soil 270:223–232

Van der Heijden MGA, Klironomos J, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396(6706):69. https://doi.org/10.1038/23932

Van der Heijden MGA, Streitwolf-Engel R, Riedl R, Siegrist S, Neudecker A, Ineichen K, Boller T, Wiemken A, Sanders IR (2006) The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. New Phytol 172:739–752

Van der Heijden MGA, Bardgett RD, Van Straalen NM (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11:296–310

Van West P, Morris BM, Reid B, Appiah AA, Osborne MC, Campbell TA, Gow NAR (2002) Oomycete plant pathogens use electric fields to target roots. Mol Plant-Microbe Interact 15 (8):790–798. https://doi.org/10.1094/MPMI.2002.15.8.790

Wagg C, Jansa J, Schmid B, Van der Hinjen MGA (2011) Belowground biodiversity effects of plant symbionts support aboveground productivity. Ecol Lett 14(10):1001–1009. https://doi.org/10.1111/j.1461-0248.2011.01666.x

Walker V, Bertrand C, Bellvert F, Moënne-Loccoz Y, Bally R, Comte G (2011) Host plant secondary metabolite profiling shows a complex, strain-dependent response of maize to plant growth-promoting rhizobacteria of the genus Azospirillum. New Phytol 189:494–506. https://doi.org/10.1111/j.1469-8137.2010.03484.x

Weston LA, Ryan PR, Watt M (2012) Mechanisms for cellular transport and release of allelochemicals from plant roots into the rhizosphere. J Exp Bot 63:3445–3454. https://doi.org/10.1093/jxb/ers054

Whitelaw MA (2000) Growth promotion of plants inoculated with phosphate solubilizing fungi. Adv Agron 69:99–151

Wu Y, Fang W, Zhu S, Jin K, Ji D (2008) The effects of cotton root exudates on the growth and development of *Verticillium dahliae*. Front Agric China 2(4):435–440

Yaxley JR, Ross JJ, Sherriff LJ, Reid JB (2001) Gibberellin biosynthesis mutations and root development in pea. Plant Physiol 125:627–633. https://doi.org/10.1104/pp.125.2.627

Young IM, Griffiths BS, Robertson WM (1996) Continuous foraging by bacterial-feeding nematodes. Nematologica 42:378382. https://doi.org/10.1163/004425996X00100

Zakharova EA, Iosipenko AD, Ignatov VV (2000) Effect of water-soluble vitamins on the production of indole-3-acetic acid by *Azospirillum brasilense*. Microbiol Res 155:209–214. https://doi.org/10.1016/S0944-5013(00)80034-8

Zhang H, Kim MS, Krishnamachari V, Payton P, Sun Y, Grimson M (2007) Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in *Arabidopsis*. Planta 226:839–851. https://doi.org/10.1007/s00425-007-0530-2

Zhou CX, Liu JY, Ye WC, Liu CH, Tan RX (2003) Neoverataline A and B, two antifungal alkaloids with a novel carbon skeleton from *Veratrum taliense*. Tetrahedron 59:5743–5747