



# Beneficial Root Microbiota: Transmogrifiers of Secondary Metabolism in Plants 16

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## Abstract

All plants in the ecosystem are found in close association with complex group of microbes both belowground and aboveground surfaces. Reports suggest that the association can be harmful, neutral, or beneficial to the plants depending upon the category of colonizing microbes. It is among them that certain microorganisms bring about modification in the plant metabolome, maneuvering to modifications in the biosynthetic pathway of plant metabolites of known and unknown origin. Plant secondary metabolites are exceptional group of chemicals released as an end product of biosynthetic pathways which have numerous secondary roles in survival and growth of the plants. Among the multifarious roles played by the metabolites, some of the important traits include repulsion of pathogens and attraction of beneficial group of microbes. The present chapter thus summarizes the till-date understanding of the role of root microbiome on the secondary metabolic status of plants, how the remodeling affects the health and defense status of the concerned plants, and finally the knowledge hiatus that needs to be fulfilled for harnessing the full potential of microbes.

## Keywords

Root microbiome · Secondary metabolites · Plant defense · Cross kingdom communication

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## 16.1 Introduction

Host-associated microbial populations are reported to be engaged in elementary roles like nutrition status, different developmental phases, and immunity of both animal and plant kingdom. The different factors which help in architecturing the host–microbiome interactions are inadequately understood, which hold an important place in evolutionary and ecological sciences (Fitzpatrick et al. 2018). Talking about the plants, the roots bring together two different microbial sections namely rhizosphere and the endosphere. The colonization at the rhizospheric surface by microbes can either be beneficial, neutral, or harmful associations, depending upon the relationship they share with the host plant. With the advancement in technologies, especially pertaining to sequencing, the picture of different root-associated microbiomes is getting clearer day by day (Rout and Southworth 2013). The most recent information which is coming out from the experimental evidences is that the role of microbiome differs not only with plant tissues but also with the change in environmental conditions too (Yu et al. 2019). The Next Generation Sequencing (NGS) data clearly demonstrates that amazing number of taxonomically dissimilar microbes colonize the plant system, whose density can be sometimes much higher than the plant cells figures (Mendes et al. 2013; Panke-Buisse et al. 2015). The colonization affects the plant system either directly or indirectly either by facilitating nutrient uptake, phytohormone production, induction of systemic resistance, formation of physical barriers, and changes in secondary metabolite status of concerned plants (Etalo et al. 2018). The most recent area of current research in plant–microbe interaction is changes in metabolomic status of plants leading to alteration in some key metabolites of agricultural and medical importance (Etalo et al. 2018). Hence, it is hypothesized that exploring plant–microbe communication will pave way for not only boosting production of metabolites of pharmaceutical importance but other unknown secondary metabolites too. The current chapter has thus been written with the aim to provide exhaustive information about the key players involved in alteration of secondary metabolites in plants with special emphasis on beneficial microbes, root exudates, and bioactive metabolites.

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## 16.2 Root Microbes

Microorganisms have been defined as smallest organisms that cannot be seen with the naked eye and can only be seen with a special equipment called microscope. Among the diverse range of microbes, we in this chapter have specifically discussed about the microbes colonizing the root zone of plants. Microorganisms are mostly found as free-living microbes and when they stick around the plant roots and root hairs, they are called root microbes.

Root microbes are classified into two types:

1. **Beneficial microbes** are those microbes which work toward enhancing the yield and overall well-being of plants and which can easily perform plant growth promotion, for example *Pseudomonas*, *Bacillus*, etc.
2. **Harmful microbes** are the category of root microbes that inhibits the growth of plants by destroying the plant cells, making the plants nutrients deficient, and killing the beneficial microbes.

### 16.2.1 Beneficial Root Microbes

In the early 1904, Lorenz Hiltner observed and stated that there are numerous microorganisms which live in the soil near the rhizospheric region than the distant part of soil (Hiltner 1904). Soil is been widely accepted as the home for array of microbial species, fungi, invertebrates, archaea, and mostly bacteria (Tringe et al. 2005). Hiltner gave the term **Rhizosphere** for that region where microbial population was the highest near plant roots. It has also been derived that some region of soil which is conventionally benefitted by root secretion and associated with microbes of soil is referred to as root microbiome. Moreover, plant root system always expands through the soil and penetrates it, resulting in release of water-soluble materials such as amino acids, organic molecules, certain sugars, and carbohydrate derivatives which are essential for microorganism to survive.

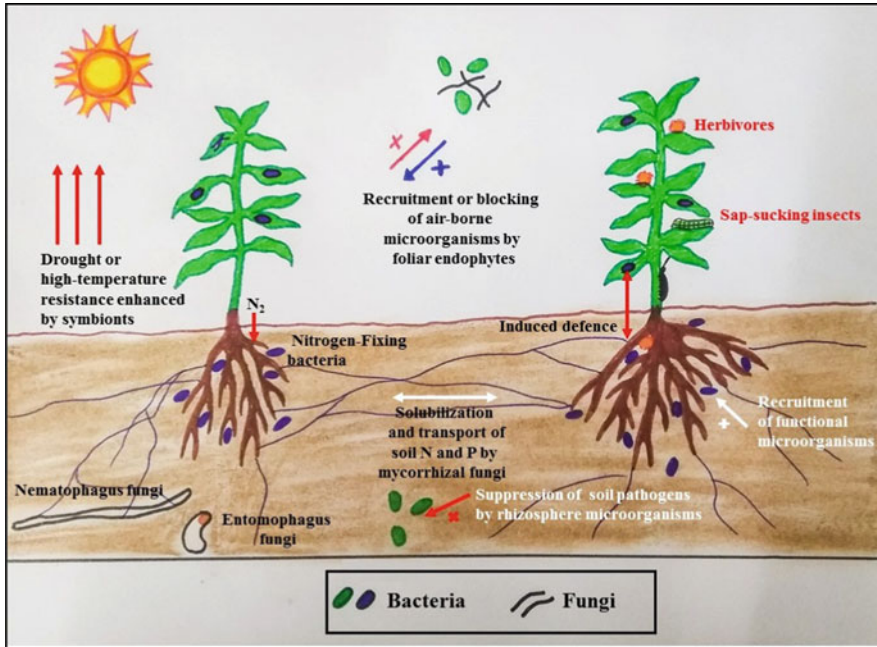
Surprisingly, plant physiologists noted that soil plays a role in providing nutrients to plants, but they forgot to add that soil is a different complex ecological system having a huge species like protists, animals, bacteria, and fungi specially (Bonkowski et al. 2009; Müller et al. 2016). The microorganisms' living in soil are the basic invisible mangers of soil fertility, and it doesn't matter if the soil condition or crop species favour them or not, because it is the nature which promotes microbes to become root symbionts. These symbionts promote plant growth and increase yield by different actions like nutrient uptake and nitrogen metabolism resulting in nitrogen fixation, and these particular activities help plants to counter pests, diseases, and biotic and abiotic stresses (Fig. 16.1). Collectively, by the enhancement of plant capacity in photosynthesis and production of organic acids, plants derive their health and the microbes which helped throughout this process are referred as "beneficial root microbes."

#### 16.2.1.1 Types of Beneficial Root Microbes

The beneficial root microbes have been basically categorized into five different types, namely actinomycetes, bacteria, fungi, protozoans, and nematodes. The detailed information about these microbes has been discussed in the following sections.

#### Bacteria

Bacteria are the smallest living organisms and major key player of soil in bringing together the simpler forms around the root system so that the plants can firmly take up all the nutrients important to their growth and development, for examples



**Fig. 16.1** Role of rhizospheric microbial community in mitigating biotic and abiotic stressors

macronutrients like nitrogen, phosphorus, potassium, etc. Phosphorus is usually not found in available form for the plants in soil, but some of the beneficial bacteria turns the nonavailable phosphorus into available form which a plant can easily utilize. In soil system there are huge number of bacteria which enhance plant growth and have thus been referred to as plant growth-promoting rhizobacteria (PGPR) (Bonkowski et al. 2009). Moreover, in obligate symbionts, PGPRs can easily interact with the host plants and enhance growth of the plant either by direct benefit via nitrogen fixation (Müller et al. 2016; Kloepper and Schroth 1987) or indirectly by secreting certain enzymes and hormones which can suppress other pathogens' activity (Soyano et al. 2014; Ferguson and Mathesius 2014). The root hierarchy is also dependent upon PGPRs, as the structural modification in root results in better conduction of molecules into plant parts which is inversely proportional to better crop yield (Pérez-Montaño et al. 2014; Lugtenberg and Kamilova 2009; Uga et al. 2013). The projectile PGPR activity and plant growth promotion attributes are also reviewed in some articles (Ogawa et al. 2014; Ning et al. 2014).

Example – Indole-3-acetic acid production by the *Rhizobium leguminosarum* has been discussed in literature for playing a key role in promoting certain effects on rice seedlings (Biswas et al. 2000). In the same way, *Azotobacter* has been reported to do the job for maize seedlings (Zahir et al. 2000).

### Actinomycetes

Actinomycetes are spore-forming, gram-positive aerobic bacteria which form thread-like structures called filaments, and work in cycling or turning up the organic matters, mainly by decomposition of complex mixtures found from decomposed plants, animals, or fungal sheets over rocks. Somehow these enzymes and hormones also help in suppressing certain plant pathogens which pose threat to plants, for example *Streptomyces* sp. have been found responsible for nutrient uptake and plant growth in rice and chickpea plants (Gopalakrishnan et al. 2014, 2015). Likewise, *Frankia* has been found to be responsible for nitrogen fixation in *Alnus* plant (Simonet et al. 1990).

### Fungi

Fungi are multicellular, eukaryotic, heterotrophic organisms that have absorptive mode of nutrition. They live in the root zone of plants and act like natural recycling bins, help in reabsorbing soil nutrients from dead organic matter, and redistributing them back to plants roots. In addition, they also help in making nutrients available to plants through formation of siderophores. For example, mycorrhizal association is a mutual relationship which exists between roots of plant and fungus for sharing the benefits. The association is usually two ways – ectomycorrhizal when the fungus resides outside of root, or endomycorrhizal when the fungus penetrates inside of the root. It is well reported in literature that most of the rhizospheric fungus produces metabolites for the inhibition of plant pathogens (Ali et al. 2015; Saraf et al. 2014).

Example – Plant defense mechanisms can directly or indirectly be controlled by arbuscular mycorrhizal fungi (AMF) (Di Benedetto et al. 2017). *Trichoderma harzianum* are involved in active colonization of tomato root and induced systemic resistance-like defense in *Arabidopsis*. (Engelberth et al. 2001). Likewise, *Trichoderma viride* has been found to be responsible for elicitation of jasmonic acid and salicylic acid biosynthesis in lima bean (Morán-Diez et al. 2009).

### Protozoa

Protozoa are single-celled, microscopic, eukaryotic, and heterotrophic organisms (using organic carbon as a source of energy). They are non-filamentous and restricted to moist or aquatic habitats. Protozoans play important roles in the fertility of soils by eating soil bacteria and maintaining bacterial populations. Protozoans sometime help in promoting plant health by the mineralization of nutrients and alteration in the hierarchy or activity of plant root-associated families (Bonkowski 2004). It was also stated and reported that predation of some of the different plant pathogenic species has an inverse effect on the plant growth hormone production (Krome et al. 2010) or sometimes they support the beneficial microbes to survive (Jousset et al. 2010; Müller et al. 2013). Protozoans also excrete nitrogen in the form of ammonium and phosphorus as products of their metabolism, and it is because of this reason that the presence of protozoans in soil has been reported to enhance plant growth and development.

Example – *Acanthamoeba castellanii* grazing has been reported to maintain the bacterial population in the rhizospheric soil by consumption etc.

## Nematodes

Nematodes are microscopic worms which live around or inside the plant and periodically rely and feed over bacteria, fungus, and other soil microbes. Nematodes can easily carry live microbes over their bodies and also inside their digestive systems, and by this activity wherever they go nematodes deliver microbes over the roots of plant or in soil. Few nematodes are also disease causing, while others feed over disease-causing organisms which can be identified as potential biocontrol agents.

Example – *Steinernema*, *Risbravis*, *Rhabditis*, etc., are the useful nematodes responsible for decomposing the organic matter and managing attack on insects and other pests.

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## 16.3 How Useful Root Microbes Boost Crop Productivity?

Beneficial root microbes present in the rhizospheric soil near plant roots ameliorate plant productivity and its performance in a variety of ways like deterioration of pathogens, providing resistance against any infection, and help in plant growth promotion. The major mode action involves following steps:

### 16.3.1 Nutrient Availability

Rhizospheric microorganisms always take part in obtaining trace elements which are found in insoluble forms, where microbes turn this into soluble form and make them available to plants. By the use of certain molecules, like siderophore, iron chelation and conversion of complex to simpler form takes place (Aznar and Dellagi 2015). Most of the bacterial community works as key component to unlock the nutrients which are locked in the form of hydrocarbons essential for the plants. Some of the saprotrophs and fungi have been reported as nutrient extractors through solubilization or reabsorption processes, among which actinomycetes play a significant role in decaying organic matter to make it in available form (Aznar and Dellagi 2015).

### 16.3.2 Plant Growth Promotion

In a different manner we have seen PGPRs playing essential role in plant growth promotion where they produce metabolites which eventually trigger the release of plant hormones reported to play beneficial role for plants. Apart from working as PGPRs, some microbes work as bio-remediators. As a biocontrol trait, microbes effect plant pathogens through the different synthesis like regulation of ethylene level in plant, siderophore activity, acquired systemic resistance, antibiosis, quorum sensing, etc. (Babalola 2010; Olanrewaju et al. 2017). In addition, the beneficial microbes are reported to increase photosynthesis and production of hormones and enzymes as a result of improvement in crop growth. They also control various

insects and plant diseases as a consequence improvement in crop quality. The use of such kinds of microorganisms leads to reduction in the usage of chemical fertilizers.

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## 16.4 Root Exudates: Role in Shaping Root Microbiome

In natural environment, plants health status mainly depends on complex and active microbial community present in the rhizospheric soil. In plants, root system is the essential part for nutrient and water conduction, which is inhabited and encircled by a major microbial community called root microbiota or rhizomicrobiome (Del Carmen Orozco-Mosqueda et al. 2018; Hacquard et al. 2015). Complex microbial community present in the root microbiome is referred to as plant's second genomic part which consists of total rhizosphere community's interactions present in relation to plant health (Berendsen et al. 2012). Crop growth and yield inside natural environment depends on microbial interactions, that is, bacteria and fungi, actinomycetes, etc. (Schmidt et al. 2016). Attachment of microbial diversities was preferred to be connected in two steps:

### 16.4.1 Rhizosphere

Rhizosphere as a term was first coined by Lorentz Hiltner (Hiltner 1904) and reconsidered by Pinton as the zone around the plant roots in the soil which is colonized by microbial community (Morgan et al. 2005; Pinton et al. 2007).

Example – Azotobacter, Nitrobacter, Proteobacteria, Rhizobacteria, Actinobacteria, Pseudomonas are some of the ruling populations of bacteria over rhizosphere (Sylvia and Prévost 2005).

### 16.4.2 Rhizoplane

Region of surface of the plant roots with epidermis and mucilage which is direct contact with the soil and colonized by microbial community.

Example – *Burkholderia*, *Acidobacterium*, *Dyella*, and *Edaphobacter* are the major genera abundant in the rhizoplane.

The soil–microbe interactions are usually specific and depend upon coevolutionary dilemma (Dobbelaere et al. 2003; Duffy et al. 2004); (Morgan et al. 2005). In the underground world, the specific plant–microbe interactions hold a very important place in various processes governing ecosystem, just like carbon metabolism, sequestration, and nutrient cycling (Singh et al. 2004).

For the export and secretion of molecules into the rhizospheric soil, plants use a hierarchical transport technique where plant roots along with root hairs and adventitious part release root exudates either by passive or active diffusion/secretion mechanism (Badri et al. 2009; Weston et al. 2012).

**Table 16.1** Different types of root exudates released by the plants

Classes of compounds	Components identified
Amino acids	All 20 proteinic amino acids, homoserine, aminobutyric acid, mugineic acid, 1-hydroxyproline
Lignins	Coumaric acid, sinapoyl aldehyde, benzoic acid, pyroglutamic acid phloroglucinol, gallic acid, nicotinic acid, chlorogenic acid, vanillin, catechol, sinapyl alcohol, quinic acid
Proteins and enzymes	Peroxidases, PR proteins, proteases, lipase, acid phosphatases, lectins, hydrolases
Phenolics and Coumarins	Umbelliferone, Caffeic acid, cinnamic acid, coumarin, ferulic acid, salicylic acid, syringic acid, vanillic acid
Indole compounds	Indole-3-acetic acid, brassilexin, sinalexin, methyl indole carboxylate, camalexin glucoside, brassitin
Flavonols	Strigolactone, kaempferol, quercetin, genistein, myricetin, naringin, rutin, naringenin, and their substitutes with sugars
Sugars	Galactose, mannitol, fructose, pentose, rhamnose, arabinose, raffinose, ribose, sucrose, xylose and glucose
Sterols	Stigmasterol, campesterol, sitosterol
Allomones	Juglone, 5,7,4'-trihydroxy-3', 5'-dimethoxyflavone, sorgoleone, DIBOA DIMBOA
Anthocyanins	Pelargonidin, delphinidin, cyanidin and their substitutes with sugar molecules
Organic acids	Succinic acid, l-aspartic acid, l-glutamic acid, salicylic acid, oxalic acid, shikimic acid, chorismic acid, acetic acid, sinapic acid, isocitric acid, citric acid, p-hydroxybenzoic acid, tartaric acid, gallic acid, malic acid, protocatechuic acid, p-coumaric acid, mugineic acid, piscidic acid
Aurones	Sinapoyl choline, benzyl aurones synapates
Glucosinolates	Cyclobassinone, desulphoglucoalyssin, desulphoprogoitrin, desulphonapoleiferin, desulphogluconapin
Fatty acids	Palmitic acid, linoleic acid, stearic acid, oleic acid

Root exudates are usually referred to as a group of chemical molecules in rhizosphere which are secreted by plant root systems. They are a mixture of complex substances like sugars, organic acids, enzymes, amino acids, etc., which act as major source of organic carbon specifically obtained from rhizospheric soil (Hütsch et al. 2002; Nguyen 2003). Usually quality and quantity of root exudates depends upon plant species and is variable in different plants, individual plant's age, and some external factors like biotic and abiotic stresses. Knudson (1920) and Lyon and Wilson (1921) were the first who had provided indication regarding root exudation and microbe abundance in rhizosphere of the plants. Some of the important exudates usually found in the rhizosphere have been mentioned in Table 16.1.



## 16.5 Requirement of Root Exudates in Plant–Microbe Interactions

Phytochemicals secreted by plant roots mediate certain number of interactions like

- Plant–plant interaction
- Plant–microbe interaction
- Microbe–microbe interaction

Microorganisms live in the rhizospheric soil where they interact with roots and their components to enhance the plant health (Berendsen et al. 2012; Panke-Buisse et al. 2015). The interaction might be neutral in some ways and either advantageous or harmful in others (Mercado-Blanco and Bakker 2007; Raaijmakers et al. 2009). Most probably, depending on the environment, microbes also turn the table from pathogenesis to symbiotic association (Newton et al. 2010). In different examples, *Rhizobia* includes *Bradyrhizobium*, *Azorhizobium*, symbiotic nitrogen, and nitrogen-fixing bacteria like *Sinorhizobium* and *Mesorhizobium* (Davidson and Robson 1986; Zahran 1999). In nitrogen-limiting conditions, attraction and intimation of legume–rhizobia symbiosis result in secretion of flavones and flavonols by legumes (Coronado et al. 1995; Zhang et al. 2009). In the same way equal exchange of plant nutrients benefit both the partners like the mycorrhizal associations which is a common association found in almost 80 percent of the plant species (Kiers et al. 2011).

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## 16.6 Effect of Microbe–Microbe Interactions on the Soil Microbial Communities

For plants, rhizospheric zone is a kind of nutrient-rich site where the competition for food among microbes always takes place. Secondary metabolites produced by microbes are released in the environment to overcome other competitors which fight to occupy similar zone for establishing firmly itself outside or within the roots (Thomashow and Weller 1988; van Loon and Bakker 2005; Pierson and Pierson 2010; Kim et al. 2011). The metabolites released in environment consist of siderophore, lytic enzymes, toxic elements, and antibiotics (Bais et al. 2006). Some rhizospheric microbes hold a variety of genes for the production of siderophores and other antibiotics like *Bacillus amyloliquefaciens* (Chen et al. 2007) and few species of *Pseudomonas* (Paulsen et al. 2005). Antibiotics like 2,4-diacetylphloroglucinol (DAPG) and oomycin are also products of microbes (van Loon and Bakker 2005). The referred antibiotics play a significant role in restraining the pathogenic microbes (Aminov 2009; Pierson and Pierson 2010; Thomashow and Weller 1988; Kim et al. 2011).

Besides antibiotics, plant secondary metabolites also work toward altering signaling pathway and metabolic activity of plants (Přikryl et al. 1985; Brazelton et al. 2008; Costacurta and Vanderleyden 1995; Kim et al. 2011). These kinds of

microbial attributes sometime change the root exudates' composition, leading to the selective enhancement of any particular microbial partner in the rhizosphere (Přikryl et al. 1985; Bulgarelli et al. 2013). The whole scenario of communication between two bacterial communities results in release of signaling molecules which are relatively recognized by other communities via inter- and intra-species communication (An et al. 2014). In bacteria this scenario comprises of biofilm formation, motility, and cell adhesion (Sperandio et al. 2002; Chu et al. 2011); production of the virulence-associated factors; and cell proliferation. This kind of density-dependent stimulus and exchange of signals is referred to as quorum sensing (Fuqua et al. 1994; Miller and Bassler 2001; Atkinson and Williams 2009; An et al. 2014) (Yajima 2014).

In fungi, two important molecules namely farnesol and tyrosol have been reported for regulating quorum sensing-controlled traits like biofilm formation, resistance to drugs, and morphogenesis (Chen et al. 2007; Enjalbert and Whiteway 2005; Albuquerque and Casadevall 2012). Likewise, tryptophol has been reported to control morphogenetic behavior in *Saccharomyces cerevisiae* through both density-dependent approach as well via nutritional trigger (Chen and Fink 2006).

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## 16.7 Coevolutionary Relationship of Root Exudates with the Rhizosphere

Microbial communities present in the soil are involved in multilevel intercommunication which are known to influence vital environmental activities, like biogeochemical cycling of nutrients, soil quality, and plant well-being (Barea et al. 2005; Giri 2005).

The age of the plants, crop species, and types of soil determine the variation in microbial communities present in the rhizospheric soil (Wieland et al. 2001; Buyer et al. 2002); (Kowalchuk et al. 2002). In some recent evidences it was observed that specific plant species cultivate their own soil fungal community and diversity composition, and this "culture" is mediated by root exudates (Broeckling et al. 2008).

Example – In native soil, when *Arabidopsis thaliana* and *Medicago truncatula* were grown at different places, it was observed that *Arabidopsis* and *Medicago* maintained its own fungal community in their resident soil. When the plants were grown in other soil different from the native soil that did not promote *Arabidopsis* or *Medicago* plants, the microbial communities in those soils decreased considerably. Similarly, when root exudates were added to the soil, the same response was observed, thus showing that plants secrete root exudates to drive these responses and this interaction has a coevolutionary component.

## 16.8 Bioactive Metabolites

Plants play a variety of roles either in metabolism or metabolites, which are required for the sustainability of plant system. These plant metabolites could be made up of proteins, lipids, carbohydrates, or nucleic acids which are then known as primary metabolites. Metabolites are primarily known as helping hand for plant system which directly intervenes in the growth and development (Ballhorn et al. 2009). The metabolites produced by plants have been broadly categorized into two groups namely:

### 16.8.1 Primary Metabolites

Primary metabolites are certain compounds which directly benefitted the plants for their overall growth. They have been classified as carbohydrates, lipids, proteins, etc., which are likely used by the plants directly for different works (Schafer and Wink 2009).

### 16.8.2 Secondary Metabolites

Plant secondary metabolites are those compounds which do not having any direct role in plant metabolism and are often useful in respect to defense-related properties. They are usually low molecular weight around 3000 dalton (Osborn et al. 2003). The production and secretion of secondary metabolite varies from species to species and somehow difference between natural products and secondary metabolites is hard to define (Vasconsuelo and Boland 2007).

In so many different ways, secondary metabolites are involved in upregulation of primary metabolism and act as triggers for signaling any known process. Secondary metabolites often maintain the balance of plant molecules with the environment either via adaptation mechanism or by making a complementary framework to intricate fine balance (Osborn et al. 2003; Berni et al. 2018; Grayson 1998).

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## 16.9 Principal Groups of Secondary Metabolites

Plant secondary metabolites have been majorly categorized into four major classes (Goldberg 2003). These four categories include terpenoids, nitrogen-containing compounds, phenolics, and sulfur-containing compounds (GSH, defensins, and lectins) (Mazid et al. 2011).

### 16.9.1 Terpenes

Terpenoids are the on the whole most varied class of plant secondary metabolites as they have approximately 40,000 dissimilar compounds, and thus they stand out as the biggest class of important plant metabolites (Bohlmann and Keeling 2008).

### 16.9.2 Phenolics

Phenolics are molecules that have an aromatic ring bound with one or more hydroxyl groups (Nicholson and Hammerschmidt 1992). By the chemical formula and its structure, it differs from simple phenols like catechol to catechol melanins through a long chain polymer. Phenolic compounds are reported to guard plants from different herbivores and pathogens. Apart from protecting plants from above-mentioned stressors, phenolics also protect plants from UV radiation, heat shock, and frost situation (Parr and Bolwell 2000).

### 16.9.3 Alkaloids

Alkaloids are amino acids–derived nitrogen-containing compounds just like tyrosine and tryptophan. They also present in huge amount but take 20% of total metabolites (Hegnauer 1988). Alkaloids occupy a major share in drug industry and are being mainly used as narcotics or in pharmaceuticals (Hesse 2002; Yao et al. 2004). The most common alkaloids derived from plant sources are vincristine and vinblastine, morphine, and codeine (Crozier et al. 2006).

### 16.9.4 Sulfur-Containing Secondary Metabolites

Sulfur-containing metabolites are derived from two different ways; one group is formed from hydrolyzation of glucosinolates by myrosinase enzyme. Second group is made up of allin by alliinase enzyme found basically in onion and garlic. Both of these groups are in nature for a purpose which we always face off with and help in guarding plants from the herbivores (Ober et al. 2003).

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## 16.10 Role of Rhizospheric Microbiome on Plant Growth Promotion

Microbial communities are well acclaimed for playing a crucial part in the overall development and growth of plants by manipulating diverse physiological processes. The shaping of rhizospheric microbiome is a mutual process which is largely influenced by the rhizodeposits (Sharma and Chauhan 2017). Recently, people have started focusing on studying the microbiome associated with host plants in

order to expand sustainable farming customs via the utilization of microbial biopesticides and biofertilizers. Within a given set of soil type, the indigenous plants restructure and reframe the native rhizospheric microbial community by applying a selective pressure. It is exhaustively reported in literature that within a given set of soil type, the indigenous plants put forth a selective pressure on this immense biodiversity pool, thereby reshaping the rhizospheric microbial community structure.

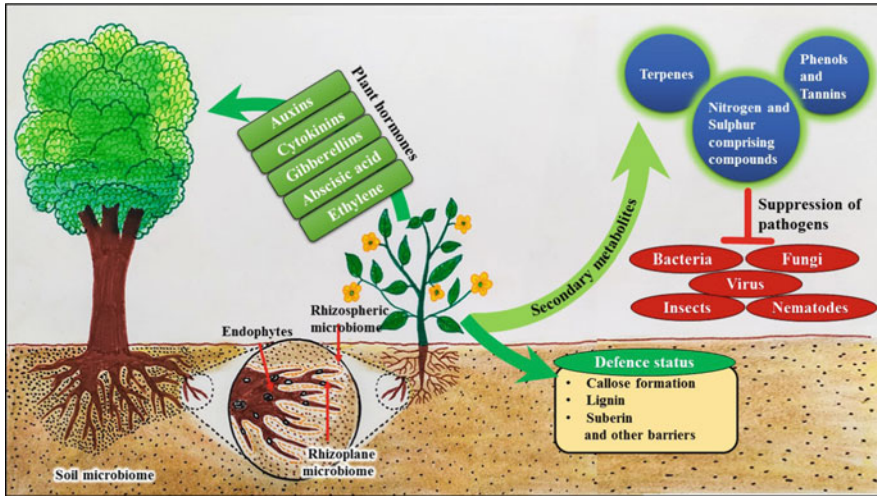
Manipulation of bacterial microbiome has attracted more attention of researchers in recent times than the other groups of organisms, as it has helped the scientists in altering numerous plant beneficial activities, namely enhancement in growth and yield, as well as suppression of phytopathogens with final effect on the usage of chemical fertilizers which is considerably reduced (Adesemoye and Kloepper 2009). Microorganisms living belowground are known to affect composition and total yield of natural plant communities directly and indirectly (Van Der Heijden et al. 2008; Turner et al. 2013). It is because of this reason that the soil microbial richness has been directly linked with the diversity and productivity aboveground plant (Lau and Lennon 2011; Wagg et al. 2011).

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### 16.11 Role of Rhizospheric Microbiome on Plant Secondary Metabolite Status

The interconnection between plants and their microbial communities is active practice in which plants interact to their surrounding environment and accordingly respond to the changes (Chaparro et al. 2012). Microbes play important role in agriculture in order to maintain environmental equilibrium (Fig. 16.2). Both the shoot and root systems of plant are directly or indirectly contact with diverse group of microorganisms. Due to the presence of infinite number of microbes, various mechanisms occur around the plant root, and one of them is secretion by root exudate. The root exudation comprises the secretion of carbon-containing compounds that are primary and secondary metabolites products and many more molecules (Uren 2000).

Elicitors are chemical compounds for stress factors which when applied in minute quantity to a living being enhances the biosynthesis of metabolites, mainly secondary metabolites (Radman et al. 2003). In context to the plant system, elicitors play vital role in defense process against pathogens and environmental stress. The biotic elicitors include bacteria, fungi, and viruses whereas abiotic elicitors involve metal, ions, and inorganic molecules. Thus, PGPR can produce elicitors which in turn will originate the synthesis of secondary metabolites (Sekar and Kandavel 2010) [Table 16.2]. The herbaceous plant *Catharanthus roseus*, which is commonly called rose periwinkle, belonging to family Apocynaceae releases bioactive compound ajmalicine under drought stress (Jaleel et al. 2009). Likewise, in another study *Pseudomonas fluorescens*, a plant growth-promoting rhizobacteria was reported to increase the production of ajmalicine under drought stress. This bacterium also increased plant biomass and helped in protecting the plants against stress condition.



**Fig. 16.2** Schematic representation of the role of rhizospheric microbiome on the growth, secondary metabolite, and defense status of host plants

*C. roseus* is also reported to secrete some metabolites like serpentine, catharanthine, tabersonine, and vindoline but among all of them ajmalicine content was found to be maximally increased (Jaleel et al. 2009).

The perennial plant *Crocus sativus*, commonly called saffron crocus, secretes crocetin, picrocrocin, and safranal compounds. In a study it was found that the contents were increased when plants were inoculated with *Bacillus subtilis* FZB24 (Sharaf-Eldin et al. 2008). Among all the compounds, crocetin was found to be increased maximally. *Trichoderma* belonging to fungal genera is usually present in almost all soil types (Hermosa et al. 2012). It has property to kill other harmful bacteria and fungi that act as biocontrol agent for the plant (Druzhinina et al. 2011). *Trichoderma* acts as a biotic elicitor for oleanolic acid which is secreted by *Calendula officinalis* plant. Oleanolic acid amount is intensified by application of *Trichoderma viride* (Wiktorowska et al. 2010).

*Scopolia parviflora* is a flowering plant belonging to family Solanaceae, which produces scopolamine compound whose concentration was found to be increased along with the amount of tropane alkaloids by different microbes such as *Bacillus cereus* and *Pseudomonas aeruginosa* (Jung et al. 2003). Tropane alkaloids concentration is high in roots as compared to stem and leaves. Tropane has cyclic amine group which has piperidine and pyrrolidine ring with single nitrogen atom and two carbon atoms (Hanuš et al. 2005). They are used as anesthetics, bronchodilators, and mydriatics (Gryniewicz and Gadzikowska 2008).

Apart from PGPRs, endophytes are those bacterial or fungal microbes that live their entire life with living cells of plant without causing any disease to the host (Wilson 1995; Sturz et al. 2000). Nowadays endophytes have been considered as an important source for secondary metabolites which include phenols, alkaloids, and

**Table 16.2** Effects of different beneficial microbes on the status of important secondary metabolites

S. No.	Plant name	Secondary metabolite	Microbes	Reference
1.	<i>Medicago sativa</i>	Luteolin	<i>Rhizobium meliloti</i>	Hartwig et al. (1990)
2.	<i>Capsicum annum</i>	Capsidiol	<i>Trichoderma viride</i>	Brooks et al. (1986)
3.	<i>Catharanthus roseus</i>	Ajmalicine	<i>Trichoderma viride</i>	Namdeo et al. (2002) and Namdeo (2004)
4.	<i>Catharanthus roseus</i>	Ajmalicine	<i>Pseudomonas fluorescens</i>	Bais et al. (2002)
5.	<i>Catharanthus roseus</i>	Serpentine	<i>Pseudomonas fluorescens</i>	Jaleel et al. (2009)
6.	<i>Salvia miltiorrhiza</i>	Tanshinone IIA	<i>Trichoderma atroviride</i>	Ming et al. (2013)
7.	<i>Gymnema sylvestre</i>	Gymnemic acid	<i>Saccharomyces cerevisiae</i>	Chodiseti et al. (2013)
8.	<i>Gymnema sylvestre</i>	Gymnemic acid	<i>Bacillus subtilis</i>	Chodiseti et al. (2013)
9.	<i>Gymnema sylvestre</i>	Gymnemic acid	<i>Escherichia coli</i>	Chodiseti et al. (2013)
10.	<i>Datura metel</i>	Atropine	<i>Bacillus cereus</i>	Shakeran et al. (2015)
11.	<i>Taverniera cuneifolia</i>	Glycyrrhizic acid	<i>Rhizobium leguminosarum</i>	Awad et al. (2014)
12.	<i>Vicia sativa</i>	7,30-Dihydroxy-40-methoxyflavone	<i>Rhizobium</i>	Zaat et al. (1989)
13.	<i>Pisum sativum</i>	Apigenin and eriodictyol	<i>Rhizobium</i>	Firmin et al. (1986)
14.	<i>Sesbania rostrata</i>	7,40-Dihydroxyflavaone	<i>Azorhizobium</i>	Messens et al. (1991)
15.	<i>Glycine max</i>	Daidzein and genistein	<i>Bradyrhizobium japonium</i>	Kosslak et al. (1987) and Bassam et al. (1988)
16.	<i>Trifolium repens</i>	7,40-dihydroxyflavone and geraldone	<i>Rhizobium</i>	Redmond et al. (1986)
17.	<i>Ocimum basilium</i>	Rosmaric acid	<i>Aspergillus niger</i>	Bais et al. (2002)
18.	<i>Glycine max</i>	(i) Iturine	<i>Bacillus subtilis</i>	Ohno et al. (1995)
19.	<i>Hyoscyamus niger</i> L.	(i) Hyoscyamine (ii) scopolamine	<i>Pseudomonas putida</i> and <i>Pseudomonas fluorescens</i>	Ghorbanpour et al. (2010)
20.	<i>Crocus sativus</i> L.	Picrocrocin, crocetin and safranal compounds	<i>Bacillus subtilis</i>	Sharaf-Eldin et al. (2008)
21.	<i>Calendula officinalis</i> L.	Oleanolic acid	<i>Trichoderma viride</i>	Wiktorowska et al. (2010)

terpenoids products. For example, hypericin is a bioactive compound which was isolated from *Hypericum perforatum* and whose production was increased upon inoculation of *Thielavia subthermophila* (Kusari et al. 2008, 2009).

*Plumbago rosea* L., commonly called Indian leadwort, is classified under angiosperms. It is used for medicinal purposes like in curing of certain kinds of chronic diseases, skin diseases, and used as an anticancer plant (Parimala and Sachdanandam 1993). It releases useful metabolite compound plumbagin from its root and *Aspergillus niger*, *Rhizopus oryzae*, *Bacillus subtilis*, and *Pseudomonas aeruginosa* have been reported to be its elicitor. Among the above-mentioned genera, fungal elicitors enhanced the content of plumbagin, whereas bacteria elicitors were not so effective (Komaraiah et al. 2002). The maize crop (*Zea mays*) discharges a compound named benzoxazinoid whose amount changed by rhizobacterium *Pseudomonas putida* KT2440, which protects the plant from pathogenic microorganism (Neal et al. 2012). These compounds function naturally toward the protection of plants. In cell culture roots of *Taverniera cuneifolia* (shrub), glycyrrhizic acid content was intensified when treated with bacteria *Rhizobium leguminosarum* as compared to the control roots. Other bacterial origin elicitors observed in *Taverniera cuneifolia* are *B. aminovorans*, *B. cereus*, and *Agrobacterium rhizogenes* which were also found to increase the amount of glycyrrhizic acid. But when it is treated with *Agrobacterium tumefaciens*, no significant increase in glycyrrhizic acid was found. In another plant, namely *Hypericum perforatum* compound hypericin and pseudohypericin is released, whose concentration is reported to be increased by *Rhizobacterium* (Mañero et al. 2012).

Alfalfa (*Medicago sativa*) belonging to family Fabaceae is a medicinal plant, which is a rich source of vitamins A, B, and C (Rashmi and Sarkar 1997). Luteolin is a bioactive compound released by alfalfa plant whose production is enhanced by plant growth rhizobacteria *Rhizobium meliloti* (Peters et al. 1986). Likewise, in *Datura metel*, *Bacillus cereus* and *Staphylococcus aureus* were found to increase the content of atropine, a compound largely used for relieving pain (Shakeran et al. 2015).

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## 16.12 Conclusion and Future Prospects

Owing to the presence of diverse variety and multidimensional role of secondary metabolites, we can assume that these organic compounds are of immense importance for the growth, development, defense, and survival of plants. Plants preferably produce these compounds when they encounter herbivores or pathogen attacks. In totality, these compounds are also produced when plants face challenges like abiotic stresses, that is, salinity, drought, UV radiations, heavy metals, and harsh climate. In addition to the above, the biotic elicitors, namely rhizospheric microbes many times positively change the status of plant secondary metabolites production. Additionally, being relatively an unexplored area, the rhizospheric microbiome offers a huge potential for not only manipulating the plant growth but also the secondary metabolite status of plants too.



Therefore, though significance of the microbiome present in the rhizosphere has been identified way back, but still tremendous efforts needs to be put in to explore the potential of organisms which might have good properties for our plants and surrounding environment. Pairing traditional techniques with high-end, next-generation sequencing techniques for identifying cues, exudates and other molecules will really help in understanding the complex underground communication existing between plants and microbes.

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