Chapter 16
From mycorrhizosphere to rhizosphere microbiome: The paradigm shift

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Abstract Mycorrhizosphere, the niche of mycorrhizal roots, is made of diverse microorganisms and represents a complex phenomenon in terms of microbe-root-environment interactions. Synthetic microbial consortia, i.e. co-cultures of microbial species with specific functions such as biofertilizers or biocontrol agents that are developed to accomplish specific targets of crop productivity in agro ecosystems, are mainly based on management microbial interactions. In order to develop a viable system for increasing soil fertility and crop production through application of these bioinoculants, it is necessary to have a clear understanding of the diversity, interactions and functioning of microbiome associated with roots. The present chapter introduces paradigm shift from usage of term mycorrhizosphere to microbiome of mycorrhizal roots, along with certain important concepts like, core and minimal communities, rhizosphere engineering etc. The content is divided into different sections, which deal with diversity, interaction, and management of mycorrhizal microbiome for better plant health and crop productivity.

16.1 Introduction

Mycorrhiza is the symbiotic association between the plant roots and the soil fungi. Almost all plants form mycorrhiza. It is estimated that c. 74% of all plant species form arbuscular mycorrhiza (AM), 9% form orchid mycorrhiza, c. 2% form ectomycorrhizal (EM) associations and 1% form ericoid mycorrhiza (van der Heijden et al. 2015). These fungal-root associations have a key role in terrestrial ecosystems as they regulate nutrient and carbon cycles. Mycorrhizal fungi provide up to 80% of the plant's N and P to get bread (carbohydrates) and butter (lipids) in return (Rich et al. 2017). The roots, both mycorrhizal and non-mycorrhizal, are the key source for providing various organic compounds in the habitat in the proximity of, on, and inside the root, which affects the composition, aeration properties, and biological activities of soil.

The term 'mycorrhizosphere' is derived from 'mycorrhiza' and 'rhizosphere' (the region around roots). Since plant roots are commonly mycorrhizal, the rhizosphere concept was widened to include the fungal component of the symbiosis into it (Linderman 2008). Thus, the mycorrhizosphere is the zone influenced by both the root and the mycorrhizal fungus and includes the more specific term 'hyphosphere', which refers only to the zone surrounding individual fungal hyphae (Johansson et al. 2004). The microbial

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habitats in the mycorrhizosphere are further divided into rhizosphere (soil-root interface), rhizoplane (root surface), and root endosphere (inside root). The three sub-habitats usually harbor different microorganism (Fig. 16.1). Microbiota thriving on rhizoplane and within roots is selected by a host genotype-dependent differentiation (Bertin et al. 2003), which, in turn, influence the plant resistance to pests, support beneficial symbioses, alter the chemical and physical properties of the soil, and inhibit the growth of competing plant species.

The mycorrhizosphere region is characterized by increased microbial activity stimulated by the leakage and exudation of organic substances from the root, called as root exudates (Bansal and Mukerji 1994, 1996; Bansal et al. 2000; Edwards et al. 2015). Plants release 10-20% of their photosynthates as exudates, which alter the physical and chemical properties of soil that in turn provides suitable niches for microbial proliferation (Edwards et al. 2015; Yuan et al. 2016). Root exudates include a wide range of compounds, like carbohydrates, amino acids, organic acids, fatty acids, nucleotides, flavones, vitamins, and enzymes (Bansal and Mukerji 1996). A positive correlation was indicated between mycorrhiza-induced changes in the qualitative and quantitative pattern of root exudation and mycorrhizosphere mycoflora (Bansal and Mukerji 1994).

Rhizosphere microbiome is a relatively new term, which refers to the diverse and dynamic community of microorganisms associated with plant roots that is not much different from (mycor) rhizosphere in its essence. However, it certainly indicates that the microorganisms studied are genomes or virtual taxa, using metagenomics methods. Studies of rhizosphere microbiome present a holistic view of diversity and interaction across the habitat. Consistent with the terminology used for microorganisms colonizing the human body, the collective communities of plant-associated microorganisms are referred as the plant microbiome or as the plants' other genome (Qin et al. 2010). In this context, plants are viewed as 'superorganisms' which is partly dependent on their microbiome for specific functions and traits. This includes all plant associated microbe habitats such as rhizosphere, spermosphere (seed surface), phyllosphere (leaf surface), and the stem microbiome. Recent applications of microbial metagenomics, metatranscriptomics, and metabolomics to plants and their surroundings have confirmed a key role of mycorrhizal fungi, rhizosphere bacteria and fungi in determining the make-up of rhizosphere microbial community and suggested a world of hitherto undiscovered interactions in the rhizosphere (Dickie et al. 2015). This knowledge is leading to a paradigm-shifting view that plants are to be considered as a meta-organism or holobionts instead of isolated individuals.

Metagenomic analyses have provided a powerful lens for a holistic view of the microbial world in the rhizosphere and improved our understanding of entire rhizosphere functioning and microbial community interactions. Since the taxonomic identification of interacting microflora is not mandatory for biome level studies, all rhizosphere microflora in soils could be characterized in workable details. This also overcomes the difficulties associated with the study organisms whose culturing is difficult –AM fungi, which cannot be cultured axenically and their taxonomy is difficult (Powell and Bennett 2016). Recent characterization of barcode sequences (Krüger et al. 2012) and development of dedicated environmental sequence databases such as, MaarjAM for AM fungi (Opik et al. 2010, 2016), has made it possible to study and characterize AM fungal genomes in environmental samples. Powerful amplicon-based deep sequencing techniques provide more detailed and accurate insights into the diversity, structure, and assembly of microbial communities than previous clone library sequencing or PCR-DGGE (denaturing gradient gel electrophoresis) approaches (Guttman et al. 2014). Small-subunit ribosomal RNA (16S SSU) gene and nuclear ribosomal internal transcribed spacer (ITS) or large-subunit ribosomal RNA (28S LSU) have often been used as barcodes for amplicon sequencing of bacterial and fungal communities (Qin et al 2010; Krüger et al. 2012).

It is becoming evident with recent studies that interactions of mycorrhizal microbiomes play an important role in soil nutrient uptake and management of soil-borne diseases in sustainable agricultural practices (Berruti et al. 2016). Different levels of interaction in rhizosphere microbes change their nutrition equation, which could be related to plant health (Kier et al. 2016). It is suggested that these microbiomes are not passive players rather, microbes can alter host development, physiology, and systemic defenses, enable toxin production and disease resistance (Weller et al. 2012), increase host tolerance to stress and drought, modulate niche breadth and change fitness outcomes in host interactions with competitors, predators, and pathogens (reviewed by Berg et al. 2014). In return, plants deposit their photosynthetically fixed carbon into their direct surroundings (Raaijmakers et al. 2009), thereby feeding the microbial community, and influencing their composition and activities.

The present chapter primarily focuses on different aspects of the microbial community associated with mycorrhizal roots including diversity, interaction, and applications in enhancing the crop productivity. The main concepts and recent terminology used in rhizosphere microbiome studies, which are equally applicable to both mycorrhizal and non-mycorrhizal roots are included.

16.2 Diversity and interactions across mycorrhizal microbiome

The rhizosphere (mycor) is considered as one of the most complex ecosystems on earth, which harbors numerous microorganisms. Number of (micro) organisms that constitute rhizosphere microbiome is much greater than the number of plant cells (Mendes et al.2013). In addition, the number of microbial genes in the rhizosphere outnumbers the number of plant genes in a microbiome (Fig. 16. 1). Organisms found in the rhizosphere (mycor) include bacteria, fungi, oomycetes, nematodes, protozoa, algae, viruses, archaea, and arthropods (Bansal et al. 2000). The interactions among them can be physical i.e. for space, or physiological, but are directed towards nutrient acquisition. Most members of the rhizosphere microbiome compete for the large amount of nutrients released by the plants as root exudates.

Several criteria have been used to group rhizosphere organisms. Mendes and coworkers (2013) classified them as ‘good’, ‘bad’ or ‘ugly’ on the basis of their role in the rhizosphere. Microorganisms those have been well studied for their beneficial effects on plant growth and health are classified as ‘good’ component of rhizosphere microbiome. These include the nitrogen-fixing bacteria, mycorrhizal fungi, plant growth promoting rhizobacteria (PGPR), biocontrol microorganisms, mycoparasitic fungi, and protozoa. Rhizosphere microorganisms those are deleterious to plant growth and health are classified as ‘bad’. These include the pathogenic fungi, oomycetes, bacteria, and nematodes. A third group of microorganisms, those are found in the rhizosphere are the human pathogens. These are classified as ‘ugly’. Over the past decade, there are an increasing number of reports describing the proliferation of human pathogenic bacteria in the rhizosphere soil (Kumar et al. 2013).

Microbial community present in different sub habitats of rhizosphere (mycor) microenvironments are frequently separated into rhizosphere, rhizoplane and endospheremicroflora, each possessing distinct features to which microorganisms have to adapt (Fig 16.1) (McNear 2013; van der Heiden and Schlaeppi 2015; Edwards et al. 2015). There is evidence that plant roots select these specific microbes in early growth stages and sustain a relatively stable community irrespective of growth stage (Edwards et al. 2015; Yuan et al. 2016). Vandenkoornhuyse coworkers (2015) found that in almost all the cases the diversity of microbes decreased from rhizosphere to endosphere, suggesting some strong filtering mechanism of habitats. The endosphere of roots have well adapted microbial communities due to the pressure exerted by host plant (Hernández et al. 2015). However, a systematic understanding of how overall rhizosphere communities and their members differ from or complement each other, in terms of functioning within the plant, across the plants and between the taxa, is still lacking.

Investigations on diversity and interaction of rhizosphere microbiome hold a great promise in solving the food and grains problem. Survey of research papers published in the year 2017(until now), revealed that rhizosphere microbiome has been investigated extensively, and holds a potential to increase plant growth and production of important crop plants. Up to 37% percent of the total studies examined from citations in Google scholar, JSTOR and Catalogue Harvard Library were devoted to application of rhizosphere microbiomes in increasing growth and productivity (Fig 16.2). Many more paper have investigated microbial diversity with an indirect aim of increasing crop production.

Different plant species support unique microbiomes. Plant microbiome structure and function under different natural and agricultural environments have been explored in many plant species, including, *Arabidopsis thaliana* (Schlaeppi et al. 2014), barley (*Hordeum vulgare*) (Bulgarelli et al. 2015), soybean (*Glycine max*) (Rascovan et al. 2016), corn (*Zea mays*) (Aira et al. 2010), wheat (*Triticum aestivum*) (Donn et al. 2015), rice (*Oryza sativa*) (Edwards et al. 2015) and cotton wood trees (*Populus trichocarpa*) (Shakya et al. 2013). Efforts are being made to develop a complete catalog of microbial species thriving in the rhizo- and endosphere of some model plants including *Arabidopsis thaliana* and *Populus* spp. (Hacquard and Schadt 2015; Lundberg et al. 2012) and crops such as maize and rice (Edwards et al. 2015; Peiffer et al. 2013) grown in their natural habitats, agricultural soils or controlled artificial conditions. The rhizosphere microbiome communities associated with different genomic clones of wild type and transgenic clones were reported to be different in *Populus* sp. (reviewed by Hacquaed and Schadt 2015). Studies conducted in *Arabidopsis thaliana* (Lundberg et al. 2012; Wagner et al. 2014), *Zea mays* and *Populus* demonstrated that within a host species, habitat, soil type, rather than host genetic background have a larger influence on overall structure of microbiome (Bulgarelli et al. 2012; Lundberg et al. 2012; Peiffer et al. 2013).

Rhizosphere communities differ in different environments. Soil type and plant species are often believed to be the main factors affecting the structure of microbiomes (Agler et al. 2016; Lakshmanan et al. 2014; Lakshmanan 2015). In addition, climatic conditions, biogeography, agricultural practices, and plant domestication have also been suggested to contribute to the variation in the plant microbiome (Coleman-Derr et al. 2016; Pérez-Jaramillo et al. 2016; Sessitsch and Mitter 2015). Rhizosphere and root microbiomes have also been investigated in extreme environments, such as, arid and saline soils (Soussi et al. 2015; Coleman-Derr et al. 2016; Fonseca-García et al. 2016; Valverde et al. 2016) and marine plants (Cúcio et al. 2016). These studies helped to clarify how plant in different habitat/ niches, host environmental, soil and geographic factors influence the rhizosphere microbiome community.

In a rhizosphere microbiome, not all of the microbes are needed to fulfill the ecological services to plants. The existence of functional redundancy in microbial communities across diverse environments is common (Dopheide et al. 2015; Souza et al. 2015). Based on relative occurrence of microbes in microbiomes can be classified as core or minimal microbiome. A core microbiome (CM) is comprised of the members common to two or more microbial assemblages associated with a habitat (Turnbaugh et al. 2007; Hamady and Knight 2009) (Fig 16.3). There are various ways to define the CM within a habitat using bioinformatics-based approaches. Shade and Handelsman (2012) suggested five parameters, including membership, composition, phylogeny, persistence, and connectivity, to discover the core microbiota based on a Venn diagram analysis. However, taxa occurring with low relative abundances may also be crucial in maintaining the community functions (Shi et al. 2016), thus less abundant taxa should not be overlooked. The concept of minimal microbiome (MM) implied the smallest but functionally indispensable subset of the total microbiome (Raaijmakers 2015). The MM is composed only of indispensable members that can retain the key features of natural communities and thus are important for community assembly. Accessory microbes are those additional members that are not obligatory for community and could be replaced by other microorganisms. The ultimate goal of identifying such CMs or MMs is to exploit them in reconstruction of synthetic microbial consortium (SMC) with desirable member microbes (de Vos 2013; Hacquard 2016). SMCs are composed of multiple species with well-defined genetic background and help in accomplishing specific function through interactions among microorganisms.

16.3 Managing rhizomicrobiome for better plant health: The rhizosphere engineering

The rhizosphere microbiome engineering implies a multi-generational, artificial creation or selection of hosts that vary in microbiome content, thereby, affecting the host traits (reviewed by Mueller and Sachs 2015; Dessaux et al. 2016; Ahkami et al. 2017). Rhizosphere microbiome diversity and their inheritance had been projected to be equally important as that of plant genome, since number of genes in plant microbiome is more than number of genes in a host (Mendes et al. 2013). The plants and the associated microbes are not seen individually as a unit of inheritance and evolution, rather as a holobiont or a superorganism. The approach involves microbial population engineering rather than single strain engineering. The rhizosphere engineering holds great promise for future plant breeding programs and biotechnological application.

It is widely known that plant phenotype is determined by plant genotype and environmental properties. The plant phenotype under the influence of local adaptation to abiotic stress (environment) is also a manifestation of change in subset of microbes associated with it. Microbiome assembly can be very sensitive to host genetic and environmental parameters and can vary even between different plant tissues. The rhizosphere management methods should primarily focus on the hypothesis of increase in yield by altering the dynamics of host genotype-x-environment-x-microbe interactions (Busby et al. 2017).Our ability to manage and manipulate microbiome is limited. There are three main approaches in building a productive microbiome – the first one relies on construction of a high yielding microbial consortium, second and third approaches involve manipulating the plant or the superorganism respectively.

1. Developing microbial consortium - The most direct way to alter the microbiome is through inoculation with several strains or mixed cultures of AM or EM fungi, rhizobia, endophytes etc. designated as biofertilizers. The concept of SMC is different from co-cultures, mixed cultures, microbial consortia and other similar concepts in a way that it includes, not only living together but also labor division (Fig 16.3) (Whipps 2001; Rosier et al. 2006; Großkopf and Soyer 2014; De Roy et al. 2014; van der Heijden et al. 2016). There are two ways for designing and constructing SMCs (Jiao et al. 2016). The first one is to re-engineer naturally occurring microbial consortia, the top-down method. This starts from studies based on multiple omic analysis, macroscopic microbial consortium and molecular mechanism in a natural field environment. The other one is bottom-up-method, which begins with design and construction of artificial microbial consortia, based on engineering principles to obtain microbial consortia with higher efficiency, stability, and controllability. This method is more popular and is applied more commonly.

   Products containing one or several species microbial consortia have been commercially available for decades-are in practice of being tried for most of important crops. However, most of these microbial species were isolated under traditional culture conditions, thus did not emulate the soil chemical environment (Verbruggen et al. 2013). Because of this reason, the inoculants often showed promising results under controlled lab and greenhouse conditions but did not consistently produce equivalent under natural field conditions in agricultural soils. Not only do key attributes like pH, nutrient stoichiometry, and texture differ among soils, but also the climate regime experienced by microbes in the field spans a broad range. The conditions used to develop the synthetic microbial consortia must overlap with the multi-dimensional niche of the host plant for them to have a chance to survive, reproduce, and function. Another important issue that should be taken into account is the number of species to be included in SMCs. No general-purpose framework for the reconstruction of SMCs used to promote plant health is yet available (Busby et al. 2017).

Inoculation by recombinant strains of microbes is another strategy to enhance plant performance (reviewed by Quiza et al. 2015). Recombinant strains of mycorrhizal fungi are not yet developed, however different combination of recombinant soil bacteria have been extensively studied. For example, soil polluting compound trichloroethylene (TCE) was removed from soils by using a wheat rhizosphere established by coating seeds with a recombinant, TCE-degrading *Pseudomonas fluorescens* strain that expresses the *tomA*$^+$ (toluene *o*-monooxygenase) genes from *Burkholderia cepacia* (Dennis et al. 1998).

2. Engineering plant traits - Plant-based strategies are designed to improve the plant productivity through the selection of a better-adapted microbiome. Approaches for engineering plant traits mainly include, host plant genetic modifications and breeding (cultivar selection) (Nogales et al. 2016). Variations are induced by altering the physical and chemical environment in the rhizosphere through plant- affected characters, which change the spectrum of the fitness and interactions among microbes and evolution of new microbes better suited to the rhizosphere environment (Lambers et al. 2009). These changes in microbiome structure and function are usually attributed to differences in root exudate chemistry (Bais et al. 2006; Rasmann and Turlings 2016), root architecture and in plant nutrient uptake rates (Bell et al. 2015) which makes it possible to engineer these traits into crops through gene editing tools. Since many genes controlling exudates have been identified, there have been few attempts to engineer the rhizosphere by manipulating the root exudates. One such example is transgenic rice and tomato plants transformed with the *Arabidopsis* vacuolar H^+-pyrophosphatase *gene* AVP1, which showed approximately 50% greater citrate and malate efflux than wild-types when treated with $AlPO_4$ (Yang et al. 2007). This was interpreted as a means to enhance resistance to Al^{3+} stress and improve the ability to utilize insoluble phosphorus. However, it is important to note that plant engineering to impact rhizosphere could be a very complex process due to degradation or inactivation of the engineered compound in the soil, small rate of exudation to influence the rhizosphere. More studies on the root exudates composition and effect of change of exudate release time and levels on plant development would expedite the application of this approach (Huang et al. 2014).

   Selecting a naturally occurring plant species or cultivar with a high capacity to recruit a beneficial microbiome is other approach that has been explored. This approach seems promising as it emulates the interactions that support beneficial microbes in natural systems and which were selected through evolution of the holobiont. Some of the plant traits under breeding selection are already known to be linked to the microbiome. For example, plant phenology, nutrient uptake, and defense have been shown to be influenced by the soil microbiome (Wagner et al. 2014; Panke-Buisse et al. 2015). Plant breeding programs, which include specific microbiome functions target only a very specific taxa or function of that taxon.

3. The Meta-Organism Route- The Meta-organism or superorganism approach is based on the fact that both microbiome and the plants are highly dependent on each other as the microbiome contributes a significant portion of the secondary genome of the host plant. The heritability of the meta organisms is not solely dependent on the genetics of microbes but the genetics of host plant as well. The study conducted on 27 modern inbred maize rhizosphere revealed that heritability of microbiome also depends on other factors like host plant species and physical and chemical properties of soil also (Peiffer et al. 2013). However, this route needs to be explored with more plant species.

16.4 Concluding remarks

The rhizosphere microbiome includes all the microbial partners of plant root present in the soil. Microbiome research of both mycorrhizal and non-mycorrhizal roots, which targets to increase the crop productivity should following five research priorities as summarized by Busby et al. (2017).

1. Develop model host-microbiome systems for crop plants and non-crop plants with associated microbial culture collections and reference genomes.
2. Define core microbiomes and metagenomes in model host microbiome systems.
3. Elucidate the rules of synthetic, functionally programmable microbiome assembly.
4. Determine functional mechanisms of plant microbiome interactions.
5. Characterize and refine plant genotype-by-environment-by-microbiome-by-management interactions.

Considering the wide potential applications of microbiome research, startups focus on the microbiome as an organic solution to increase crop yields. For example, NewLeafSymbiotics (https://www.crunchbase.com/organization/newleaf-symbiotics#/entity), BioConsortia (http://bioconsortia.com) and Indigo (www.indigoag.com), the start-up companies, have generated several robust pipelines for identifying microbial consortia for improving almost all plant traits. We still look forward for more microbiome-based products to be discovered in the future.

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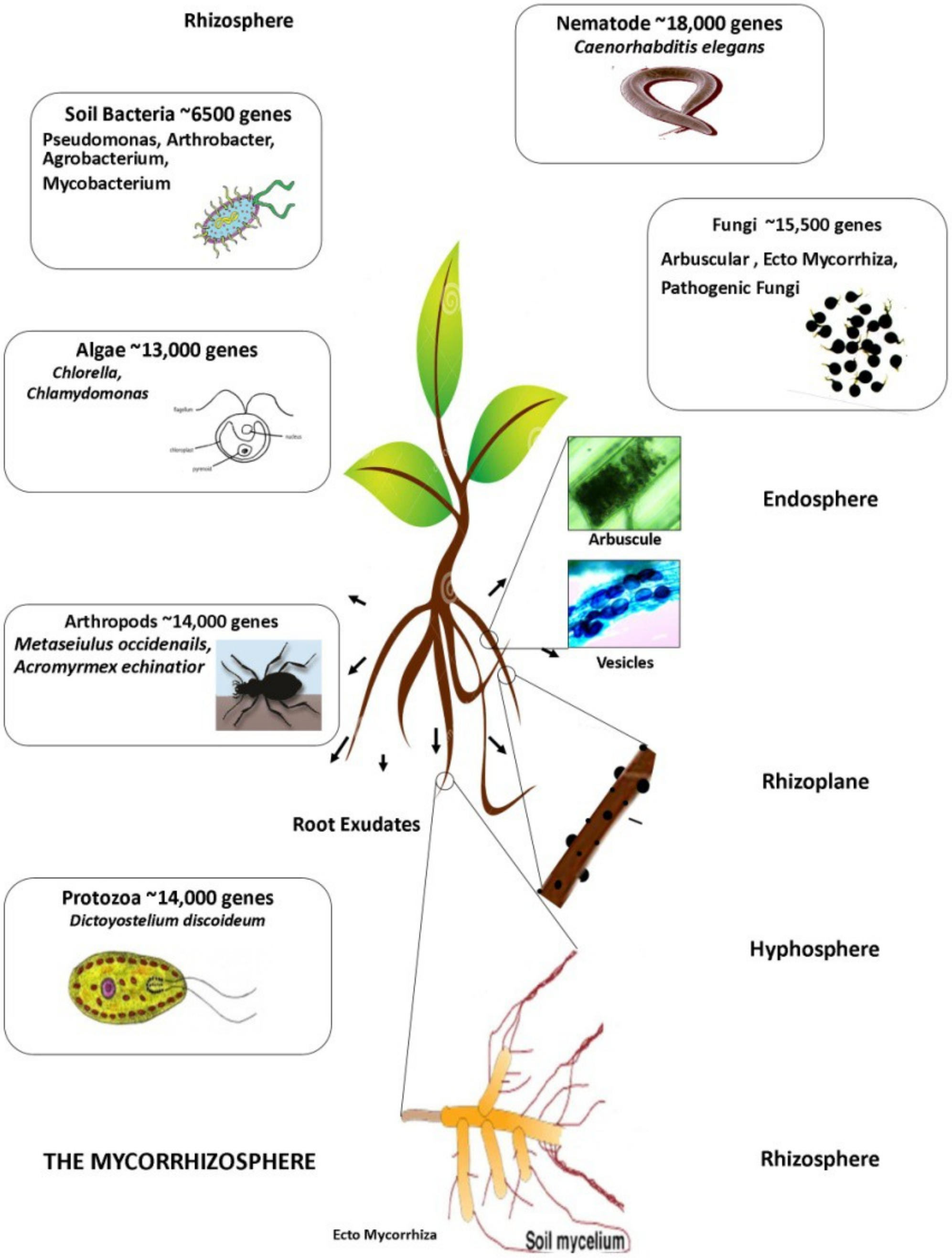

Fig. 16.1 Overview of mycorrhizosphere. The genome data given here is based on information given in Mendes et al. (2013).

Fig 16.2 Graphic representation of percentage studies on different aspects of rhizosphere microbiome in the year 2017(till now) as revealed by Google scholar, JSTOR and Catalogue Harvard Library.

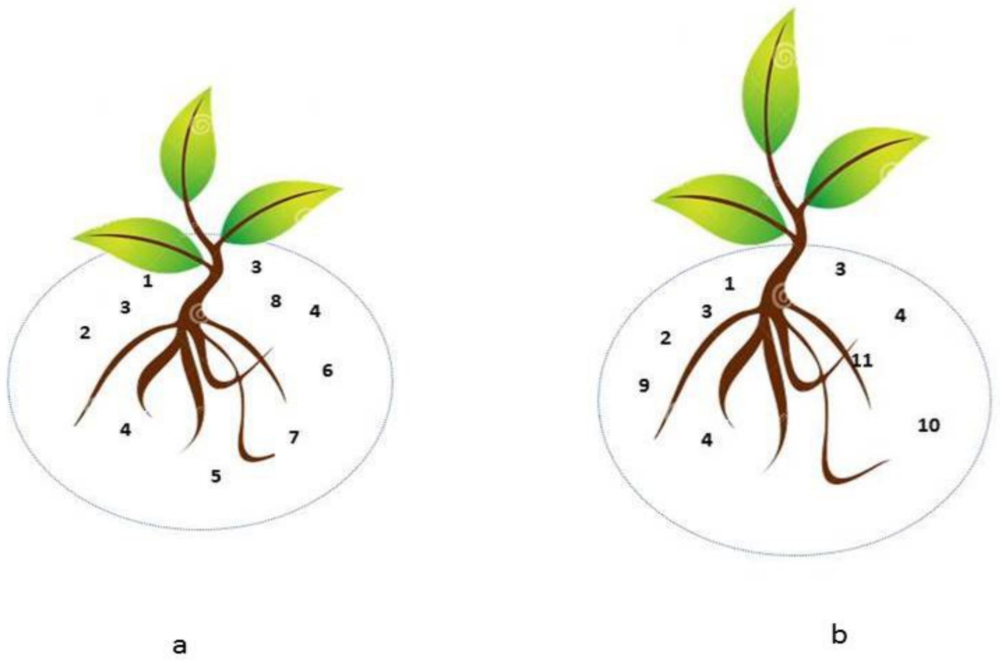

Fig 16.3 Diagrammatic representation of different microbial communities present in rhizosphere in a given habitat. a and b represent communities present in natural environment and synthetic community respectively. Species numbers 1,2,3,4 are part of core community in the given habitat. Species 1and 2 represent the minimal community without which plants do not survive, 5 to 8 are part of accessory microbiome, which can be replaced by other beneficial microbes, 9 to 11 are synthetic beneficial microbes.