Manoeuvring Soil Microbiome and Their Interactions: A Resilient Technology for Conserving Soil and Plant Health

19

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Abstract

The soil microbial community hugely affects the growth and development of the plants through direct or indirect interactions. The rhizospheric microbial community dwelling in the soil are major drivers of this phenomenon. Manipulation of soil microbial population and community through various treatments of an array of beneficial microbes such as plant growth-promoting rhizobacteria, plant growth-promoting fungi, endophytic bacteria, biocontrol agents, etc. helps in alleviating various abiotic and biotic stresses of the plants. This, in turn, leads to the achievement of the yield which is close to the potential yield of the crop. Apart from increasing the yield of the crop, some of the beneficial microbes also enhance the nutrient content in the soil and availability of certain minerals to the plants eventually leading to conservation of soil health. Thus, manipulation of plant–soil microbiome paves the way for sustainable and green agriculture without imparting excessive monetary expenses, thereby creating increased crop production and embellishment of soil health. This chapter will so focus on the strategies and methods that are adopted to manipulate the plant–soil microbiome interactions, various mechanisms that are involved in the interactions, and the impact of this technology on the plant and soil.

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Keyword

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19.1 Introduction

The agricultural ecosystems are experiencing an enormous pressure of providing the food to the growing population along with maintaining environmental sustainability. The agricultural lands are constantly degrading because of the faulty farming packages, changing climate, invasion of foreign species, accumulation of pollutants and chemicals, and many other reasons. Since the soil is at the receiving end of this cycle, the organisms which thrive on it are also very gravely affected as it is the most complex and diverse habitat. The crops permanently require a soil system to grow as it provides the base and required nutrients to them, with exception to hydroponics and aeroponics. The microorganisms which dwell in the soil are also at risk which is also a reason to worry as they are the critical players of various functions and services provided by the agricultural ecosystem (Jiao et al. 2019). Soil microbiome can be defined as the total count of microorganisms inhabiting the soil which co-exist together in the rhizospheric as well as the non-rhizospheric zones and are able to perform various functions either individually or together that ultimately changes the properties of soil and health of plants grown on them. These microbes include bacteria, fungi, protozoa, algae, and actinomycetes. These microbes are diverse in nature and range from beneficial ones to harmful ones. The beneficial ones support plant growth and development either directly and/or indirectly by providing the nutrients, stimulating plant growth, and acting as antagonists to phytopathogenic microbes. The major component of soil microbiome is fungi, bacteria, and archaea groups, which altogether makes more than 99% of soil microbial biomass (Fierer 2017). Additionally, various saprophytic, mutualistic, and phytopathogenic microbes also constitute the soil microbiome which also has important roles to play (Peay et al. 2016). The effects of soil microbiome on plants and soil are now very much evident and it is now a proven fact that a right microbial composition is essential for the betterment of both.

The relationship between soil, plants, and soil microbiome is now deciphered day-by-day, and now a new tier of connection is also added to it which is animals (Attwood et al. 2019). This new connection is very well evident from the proof that different ecto-endophytic plant microbes which pass onto plants from soil microbiome also enter the rumen of animals and aid in digestion (Kingston-Smith et al. 2008). The interactions between plants and the soil microbiome are also highly coordinated and dependent on various factors such as biotic or abiotic stresses, microbial population, climatic condition, soil, host plant, root exudates, and microbial secretions (Bais et al. 2006; Lakshmanan et al. 2014). This along with various other functions is carried out by the soil microbiome that is essential for the vitality of earth. It is so grievous that the soil microbiome is under threat due to urbanization, industralization, climate change, land degradation, changing rainfall pattern, malformed agricultural practices, and poor land management practices (Amundson et al. 2015). Additionally, the pressure of feeding the population has adjured farmers to increase the agricultural production by adopting intensive agriculture which in turn has led to detrimental effects on soil physical and chemical properties and also loss of soil microbial diversity. The consequence of all these factors and their impact on soil microbiome is still poorly understood and needs more focus in order to make a sustainable agricultural blueprint (Köhl et al. 2014; Kumar et al. 2015). Hence, in recent times the scientific farming community is having enhanced interest and attention manoeuvring soil microbiome as a means for increasing crop production and/or productivity, soil restoration, and ecological balance (Calderón et al. 2017).

The habitat of soil-derived plant microbiome ranges from the whole plant to specific organs to the zone of interactions between plant and soil, i.e. rhizosphere and plant and atmosphere, i.e. phyllosphere (Rout and Southworth 2013). The rhizospheric region of the soil is dynamic in nature and is constantly remodelled by the influences of growing plants through exudation/secretion/deposition of various molecules and compounds (Bais et al. 2006; Badri and Vivanco 2009; Hinsinger et al. 2009; Shi et al. 2011; Moe 2013). The plants thereby through these influences bring changes in inhabiting microbiome. Reciprocally, the microbiome also brings changes in plants through production of different regulatory compounds which can have a positive or negative impact on the growth and fitness of the former (Carney et al. 2007; Mendes et al. 2011; Lebeis 2015). The soil microbiome thus behaves as an immensely evolved exterior force which possesses excellent potential of making changes in the cultivating crop plants (Philippot et al. 2013; Turner et al. 2013; Spence et al. 2014; Vaishnav et al. 2019); therefore, it is also aptly called as plant's second genome (Berendsen et al. 2012). Higher buffering capacity and reproduction potential of microbes have led to advanced genetic evolution in them which enables them to adapt to different environmental conditions. The stability of microbes under wavering soil conditions is also because of their abundance, physiological tolerance, molecular flexibility, widespread dispersal, and horizontal gene transfer (Allison and Martiny 2008; Fuhrman et al. 2015). The three main mechanisms which function behind their stability are resilience, resistance, and functional redundancy (Allison and Martiny 2008). The mechanism of resilience can be described as the ability of microbes to recover very readily to its stable state after the changes brought by any of the disturbances (Griffiths and Philippot 2013; Hodgson et al. 2015). Resistance in microbes is the ability to exhibit a significant magnitude of tolerance against any disturbances. The microbial functional redundancy is described as the phenomenon where the disturbed microbial ecosystem possesses the same traits to that of original one even though the community is significantly modified without recover (Allison and Martiny 2008).

The manoeuvring of plant's soil microbiome is one of the best alternatives which can ease of the dual pressure of increasing the agricultural production but with eco-friendly and sustainable agriculture, without imparting excessive monetary expenses. A particular strain of microbe or a consortium of many compatible microbe scans be thereby used for increasing agricultural production and enrichment of soil health (Yadav et al. 2019; Mukherjee et al. 2020; Patel et al. 2020). There are many commercial microbial formulations present in the market which are even utilized by the farmers successfully as biofertilizers and seed inoculants (Patel et al. 2019; Prabha et al. 2019). Since both soil and plants are meta-organism, our knowledge and understanding about the precise mechanisms and processes which are involved during their interactions with the microbial community and their outcome are still insufficient. In this chapter, we will mainly focus on knowledge of the importance of soil microbiome, its composition, their interactions with host plant and their outcome, their effects on soil health, and the role of soil microbiome in achieving sustainable agriculture along with increased production and productivity.

19.2 Composition of Soil Microbial Community and Population

Soil and the microbes inhabiting in them together make the base of food webs carrying out functions like maintenance of terrestrial life, nutrients recycling, and elemental cycling pathways of production and degradation (Wilpiszeski et al. 2019). Microbes are known to form communities that are complex in nature, having varying structure, interactions, and functions. They are the most diversified form of life and have an indispensable role to play in different ecological functions and biogeochemical cycles. The soil microbial community lives in close association with the soil particles in the form of a single cell or as matrix embedded biofilms (Maier et al. 2009; Kamal et al. 2010). The diversity of soil microbes and their composition in different communities are the major indicators of soil fertility and productivity (Wang et al. 2019). The soil microbial community constitutes of bacterial species, archaeal species, and species from eukaryotic taxa (Curtis et al. 2002). The bacterial and archaeal species are the most ancient microbial life-forms and are thus found in more diverse environmental conditions. Among the eukaryotic taxa, fungal species are more prominent ones which are comparatively more modern microbial life-form in their appearance and are evolved in close association with the plants (Maier et al. 2009; Kamal et al. 2010). The total life from an estimate in the soil varies diversely, among which the bacterial species solely range from over thousands to millions in one gram of soil (Curtis et al. 2002; Torsvik and Øvreås 2002; Schloss and Handelsman 2006). These soil microbes are either the supporter or inhibitor of the plant's growth and development through direct and indirect means. The supporters are known as the beneficial microbes which function as symbionts, mutualists, or endophytes. The inhibitors are known as the phytopathogens and negatively affect plants through tissue damage and the production of toxins (Roper and Gupta 1995; Mukherjee et al. 2020). In addition to bacteria and fungi, the soil microbial population also has viruses and protozoan species (Jansson and Hofmockel 2019). The abundance level of soil microbial population is so much so that it constitutes about 60% of the earth's biomass (Bar-On et al. 2018).

The microbial population in the soil is majorly categorized into three groups. The first group comprises beneficial microorganisms like nitrogen-fixing bacteria, plant growth-promoting rhizobacteria, mineral solubilizing bacteria, mycoparasitic fungi, mycorrhizal fungi, biocontrol agents, etc. which is the most studied one. The second group comprises phytopathogenic microorganisms which are deleterious to plant and the third group comprises human-pathogenic microorganisms which are deleterious to human health (Teplitski et al. 2011; Kaestli et al. 2012). The plant growth-promoting rhizobacteria (PGPR) are free-living bacterial species which are found in the rhizospheric region of the soil and expend beneficial effects on plants through direct and indirect means. They provide nutrients to plants by nutrient acquisition, help in signal transduction and growth by phytohormones production, and form a channel of cross-talk with other microbes in soil and plants (Backer et al. 2018; Patel et al. 2020). The nitrogen-fixing bacteria are the symbiotic bacterial species which fixes atmospheric nitrogen in the soil and is majorly found associated with legume crops with some exceptions to non-leguminous crops (Mahmud et al. 2020). The mineral solubilizing bacteria are yet another group of bacterial species which aids in mineralization of nutrients that are present in fixed states in the soil (Mukherjee et al. 2019). The mycoparasitic fungi and the biocontrol agents are the species of microbes which are parasitic to pathogenic fungi and microbes, respectively. The mycorrhizal fungi is another group of fungi that lives in a symbiotic association with plants performing the functions of nutrients mineralization and activation of defence genes in plants against phytopathogens (Maharshi et al. 2019).

There are now many modern and efficient methods of estimating the soil microbial population but the classical ones are still more reliable. The classical method of estimation of soil microbial population is serial dilution along with isolation and culturing on different mediums (Lakshmanan et al. 2014). The population is calculated by counting the number of colonies of microbes formed at a specific dilution level of the soil. The only drawback of this method is that we do not get the exact population level as the unculturable microbes are not counted. Once the microbes are in pure culture form, then they can be identified through PCR methods and also evaluated for their potentiality as plant growth promotion microbes, biocontrol agent, and others (Forchetti et al. 2007; Beneduzi et al. 2008; Taulé et al. 2012). The exact estimation of soil microbial population is also dependent on sampling and sequencing techniques. In modern times, the soil microbiome population and diversity are calculated through the high-throughput sequencing methods, DNA/RNA SIP method, and DNA arrays (Mendes et al. 2011; Uhlik et al. 2013; Nkongolo and Narendrula-Kotha 2020). The sequencing methods also provide only a partial coverage as it is estimated that one gram of soil contains up to 1000 Gbps of metagenomic DNA (Frisli et al. 2013). The structure and function of soil microbial population are controlled by different factors which are host-dependent and host-independent. The host-dependent factors include host-plant species, host-plant genotype, host-plant signalling pathways, secretions from host-plants root, etc. The host-independent factors include soil type, temperature, soil pH, moisture, soil porosity, etc. (Lakshmanan et al. 2014). The taxonomic diversity of microbes found in the rhizosphere of different plants is given in Table 19.1.

Table 19.1 Composition of soil microbes in rhizosphere of different plants

Host	Main rhizospheric microbiome	References
Erica andevalensis	Actinobacteria, followed by the acidobacteria, and proteobacteria. Archaea: community was composed of crenarchaeota	Mirete et al. (2007)
Zea mays	Azospirillum, bradyrhizobium, and ideonella	Roesch et al. (2007)
Avena sativa	Proteobacteria, firmicutes, actinobacteria, verrucomicrobia, and nitrospira	De Angelis et al. (2009)
Deschampsia antarctica and *Colobanthus quitensis*	Firmicutes, few acidobacteria Bifidobacterium (phylum actinobacteria), Arcobacter (phylum proteobacteria), and Faecalibacterium (phylum firmicutes)	Teixeira et al. (2010)
Oak	Proteobacteria, acidobacteria, and actinobacteria.	Uroz et al. (2010)
Beta vulgaris	Proteobacteria, firmicutes, and actinobacteria. Gamma- and betaproteobacteria and firmicutes	Mendes et al. (2011)
Solanum tuberosum	Proteobacteria, firmicutes, actinobacteria, bacteroidetes, and acidobacteria. Bacterial families streptomycetaceae, micromonosporaceae, and pseudomonadaceae	Weinert et al. (2011)
Rhizophora mangle and *Laguncularia racemosa*	Halobacteria, methanobacteria, methanomicrobia, and thermoprotei	Pires et al. (2012)
Mammillaria carnea	Acidobacteria, actinobacteria, proteobacteria, and bacteroidetes	Torres-Cortés et al. (2012)
Arabidopsis thaliana	Acidobacteria, proteobacteria, planctomycetes, and actinobacteria	Bulgarelli et al. (2012)
Glycine max	Proteobacteria	Vaishnav et al. (2018)
Vitis vinifera	Proteobacteria, actinobacteria, acidobacteria, bacteroidetes, ascomycota, basidiomycota, and zygomycota	Berlanas et al. (2019)
Glycine max	Proteobacteria, acidobacteria, actinobacteria, bacteroidetes, firmicutes, verrucomicrobia, and planctomycetes	Liu et al. (2019)
Adenium obesum, Aloe dhufarensis, and *Cleome austroarabica*	Actinobacteria, proteobacteria, bacteroidetes, planctomycetes, acidobacteria, verrucomicrobia, ascomycota, basidiomycota, and mucoromycota (only in *A. obesum* and *A. dhufarensis*)	Khan et al. (2020)
Panax ginseng	Proteobacteria, actinobacteria, acidobacteria, bacteroidetes, chloroflexi, firmicutes, gemmatimonadetes, plactomycetes, nitrospirae, latescibacteria, mucoromycota, ascomycota, and basidiomycota	Wei et al. (2020)

19.3 Effects of Soil Microbiome on Plants

As stated earlier, there is a massive count of microbes which colonize plant roots and offer distinct valuable assistance to them. These microbes can work independently or in interaction with each other also. In a recent study, it was shown that the arbuscular-mycorrhizal parasites and the plant growth-promoting rhizobacteria could live as symbionts in a model grassland system and supplement each other for better acquirement of nutrients. Thus, consequently, it was deduced that symbionts possessing diverse functions could supplement the root microbiome which would help in mitigation of nutrients constraint (Van Der Heijden et al. 2015; Vyas et al. 2018). From the evolution of life-forms from amphibian to terrestrial habitat, plants got exposed to a considerable array of microbes constituting of bacteria, fungi, and protists (Kenrick and Crane 1997). This exposition of land plants to microbes led to the establishment of different interactions between them and making up of a flawless soil microbiome which became a trademark characteristic of plants in adapting to a new habitat. Evidences from the fossil remains showed that the plants which were engaged in advantageous interactions with the arbuscular-mycorrhizal fungi and other microbes, were well equipped with improved nutrient uptake from the soil and came into being 400 million years ago (Lambers et al. 2009). The phyletic examinations also support the hypothesis that developmental advancement of land plants in solitary mode happened only 100 million years ago which is later than mutualistic mode as mentioned. This was concluded by studying the ability of angiospermic plants to create a specific positive association with the nitrogen fixers (Werner et al. 2014). The modern researches aided with computational techniques have enabled scientist to declassify microbial diversity and their possible interactions with plants (Lebeis et al. 2012). The researches have shown that plants have dynamic and conglomerated microbial communities consisting of fungal, bacterial species working in a consortium as mutualist, commensals, and parasites (Schlaeppi and Bulgarelli 2015).

Advanced disclosures from the experiments have proved that the immune system of a plant is an outcome of its interactions with the soil microbial community. As, for example, in *Arabidopsis thaliana*, a complete defence system is established by a consortium of non-pathogenic endophytes, and root microbes (Lebeis et al. 2015; Hiruma et al. 2016). This perception is also supported with the revelations that soil microbial partners are also equipped with different machineries which tune the defence system of plants, for example, the T3SS (type III secretion system) in bacterial species (Guttman et al. 2014). The soil microbes which can have beneficial effects on the plants essentially have two kinds of mechanisms. First category is made of the mechanisms which have a direct effect on plants growth and development. It includes protections from phytopathogens (Lugtenberg and Kamilova 2009), improved nutrient acquizition (Pii et al. 2015; Terrazas et al. 2016), and regulation of phytohormones (Glick 2012). The second category is made of the mechanisms which have indirect effects on plants growth and development. These include activation of induced systemic response (ISR), inducing the production of stress-related molecules (Parray et al. 2016; Vaishnav et al. 2014), and all the

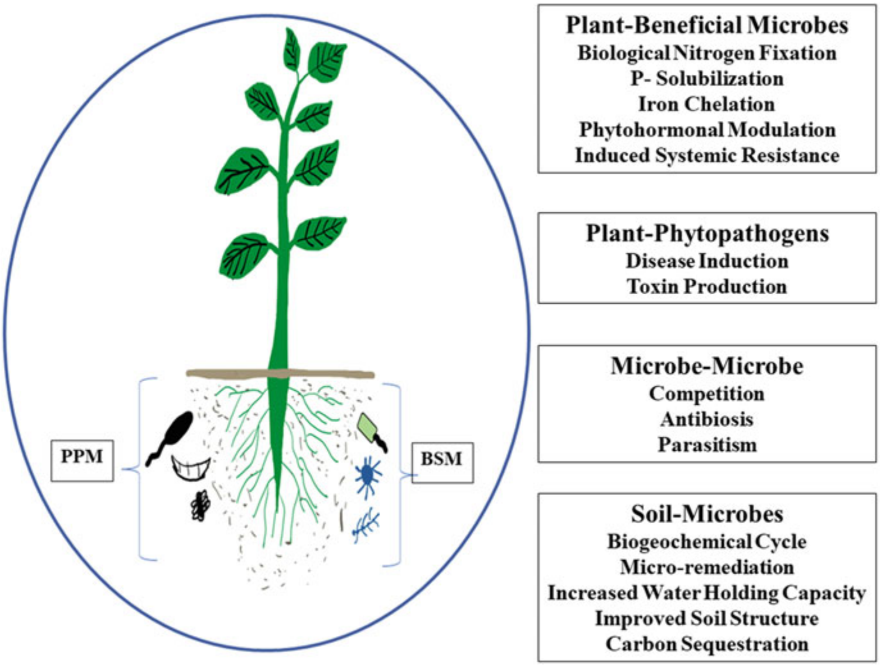

Fig. 19.1 The effects which come out after interactions between plant–soil microbes. *PPM* phytopathogenic microbes, *BSM* beneficial soil microbes

different activities which indirectly shield plants from phytopathogens (Lugtenberg and Kamilova 2009) as given in Fig. 19.1.

1. *Direct effects*: The major mechanisms of soil microbiome which have a direct effect on the plants are improvement in the availability of nutrients, production of phytohormones, and inciting of plant diseases. Nutrients bioavailability in the rhizospheric region is most important for the plants as its development and profitability firmly rely on them. Some of the primary mechanisms involved in minerals bioavailability for plants are nitrogen fixation, phosphorus solubilization, and siderophore production (Pii et al. 2015; Terrazas et al. 2016). The phytopathogenic microbes also have a direct impact on the plant through the production of phytotoxins and incitation of plant diseases. Additionally, the beneficial soil microbes also help plants to survive under different abiotic stresses such as drought conditions through direct mechanisms, i.e. through the production of extracellular polysaccharides (EPS) (Lakshmanan et al. 2017; Naylor and Coleman-Derr 2018). There is also a massive surge in the researches where the soil microbes can be used as inoculants to support plants against the changing environment (Compant et al. 2010). The osmotic stress in plants is also alleviated by rhizospheric microbes through the production of specific metabolites and

inducing aquaporins in plants (Casanovas et al. 2002; Pereyra et al. 2012; Quiroga et al. 2017; Kapilan et al. 2018).

a. *Biological nitrogen fixation (BNF) and nitrate availability*: This is one of the most studied direct mechanisms of beneficial microbes on plants as well as soil. Many of the commercial formulations of microbes are available in the market, which is used for nitrogen fixation in crop plants (Yadav et al. 2019). It is also one of the functions of soil microbes which is applied to a large scale in the agricultural sector. Biological nitrogen fixation is the process in which atmospheric nitrogen (N_2) is converted into nitrate forms which can be taken up by plants, by different microbes with the help of nitrogenase enzyme (Kim and Rees 1994). These microbes are symbiotic nitrogen-fixing bacteria like *Rhizobium* and *Frankia* and also free-living bacteria like *Azotobacter*, *Azospirillum*, *Azoarcus* (Bhattacharyya and Jha 2012; Bhat et al. 2015; Yadav et al. 2019; Vaishnav et al. 2017). Among the two, free-living bacterial species can only provide a limited quantity of atmospheric nitrogen fixation, while the symbiotic ones are more productive (Jones et al. 2007); nevertheless, both are equally important as symbiotic ones can be only used with legumes with a few exceptions (Yadav et al. 2019). Arbuscular-mycorrhizal fungi are also known for making nitrogen available to plants. They utilize the ammonia present in soil and reduce the production of nitrous oxide (Jansson and Hofmockel 2018).

b. *Phosphorus solubilization*: Soil contains an enormous quantity of phosphorus (P) in both organic and inorganic state but, unfortunately, less than 1% is available for uptake by plants (Bhattacharyya and Jha 2012; Alegria Terrazas et al. 2016). It is an essential nutrient for the plants which is required in macro-quantity. The immobilized form of phosphorus in inorganic forms is mineralised by different acids like formic acid, shikimic acid, gluconic acid, and 2-ketogluconic acid produced by different microbes like *Bacillus*, *Aspergillus*, *Trichoderma*, *Pseudomonas*, *Klebsiella*, *Lactobacillus*, and *Enterobacter* (Hinsinger et al. 2009; Sharma et al. 2013; Hunter et al. 2014; Azeem et al. 2015).

c. *Iron chelation*: Iron is one of the essential micronutrients for the plants which is found in two states, viz: Fe^{2+} and Fe^{3+} of which the latter one is the non-available form of iron to plants and microbes (Colombo et al. 2014; Mimmo et al. 2014). Many soil microbes produce a low molecular weight iron-chelating compounds that have a high affinity to Fe^{3+} ions and aid in the absorption of iron across different membranes (Neilands 1981; Guerinot 1994; Lemanceau et al. 2009; Hider and Kong 2010). The chelated Fe^{3+} ions by the microbial siderophores are also taken up by the plants (Crowley et al. 1988; Walter et al. 1994; Jin et al. 2006; Robin et al. 2008).

d. *Phytohormone modulation*: Phytohormones are known to play various key roles in developmental processes of a plant (Taiz and Zeiger 2006; Glick et al. 2007). The activity and movement of phytohormones in plants are dependent on the versatility of the root system which responds according to nutrients availability (Kloepper et al. 2007). Phytohormones like auxins, cytokinins, and gibberellins are produced by many PGPRs which affect the plant's root system (Vacheron et al. 2013). The cytokinins and gibberellins produced also have a profound effect on the plant growth and development; however, the exact underlying mechanism is still not precise (Glick 2012). Auxins are also produced by different microbes that are discharged to the external environment (Scagliola et al. 2016) which modulate cell division, cell differentiation, development of vascular bundles, and many other processes in plants (Sachdev et al. 2009; Overvoorde et al. 2010). They also lead to an increased root growth in a plant which alternately provides better access to nutrients and water which relives plants from water stress also (Xie et al. 1996; Mayak et al. 1999; Armada et al. 2015; Lakshmanan et al. 2017). Indole acetic acid (IAA) is one of the auxin molecules which is produced by microbes that are known to act as a signalling molecule and induce different gene expressions in plants and microbes itself (Spaepen and Vanderleyden 2011). PGPRs also produce an enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase which catalyses ACC, a precursor of ethylene (Arshad et al. 2007) and thus facilitating plant growth through ethylene modulation (Glick 2014). Ethylene is believed as the stress-hormone (Abeles et al. 2012) and thus its modulation leads to induction of defence responses during stress conditions as well as detrimental responses such as chlorosis, senescence, abscission during prolonged stress condition (Glick 2014). The phytohormone modulation also helps plants to overcome drought stress through accumulation of osmolytes and scavenging of reactive oxygen species (ROS) (Lakshmanan et al. 2017; Vurukonda et al. 2016; Vaishnav et al. 2019).

e. *Disease induction*: Contradictory to the beneficial soil microbes, there are certain other species of microbes which are known for inhibition of plant growth and hampering of plant health, thus, are accordingly called as phytopathogenic microbes or phytopathogens. They are a threat to global food security. The soil-borne phytopathogenic microbes are known to survive in the bulk soil, and the rhizospheric region is also an important niche for them where they live as parasites either on the root surface or inside the roots of plants. The exudates from plant roots activate and attract its pathogenic microbes present in soil towards itself (Agrios 2005). The bacterial phytopathogens are known to enter a plant through natural opening and wounds leading to disease development. Some of them colonize in the xylem vessels and caused wilt in plants like *Ralstonia* spp. (Genin and Boucher 2004), while some of them transmit their nucleic acid into the plant's cells and cause irregular growth of cells as in the case of *Agrobacterium tumefaciens* (Nester et al. 2005). Fungal phytopathogens are more advanced and used different mechanisms for penetrating the root cells and inciting diseases. Most of the soil-borne phytopathogenic fungi are necrotrophic but some of them are biotrophic like *Plasmopara* spp. and *Plasmodiophora* spp. (Friskop et al. 2009) They penetrate the root surface by germ tubes and by infecting the epidermal cells. This is achieved either by cell wall degrading enzymes or by the action of hydrostatic force. Additionally, both bacterial and fungal phytopathogens produce phytotoxins which are harmful to plants.

2. *Indirect effects*: The major mechanisms of soil microbial complex, which alternatively has indirect effects on the plants, are competition, induced systemic resistance, antibiotics production, and production of lytic enzymes. There has been a very strong agreement among the farm scientific community to utilize these mechanisms in mainstream management practices for controlling phytopathogens instead of chemical pesticides.
    a. *Competition*: It is a type of negative interaction between the soil microbes where they compete for the nutrients and space at intra-specific and inter-specific level. Competition leads to the evolution of superior microbial phenotypes which are able to outcompete and remove incompetent ones. The competition is generally higher during the first encounter between the soil microbes and reduces over time due to partitioning of niche or spatial separation or competitive exclusion; thus, they are able to coexist stably (Ghoul and Mitri 2016). During the competition, different microbes compete for niches or nutrients or both. PGPRs are known to compete for the phytopathogens in the rhizospheric region of soil and thus reduce the incidence and severity of diseases. PGPRs also produce siderophores in higher quantities than the phytopathogens. The siderophores solubilize different micronutrients like iron, making them unavailable for the phytopathogens. This ultimately leads to hampered capacity of phytopathogens to multiply and provide an indirect benefit to plants (Schippers et al. 1987; Lugtenberg and Kamilova 2009).
    b. *Induced systemic resistance (ISR)*: Many of the non-pathogen soil microbes are known to activate a defence response system in plants which enables them to protect themselves from phytopathogens by acting sooner (van Loon et al. 1998). ISR activates plant's innate defence barriers, thereby enhancing the defence response. This upgradation of the defence system is not just activated at the site of infection but is systemically throughout the plant by jasmonic acid or ethylene signalling pathways (Verhagen et al. 2004; Jain et al. 2017). The different bacterial products which are known to induce ISR are chitin, flagellar proteins, glucans, and surfactants (Annapurna et al. 2013).
    c. *Antibiotics and lytic enzymes production*: Another mechanism of soil microbes which has an indirect effect on plants is the production of certain metabolite that can inhibit the growth and multiplication of other microbes. The phenomenon is known as antibiosis and the metabolites are known as antibiotics (Waksman 1947; Selwyn 1981). Lytic enzymes are sub-group of antibiotics which have the ability to hydrolyse the peptidoglycan layer of microbial cell wall (Fischetti 2010). Lytic enzymes are also known as lysozymes and are majorly produced by bacteriophages and bacteria (Ohbuchi et al. 2001; Loessner 2005; Lortal and Chapot-Chartier 2005; Salazar and Asenjo 2007; Fischetti 2010; Oliveira et al. 2012). The focus on lysozyme production by the filamentous fungi is given very less attention (da Silva et al. 2014). Cellulases, chitinases, proteases, glucanases, and lipases are different lytic enzymes which are produced by soil microbes which have an adverse effect on

phytopathogenic microbes. Many of the antibiotics such as tensin, phenazine, xanthobaccin, pyrrolnitrin, and zwittermicin A are produced by PGPRs which enable them to function as a biocontrol agent, thus providing indirect benefit to plant (Whipps 2001; Haas and Keel 2003; Compant et al. 2005; Mazurier et al. 2009).

19.4 Effects of Soil Microbiome on Soil

Soil health is a very important point which is always addressed in any of the discussion pertaining to sustainable agriculture. Management of soil is fundamentally essential for agricultural systems, but mining activities, climate change, land degradation, growing industrialization and urbanization, etc. are causing a detrimental effect on soil health and thus threatening the sustainable agriculture. Soil microbiome plays an important role in the restoration of soil health and productivity, as shown in Fig. 19.1. Soil plays as a diverse role in sustenance and functioning of the ecosystem such as providing the base for the biogeochemical cycle of various elements that also enriches its health (Aislabie et al. 2013). There are many beneficial soil microbes that have been identified which are utilized for improvement of soil health in addition to plant growth. However, unfortunately, only less than 10% of such soil microbes have been described yet (Callaway 2016). As the global food demand is going to be doubled by 2050, it is thus necessary to deploy these microbes for increasing the resistance to various stresses caused by biotic factors present in soil (Vorholt et al. 2017; Zavala-Gonzalez et al. 2017). These microbes not only provide help in providing resistance to plant and playing a role in various biogeochemical cycles but also enhances the nutrient uptake in a plant by making it in available form.

The microbes enhance soil health by making the various nutrients in available form, orchestrating various biogeochemical cycle of elements, increasing water holding capacity, improving soil structure, carbon storage, and root growth and also by favouring the growth of various flora (Nannipieri et al. 2017). There are certain beneficial microbes that have an antagonistic effect on various soil-borne pathogens, hence increase the crop productivity by providing protection against pest and disease outbreaks as described earlier (Bonanomi et al. 2018). They enhance the growth of the plant by improving the uptake of various macro- and micronutrients by bringing changes in characteristics of soil through degrading the organic matter, mineralization, solubilization, and weathering of rocks (Van Der Heijden et al. 2008). There is a huge number of soil microbes which are found in plants rhizosphere that can act as symbionts, enhancing the growth and production of plants by complementing each other with limiting nutrients (Vyas et al. 2018). Earth’s crust is a huge reservoir of organic matter and various minerals where different biological phenomenon by soil microbial complex regulates the store and release of carbon and various minerals (Amundson et al. 2015). The soil microbiome decides the physical property of soil and hence often regarded as bioindicator for soil health (Liu et al.

2019). Arbuscular-mycorrhizal fungi have the capacity to reduce leaching of plant nutrients from the soil as well as phosphorus scavenging, thereby ultimately embellishing the nutrient-use efficiency of soil (Cavagnaro et al. 2015; Kumar et al. 2015).

The soil microbes also help in restoration of soil health by carrying out bioremediation and biodegradation processes. The process of remediation is divided into three groups on the basis of the biological entity involved, namely phytoremediation (carried out by plants), micro-remediation (carried out by microbes), and rhizomediation (carried out by plants in association with rhizospheric microbes). There are many genera of arbuscular-mycorrhizal fungi whose potential has been described for degradation of soil contaminants and toxic materials which are leftover as residues like *Gigaspora* spp., *Glomus* spp., and *Acaulospora* spp. (Khan et al. 2014). Additionally, these fungi also have a role to play as bio-surfactants for removing metal ion contaminations in soil and bring them down below threshold level (Thavasi et al. 2011). As stated earlier also, soil microbes also perform the process of biodegradation in soil and convert the complex organic materials into their monomeric forms, accompanied by the release of carbon dioxide and water (Ramana and Singh 2000). The process of biodegradation is done by various chemical and physical mechanisms of various soil microbes (von Wirén-Lehr et al. 2002). Many soil-borne fungi have been reported to decompose compounds such as hydrocarbons, nitrilases, nitro-reductases, radionuclides, polyaromatic hydrocarbons, polychlorinated biphenyls, and even the chemical pesticide dichloro-diphenyl-trichloro-ethane (DDT) (Patil et al. 1970; Chaudhry et al. 2005; Glick 2010).

There are a majority of soil-borne beneficial microbes which have been well-studied for their positive effects on soil but their application is only limited to disease management. Since these microbes are native to the soil, they are major drivers of soil organic matter and nutrients apart from providing resistance to pest and diseases in plants (Dubey et al. 2019). As we all are aware that the overdependence of the farming community on various inorganic fertilizers and chemical pesticides has hampered the environment and soil health. So, its high time for moving towards the green and sustainable agriculture for which we must have to explore more and more soil microbes and deploy them for achieving sustainability. The utilization of various modern biotechnological tools and its application on microbes has enormous potential to enhance the quality of soil, environment, and sustainable agriculture (Peng et al. 2016). There are some important microbes like arbuscular-mycorrhizal fungi that contain multinucleated genetic system which cannot be engineered. For such microbes, classical method of isolation, selection, and culture should be applied in order to make them operational for soil amelioration (Muleta 2017; Charubin and Papoutsakis 2019).

19.5 Methods of Soil Microbiome Management

With our increasing knowledge about the role of soil microbiome on plants and soil itself, different management practices have been devised for utilisation of such microbiome for beneficial effects. These management practices of manoeuvring soil microbiome form under two categories, namely: direct and indirect manipulation of soil microbiome by bringing changes in agricultural practices. Some of the methods for management of soil microbiome are explained as below:

1. *Organic farming*: The organic farm management practices lead towards achievement of more diverse and stable soil microbiome which has a beneficial effect on both plants and soil and is strictly advised for barren agricultural lands (Chaparro et al. 2012). This type of farming is based on principles of minimising the off-farm inputs which aids in restoring, maintenance, and enhancement of ecological harmony (Gold 2007). Since the use of chemical fertilisers and synthetic pesticides is not done during cultivation of land and growing of the crop, their harmful effect of soil microbial evenness and diversity reduction is completely alleviated (Liu et al. 2007; Crowder et al. 2010; Sugiyama et al. 2010; Krauss et al. 2011). On the contrary, organic farming promotes the use of microbial diversity for providing nutrients to plants and controlling plants diseases and pests (Sugiyama et al. 2010). Soil microbial complexity and richness are also affected by land use pattern, degree of stress and disturbance which are least in organic farming and thus further adding to the benefits (Degens et al. 2000, 2001).
2. *Beneficial microbes as inoculants*: The beneficial soil microbes which can inhabit the rhizospheric region and help plants in counteracting stresses can be used as seed inoculants or as supplement to standing crop in either solid or liquid formulations (Prabha et al. 2019). Seeds or planting materials are the base material which develops into plants, and therefore the application of beneficial microbes on themselves provides plants with an edge over the upcoming stresses. This is also a straightforward method of managing the soil microbiome as we do not have to physically manipulate it during advanced stages of plants. The classical example for this is the use of *Rhizobium* spp., as a seed treatment in leguminous crops for enhanced nitrogen fixation. In present time in addition to *Rhizobium* spp., various other beneficial soil microbes are available in market in different formulations which can be used as biofertilizers and biopesticides in various crops as seed inoculants (Yadav et al. 2019). Various PGPRs are also available in the form of commercial formulations which alleviate plants from drought stress (Kumar et al. 2017).
3. *Carbon sequestration*: Carbon sequestration is a process of reducing the atmospheric carbon levels by converting it into stable and non-gaseous forms by different abiotic and/or biotic processes. Plants are the dominant biological organism which performs most of the carbon sequestration, but there are also certain soil microbes which are autotrophic and perform the function of carbon assimilation (Jansson and Hofmockel 2019). Carbon compounds which are deposited by plants and other organisms are known to stimulate free-living and

symbiotic soil microbes. Soil microbial community is regulated by the carbon compounds as it passes through different microbes in bioavailable forms and lastly taking the unavailable forms. The carbon sequestration ability of soil is dependent on the soil microbial diversity with quantity and form of carbon alternatively regulating the diversity (Lal 2004). A particular soil microbe or consortium of different ones who carry out the reactions of carbon sequestration can be used for making more stable carbon products (Hicks et al. 2017). In a complementary fashion, soil microbiomes can also be manoeuvred through the addition of amendments which embellishes their capacity to consume and store carbon (Jansson and Hofmockel 2019). Root exudates of plants also affect the dynamics and makeup of soil microbes of which mostly are carbon compounds. Hence, the crop plants can be genetically engineered to produce exudates which can incite the beneficial soil microbes having the ability to trap this carbon exudates (Wallenstein 2017; Jansson et al. 2018) and also leading to more microbial diversity.

4. *Crop cover*: It is an age-old agricultural practice to cover the croplands with different crops known as cover crops during the season or time when they are not cultivated. This practice of covering agricultural land with cover crops has now attained a major role in sustainable agricultural practices (Schipanski et al. 2014; Groff 2015). The main reason behind the use of cover crops was to control the growth of weeds either by the mechanism of competition and/or allelopathy (Weston 1996; Brust et al. 2014; Cordeau et al. 2015). Additionally, they also prevent soil erosion, nutrient loss, and modify different properties of soil (Kuo and Sainju 1998; Hubbard et al. 2013). Since it is known already that the plants are major drivers of soil microbial complex, cover can thus be used for modulating the microbial communities in the soil to derive beneficial effects (Bardgett and van der Putten 2014; Schlatter et al. 2015; Vukicevich et al. 2016; Romdhane et al. 2019). Deployment of cover crops over a more extended period can lead to an enhanced nutrients availability in soil and thereby stimulating diversity and abundance of soil microbes (Schmidt et al. 2018; Castellano-Hinojosa and Strauss 2020). Cover cropping with multiple species of plants constituting of at least two legumes or non-legumes has shown to increase soil microbial diversity along with the abundance of many beneficial rhizospheric bacteria like *Pseudomonas* spp., *Azotobacter* spp., *Azospirillum* spp., and *Bacillus* spp. and beneficial mycorrhizal fungus such as *Gigaspora* spp., *Acaulospora* spp., *Scutellospora* spp., and *Archaeospora* spp. (Hamel et al. 2005; Mazzola and Manici 2012; Wortman et al. 2012; Bever et al. 2015). The outcome of increased soil microbial diversity is obvious due to application of multiple cover crop as there is a positive correlation between plant biodiversity and soil microbial diversity (Garbeva et al. 2004; Maron et al. 2011; Fanin et al. 2014; Civitello et al. 2015). Furthermore, removal of cover crop through herbicide application leads to more loss of soil bacterial diversity than through other means of removal (Moreno et al. 2009), therefore, during the cultivation period the cover crops should be terminated using any other means than herbicides.

19.6 Challenges in Shaping Plant–Soil Microbiome Interactions

From the recent microbiome research, the perception about the diverse microbial community and its impact on soil physical structure has been changed. However, we are just at the starting point of understanding the diverse microbial community and their interactions with plant and soil. With increasing need to develop alternate methods for soil health restoration and plant improvement, scientists are looking at insights to understand the dynamic role of soil microbiome and their interactions with plant and soil (Goodrich et al. 2017). As unique microbiome is present in the rhizosphere of every plant, we have to move towards the personalization of microbiome according to the host for taking the advantages from beneficial ones (Lundberg et al. 2012). Hence, for deployment of the potential soil microbiome, firstly, there is a need to develop different approaches to comprehend the diverse functions of that particular soil microbiome (Bashiardes et al. 2018). As it is an established fact that soil microbiomes are a key determiner for better crop growth and production, there is a challenge of how to apply this knowledge from lab to field (Sergaki et al. 2018) and persuade farmers for use of this technology.

Before defining the shape of plant–soil microbiome under any environment, we have a challenging task to assign a specific function to that particular microbiome group. The diverse lifestyle of the microbiome at genus or even at species level makes the task further tougher. Additionally, their nature keeps changing due to change in their genetic makeup either due to mutation or due to horizontal transfer of particular functional gene(s) (Qiu et al. 2009; Hiruma et al. 2016). This can variably bring drastic changes from the desired phenotype of soil microbiome (Lidbury et al. 2016). Although, with the advancement of various technologies like computational or modelling methods, transition from metagenomics to metamorphic and metaproteomic enables us to comprehend the critical function performed by the certain specific responsible taxa (Prosser 2015; Ofaim et al. 2017). However, there are several limitations to these, as these methods require a sufficiently high starting material, correctly assigned peptides or proteins, and appropriate computational power.

When the task of assigning the function of soil microbiome is over, next challenge forward is to specify the application of these soil microbes with assigned functions to different crops and in different soils for obtaining an interaction which should be useful to agriculturists. In order to overcome this challenge, we have to carry out a considerable number of experiments in order to find the perfect combination of soil microbiome, plant type, and soil type, which should additionally also be feasible for the farmers to adopt. Since we are working with more than soil microbes if we are taking in consideration of the microbiome, then we also have to study the interactions between the different microbes as well. For a successful achievement of soil microbiome which can benefit the plant growth and production, the consortium of microbes should have synergism between themselves and should have antagonism between them and the abiotic or biotic stresses. For achieving such elaborative information, a lot of combinational studies is required which is quite laborious and tiresome. After overcoming all these challenges, there is also a tedious task of making the microbial in the form of a formulation which should have longer shelf-life, more comfortable to apply, compatible with other sustainable agricultural inputs, and should be of spreading characteristic for higher reach in after soil application. Lastly, the adoption of this technique by the farmers is also an area of concern as mostly they tend to adopt a technique which gives immediate results. As the technique of soil microbiome manipulation is based on the medium of soil and microbial manipulation is a comparatively slow process, showing results over a longer time, there would be a low adoption rate by the farmers. Nevertheless, it can also be overpowered by educating the farmers about the benefits of soil microbiome manipulation in the long run and motivating them for adopting this technology.

19.7 Social and Economic Impacts of Soil Microbiome Management

For genuineness and successful implementation of technology, it is essential it should be socially and economically beneficial for humankind and world. Therefore, it is always important to analyse the social and economic impact of all the scientific technologies which are developed. The soil microbial community provides a consequential amount of economic and social insistence to the society and global economy on an annual basis through their role in the regulation of diverse processes and functions of the ecosystem (Sandhu et al. 2010). The global economic growth was predicted to about 3.5% in 2019 and 3.6% in 2020, which would mean that there is going to be high-income growth and therefore lead to more consumption of food. For meeting the increased consumption and food demand of the growing population, adequate measure for improvement and maintenance of soil health is essential (Lal 2009). Soil is the base for most of the ecosystems globally which provides support for both plants and animals and therefore, the soil and its services are essential too. Considering soil and its services, 90% of the soil processes are carried out by the soil microbiome (Coleman et al. 2004), making them a major player of the global agricultural economy. The ecological services which are provided by the soil microbiome are estimated to be approximately about US \$1.5 trillion year^{-1} globally, in economic terms (Pimentel et al. 1997). The biological nitrogen fixation process which is carried out by the soil microbes is solely responsible to generate an economic value of US \$50–70 billion year^{-1} globally (Sandhu et al. 2010). Nitrogen fertilizers are the synthetic source which is applied by the farmers to meet the nitrogen demands of plants which comes at a high cost. The world consumption of three primary fertilizer nutrients, namely: nitrogen (N), phosphorus (P), and potassium (K) was estimated to be about 186.67 million tons in 2016 with an annual growth of 1.5%, 2.2%, and 2.4%, respectively, from 2015 to 2020 (FAO 2017). The manipulation of soil microbiome along with application of nitrogen fixers and phosphorus solubilizers could decrease the dependence on fertilizer and also provide economic benefit to the farmers together with sustainable agriculture (Altieri 1999). The microbial inoculant industry would also get a boost and provide a new domain of employment and entrepreneurship for the youth globally. The nutrient cycling value of soil microbes was calculated to be about US \$165.62 ha^{-1} year^{-1} in organic farming system and US \$142.0 ha^{-1} year^{-1} (Sandhu et al. 2008, 2010).

Many of human communities have been surviving on the natural resources from centuries. Despite huge enhancement in agricultural production during green revolution, many of the small and marginal farmers were unable to procure the seeds and other agricultural inputs due to monetary issues. To this lack of information and technical capabilities, these farmers were not able to ripe the benefits and suffered from impaired productivity. The microbial inoculants come at a relatively cheaper cost which is affordable for these types of farmers. The manipulation of soil microbial complex is a sustainable approach; there is no need for microbial augmentation after a beneficial microbial complex is established. Majority of the farmers in South Asia, Africa, and many developing countries are poor who do not realize the importance of managing soil constraints. Since there is an inevitable linkage of human livelihood and their social well-being with soil health, the social sustainability of these farmers could be achieved by soil health maintenance (Lal 2009; Sandhu et al. 2010). Use of microbial formulation instead of pesticides will undoubtedly help in the alleviation of ill-effects that are caused by the residues of latter, thus ensuring a safer environment and human health. The increased agricultural production, reduced use of machinery, reduced use of synthetic input, reduction of soil erosion, etc. are some of the major benefits which are obtained from soil microbiome management which will help farmers in both social and economic aspects.

19.8 Conclusion

For succeeding in the long-term, it is essential to shift from conventional practices towards sustainable agriculture in order to maintain the soil health and meet the demands of the growing population. A complete insight about the structure and function of soil microbiome would undoubtedly help in increasing the crop production and productivity simultaneously with restoration of soil health. The rhizospheric region of soil is a hotspot for microbial functionality; therefore, isolation, characterization, and use of beneficial microbes from this region will help in the stimulation of plant growth and also protect them from various abiotic and biotic stresses. The knowledge of interactions between plant, soil, and microbes will undisputedly play an important role in achieving sustainable development goals. The manipulation of soil microbiome is a resilient technology which is here to stay, since microbes are insistent and stubborn to climatic vagaries. Some more advanced researches in this area would enable us to understand the interactive functions of soil microbiome and plants which will be pivotal for the utilisation of specific microbes against specific problems. The manipulation of soil microbiome is the most simple and effective method of planning future ecological functions and therefore is a key for ensuring a sustainable planet.

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