

# Chapter 5

## Phyllospheric Microbiomes: Diversity, Ecological Significance, and Biotechnological Applications



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**Abstract** The phyllosphere referred to the total aerial plant surfaces (above-ground portions), as habitat for microorganisms. Microorganisms establish compositionally complex communities on the leaf surface. The microbiome of phyllosphere is rich in diversity of bacteria, fungi, actinomycetes, cyanobacteria, and viruses. The diversity, dispersal, and community development on the leaf surface are based on the physiochemistry, environment, and also the immunity of the host plant. A colonization process is an important event where both the microbe and the host plant have been benefited. Microbes commonly established either epiphytic or endophytic mode of life cycle on phyllosphere environment, which helps the host plant and functional communication with the surrounding environment. To the scientific advancement, several molecular techniques like metagenomics and metaproteomics have been used to study and understand the physiology and functional relationship of microbes to the host and its environment. Based on the available information, this chapter describes the basic understanding of microbiome in leaf structure and physiology, microbial interactions, especially bacteria, fungi, and actinomycetes, and their adaptation in the phyllosphere environment. Further, the detailed information related to the importance of the microbiome in phyllosphere to the host plant and their environment has been analyzed. Besides, biopotentials of the phyllosphere microbiome have been reviewed.

**Keywords** Biotechnological applications · Diversity · Ecological significance · Phyllospheric microbiomes · Plant growth promotion

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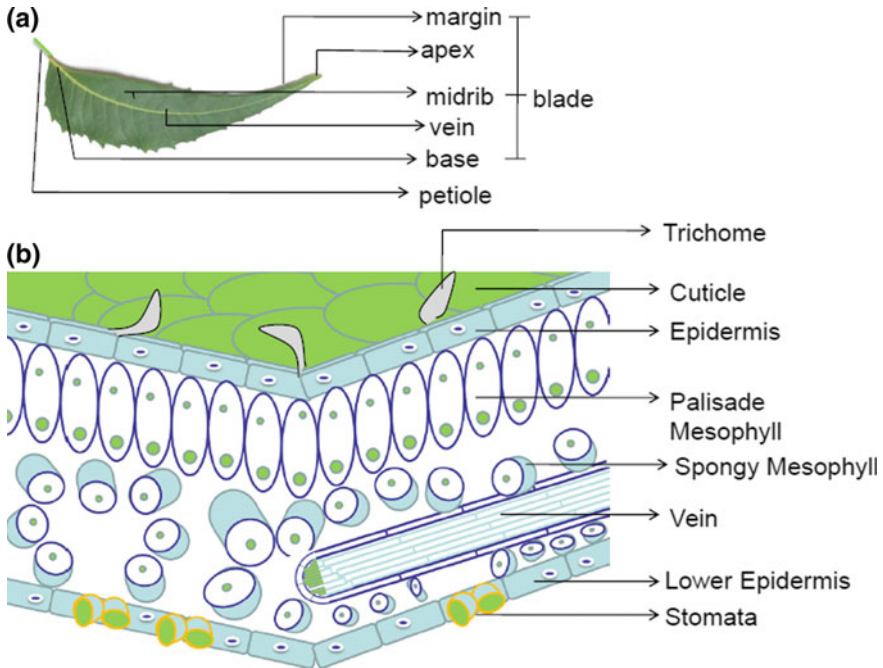
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## 5.1 Introduction

The term phyllosphere is referred to as “the aerial part of the plant or the parts of a plant above the ground usually surface of leaves, considered as a habitat for microorganisms.” This is a place where normally a variety of microorganism (bacteria, yeasts, and fungi) colonizes. The global leaf area corresponds to both upper and lower surfaces, has approximately twice as great as the land surface area (Vorholt 2012). The phyllosphere is the ambient region for microbes to colonize and establish its association with plants usually epiphytes. Microbial communities in the phyllosphere are highly complex and consist of many cultured and uncultured microorganisms (Müller and Ruppel 2014). It has a heterogeneous group of the microbial association at the micrometer scale area due to its diverse microenvironments (habitats). The phyllospheric microbes are adapted to the insensitive environmental conditions, specifically microbial epiphytes are highly exposed to atmospheric temperature, light, UV radiation, less water, and nutrient availability. These external factors affect the composition and diversity of phyllospheric microbial communities (Vorholt 2012). However, the type of plant and invading microbial populations (pathogens) are also influencing the commensals and/or mutualistic relationship with their host plant (Lindow and Brandl 2003). Less number of studies are available for the microbiology of phyllosphere rather than plant root. Moreover, with increasing anthropogenic stresses, the diversity and community structure of phyllosphere microflora have been continually modified. In this chapter, we focused on the phyllospheric microbiome, structure and diversity, epiphytic mechanism, molecular interactions, ecological significance, and the microbial importance in biotechnology.

## 5.2 Basic Understanding of Leaf Structure

The leaf is a highly organized and multi-layered plant organ (Fig. 5.1), which consists of the epidermis (upper and lower) covered by a waxy cuticle that provides a physical barrier against abiotic and biotic stresses. The epidermis involves many regulatory processes of leaf physiology including gas exchange, temperature regulation, primary production, secretion of secondary metabolites, and water mobilization. Also, a specialized epidermal cell such as stomata, hydathodes (modified stomata), and trichomes (outgrowth) are there in the epidermis. The stomata are surrounded by two cupped hand cells called guard cells, which may open or close due to internal water pressure. Inside the leaf, a layer of cells called the mesophyll, is present, usually two layers, namely, palisade layer and the spongy layer. They contain chlorophyll and photosynthesis occurs in these cells. The palisade cells are more column cells and the spongy cells are more loosely packed between the palisade layer and the lower epidermis, and it allows for gas exchange. The veins of the leaf contain the vascular tissue, xylem and phloem are found in it. Veins run from tips of the roots and are extended up to the edges of the leaves. The outer layer cells are called bundle sheath



**Fig. 5.1** Structural organization of a leaf

cells which circle the xylem and the phloem. The xylem transports water and phloem transports sugar (food).

Glandular trichome of the epidermis releases a wide spectrum of leaf exudates, such as polysaccharide salts, lipids, volatile compounds, and proteins, and its function is associated with plant–microbe and plant–insect interactions (Hirano and Upper 1983). But, non-glandular trichome involves regulation of water tension, light absorption, and protect the leaf from UV radiation and heat as well as drought tolerance (Hirano and Upper 1983).

### 5.3 Phyllosphere Habitat

The phyllosphere is a unique and dynamic habitat which constitutes irregular, and sometimes relatively large microbial community inhabitant in the ecosystem (Whipps et al. 2008). The total terrestrial phyllosphere area estimated is around  $6.4 \times 10^8 \text{ km}^2$  (Morris and Kinkel 2002), and it exhibits numerous microhabitat which represents a major source of microorganism. Variety of bacteria, filamentous fungi, and yeasts are naturally colonized on the phyllosphere region and less frequently, protozoa and

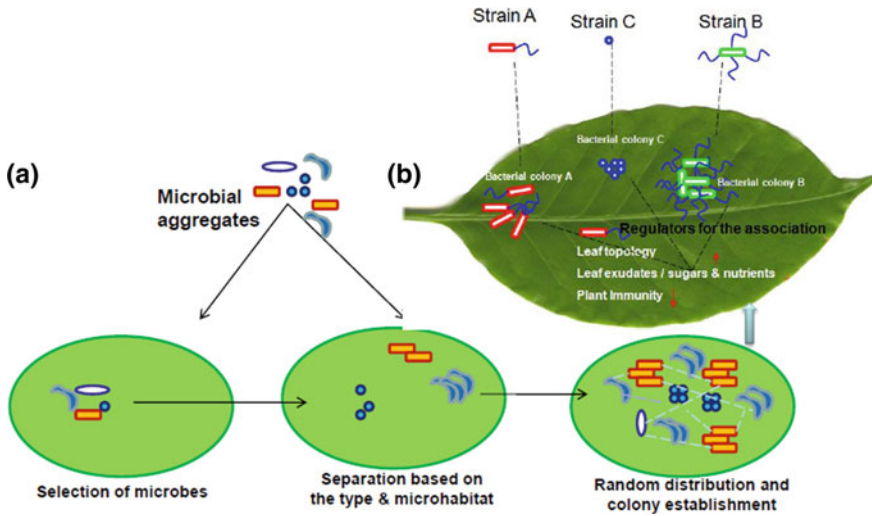
nematodes. These microorganisms exhibit commensalism and/or mutualism (symbionts) or antagonism type of relationship on their host plants. The microbial association in phyllosphere has several advantages and importance to global processes including biogeochemical cycles (carbon and nitrogen) and environmental impact.

### 5.3.1 *Microbial Assembly on Leaf*

The arrangement of leaf epidermal cells describes the leaf physiology and the microenvironment which allow the abundance and distributions of microorganisms on the leaf surface (Shiraishi et al. 2015; Esser et al. 2015). Simply, epiphytes make biofilm-like growth, most preferably larger bacterial aggregates are on the trichomes, veins, and epidermal cell groves (Brewer et al. 1991; Morris et al. 1997), where the leaf exudates containing nutrient-rich region. The presence of outer cuticle and its physiology help the microbes to colonize this site. Presence of aliphatic compounds in the cuticle layer determines the physicochemical properties of the leaf surface and renders the permeability and wettability, which facilitate the adherence of microorganisms (Sadler et al. 2016). Water permeability of this site may play a vital role in the survival and growth of the epiphytes. Moreover, leaching the nutrients along with water makes the epiphytes to utilize and develop colonies on the phyllosphere (Burch et al. 2014). The leaf surface with higher water and nutrient penetration is heavily colonized by bacterial communities (Beattie 2011). In general, bacteria maintain the cuticular permeability by secretion of biosurfactants, for example, *Pseudomonas syringae* release syringafactin on the cuticle layer of the leaf which facilitate the availability of sugar for persistent epiphytic growth (Van der Wal and Leveau 2011). Similarly, fructose availability by *Pantoea eucalypti* 299R and *Pantoea agglomerans* (Leveau and Lindow 2001). Figure 5.2 represents the phyllosphere microbial assemblage, wherein the epiphytic microorganism exploits this microenvironment for special distribution of microbes, survival as well as blooming (colonization). At the same time, surface microorganisms change the phyllosphere chemistry, and they render the heterogeneous oligotrophic mode of epiphytic life. Besides, microorganism establishes special niches on the leaf surface with the interactive mode of life (Aglar et al. 2016) in this microhabitat microbial population can be constantly maintained.

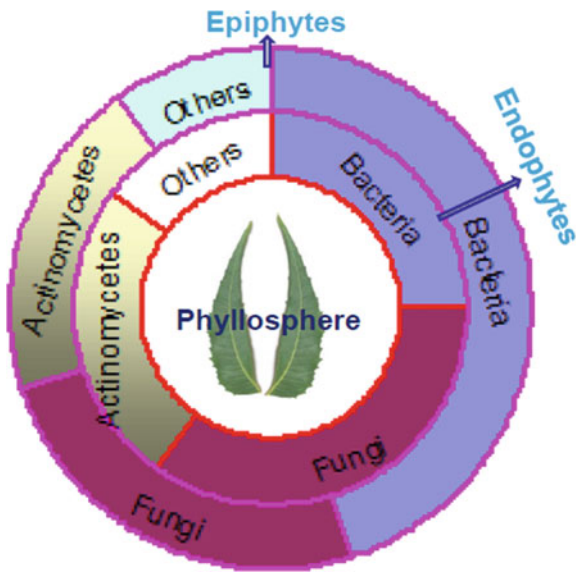
## 5.4 **Microbial Diversity in the Phyllosphere**

The phyllosphere consists of diverse numerous microbial communities including bacteria, filamentous fungi, yeasts, algae, and protozoans (Whipps et al. 2008; Verma et al. 2013, 2015, 2016a, b). The nature of various microorganisms (epiphytic and endophytic) associated with phyllosphere is given in Fig. 5.3. Among the diverse community of microbes, bacteria are the predominant community on leaves and its



**Fig. 5.2** Structure of phyllosphere microbial assemblage. **a** stages for microbial community structure development, **b** regulations for the microbial community structure in phyllosphere

**Fig. 5.3** Epiphytic and endophytic microbes in phyllosphere



range is between  $10^2$  and  $10^{12} \text{ g}^{-1}$  of the leaf (Inacio et al. 2002). The conventional culture-based method has been used for the identification of different microbial communities of the leaves. Thompson et al. (1993) identified 78 bacterial species from the sugar beet, and Legard et al. (1994) screened 88 bacterial species from 37 genera.

However, the culture-dependent method based profiling of phyllosphere communities is likely to be incorrect and miscalculates diversity (Rasche et al. 2006). The culture-independent approaches like 16S rDNA sequences of the whole microbial mass of phyllosphere could give the complete and complex microbial community structure of the environment. Molecular studies suggested that alpha-, beta- and gammaproteobacteria and firmicutes are the dominant bacterial inhabitants of the phyllosphere. Frequently, acidobacteria, actinobacteria, and cyanobacteria are also occurring in the phyllosphere environment (Kadivar and Stapleton 2006). Lambais et al. (2006) identified that 97% of the bacterial sequences of the phyllosphere have been new and unidentified. Yang et al. (2001) reported large numbers of novel bacteria from the phyllosphere of crop plants. The number of studies confirmed the diversity of yeast in the phyllosphere environment as an epiphyte.

The cultivable yeasts genera such as *Cryptococcus*, *Sporobolomyces*, and *Rhodotorula* and its species have been largely inhabitant in the plant leaf (Thompson et al. 1993; Glushakova and Chernov 2004). Moreover, the culture-dependent methods have been used to study the abundance of filamentous fungi, ranging from  $10^2$  to  $10^8$  CFU  $g^{-1}$ . Genera such as *Cladosporium*, *Alternaria*, *Penicillium*, *Acremonium*, *Mucor*, and *Aspergillus* are the frequent filamentous fungi colonizing as epiphytes and endophytes (Arnold et al. 2000; Inacio et al. 2002; Rana et al. 2019a, b, c).

However, the culture-independent strategy is the best to investigate the diversity and distribution of specific bacterial groups of interest (Miyamoto et al. 2004; Sessitsch et al. 2006). Other than the 16S/18S rDNA sequences, multiplex terminal restriction fragment length polymorphism (TRFLP) has been used to analyze several phylogenetic groups or functional genes in the microenvironment (Singh et al. 2006). Soils, water, air, tree buds, and plant debris from the previous crops are the sources for microbes in phyllosphere (Manceau and Kasempour 2002). Those microorganisms may be habited in phyllosphere either transient or residual epiphytes (Suslow 2002; Zak 2002). The atmospheric microflora, rainfall, humidity, wind, etc. can directly influence the transients of microorganisms to the phyllosphere (Lighthart 1997). During the plant growth period, the epiphytic bacterial population will increase in quantity (Inacio et al. 2002). The microorganisms on the seed or roots may be established as epiphytes or endophytes (Wulff et al. 2003). Some epiphytes may be injected into the internal space of the leaf and colonize as endophytes. The distribution pattern of the phyllosphere microorganisms is not even, mostly bacteria colonize at the epidermal wall junctions, specifically in the grooves and the veins or stomata or at the base of trichomes (Melotto et al. 2008), also found in the cuticle layer, near hydathodes and stomatal pits (Aung et al. 2018). The microbial load is higher at the lower leaf surface perhaps the lower leaf surface contains thin cuticle, stomata, and/or trichomes (Beattie and Lindow 1999). Mostly, all microorganisms that appear in the phyllosphere are capable to colonize and grow (Whipps et al. 2008), and it disperses throughout the surface by rain splash, bounce-off, wash-off, water movement, or removal by insects or pest (Kinkel 1997; Yang et al. 2001; Lambais et al. 2006).

### 5.4.1 Bacterial Diversity in the Phyllosphere

Phyllosphere is a heterogeneous environment (Koskella 2013), bacteria are considered the most abundant inhabitants of the leaves, and its average number is being around  $10^6$ – $10^8$  cells  $\text{cm}^{-2}$  (Andrews and Harris 2000; Hirano and Upper 2000). But the population of epiphytic bacteria differs depending on the plant species and its surrounding environment. The variation is mainly due to the physical and nutritional conditions of the phyllosphere. Commonly, the broad-leaf plants have the highest number of bacteria than the grasses or waxy broad-leaf plants (Kinkel et al. 2000).

Generally, the phyllosphere contains four major phyla of bacteria such as the Proteobacteria, Firmicutes, Bacteroides, and Actinobacteria (Kembel et al. 2014; Durand et al. 2018). Methylophilic bacteria are predominant in phyllosphere which includes genera such as *Methylobacterium*, *Methylophilus*, *Methylibium*, *Hyphomicrobium*, *Methylocella*, *Methylocapsa*, and *Methylocystis* (Mizuno et al. 2013; Iguchi et al. 2013; Kwak et al. 2014; Krishnamoorthy et al. 2018). *Methylobacterium* and *Sphingomonas* are the predominant genera belonging to the class alphaproteobacteria reported in several plant phyllospheres (Delmotte et al. 2009; Kumar et al. 2019a). The bacterial community organization on phyllosphere is controlled by specific assemblage regulations (Buee et al. 2009; Reinhold-Hurek et al. 2015). Normally, soil type, plant genotype and species, immune system of the plant, age, climatic condition, and the geographic region are the factors forcing the bacterial community assembly (Leff et al. 2015; Zarraonaindia et al. 2015; Copeland et al. 2015). Extensive studies are available for the soil and rhizosphere bacterial community on phyllosphere bacterial colonization in *Arabidopsis thaliana* (Bodenhausen et al. 2013; Maignien et al. 2014; Bai et al. 2015; Muller et al. 2015) and maize (Peiffer et al. 2013). *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* are the most abundant phyla colonizing the leaf and root of *A. thaliana* (Delmotte et al. 2009; Redford et al. 2010; Bodenhausen et al. 2013). *Massilia*, *Flavobacterium*, *Pseudomonas*, and *Rathayibacter* are a prevalent bacterial genus in *A. thaliana* (Bodenhausen et al. 2013), *Deinococcus thermus* on tree phyllosphere (Redford et al. 2010), and *Bacillus* and *Pantoea* dominate the lettuce (Rastogi et al. 2012).

Kembel et al. (2014) studied the bacterial communities on tropical tree leaves, around 400 bacterial taxa the phyllosphere has been dominated with Actinobacteria, Alpha-, Beta-, and Gammaproteobacteria, and Sphingobacteria. However, Archaea is the profuse members of the plant-associated microbe, commonly Thaumarchaeota, Crenarchaeota, and Euryarchaeota make the endophytic mode of life in plants (Müller et al. 2015). Durand et al. (2018) characterized the bacterial genera such as *Methylobacterium*, *Kineococcus*, *Sphingomonas*, and *Hymenobacter* of the phylum Firmicutes from the leaf surface. The phyllosphere of the grapevine contains Acinetobacter, Bacillus, Citrobacter, Curtobacterium, Enterobacter, Erwinia, Frigoribacterium, Methylobacterium, Pantoea, Pseudomonas, and Sphingomonas as dominant genera (Kecskeméti et al. 2016). Steven et al. (2018) characterized *Pseudomonas* and Enterobacteriaceae as predominant taxa from apple. Several studies revealed *Pseudomonas* as the most abundant genus of phyllosphere region (Alekkett et al. 2014;

Kecskeméti et al. 2016; Steven et al. 2018). Seed coat associated bacteria that have been reported in phyllosphere are mainly Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria (Johnston-Monje and Raizada 2011; Rodríguez-Escobar et al. 2018).

The most notable bacterial pathogen is *Pseudomonas syringae*, it causes diseases in a wide range of economically important plant species (Mansfield et al. 2012; Morris et al. 2013; Burch et al. 2014). Hamd Elmagzob et al. (2019) identified taxa such as Rhizobiales, Clostridiales, Pseudomonadales, Burkholderiales, Bacteroidales, Enterobacteriales, Rhodocyclales, Sphingomonadales, Lactobacillales, and Bacillales from the leaves of *Cinnamomum camphora* (L.) Presl. Several studies reported diazotrophic bacteria on phyllosphere (Fürnkranz et al. 2008; Rico et al. 2014). Diazotrophic bacteria can use atmospheric dinitrogen (N<sub>2</sub>) as nitrogen source for its metabolic activities. Bacterial diazotrophic include *Beijerinckia*, *Azotobacter*, *Klebsiella*, and Cyanobacteria (e.g., *Nostoc*, *Scytonema*, and *Stigonema*). Diazotrophic nitrogen fixation has been reported in many species which contains an enzyme nitrogenase (encoded by *nif* genes) (Rico et al. 2014). Recently, 16 s rRNA gene-based high-throughput sequencing technology has been used for the diversity analysis of phyllosphere, for example, the distribution of endophytic bacteria of *C. camphora* (L.) Presl leaves has been analyzed by 16S rRNA gene metagenomics, revealing Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, Gemmatimonadetes, Acidobacteria, Planctomycetes, Chloroflexi, and Fusobacteria are the major phyla of the polymicrobial community (Hamd Elmagzob et al. 2019).

#### 5.4.2 Fungal Microbiota of Phyllosphere

Fungi are saprophytic and they may be associated with plants either epiphytic or endophytic, and mostly they are known for their pathogenesis on plant system (Voříšková and Baldrian 2013; Yadav et al. 2019b, c, d). There are several reports revealed that phyllosphere fungi have a profound role in the residing host. Both epiphytic and endophytic fungi inhabiting the leaf are of high species diversity with diverse metabolic functions (Yao et al. 2019), such as leaf litter decomposition and recycling the carbon and nitrogen (Kannadan and Rudgers 2008; Guerreiro et al. 2018). In general, endophytic fungi can help plant growth and also provide resistance to biotic (pathogens) and abiotic (drought and salinity) stresses, (Arnold et al. 2007; Purahong and Hyde 2011; Guerreiro et al. 2018; Yadav et al. 2018c). In culture-dependent approaches, several fungal species have been isolated from small herbs to larger woody plants. Inácio et al. (2010) reported that the density of yeast-like fungi may vary from plant to plant and approximately  $5 \times 10^4$  cells cm<sup>-2</sup>. *Aureobasidium pullulans* are yeast-like fungi abundant in phyllosphere (Cordier et al. 2012; Setati et al. 2012). Apart from yeast-like fungi, many filamentous fungi have been reported from health as well as infected plant leaves. Through the culture-dependent method, Ripa et al. (2019) isolated *Aspergillus niger*, *Fusarium oxysporum*, *Penicillium aurantiogriseum*, *Fusarium incarnatum*, *Alternaria alternata*, *Alternaria*



*tenuissima*, *Cladosporium cladosporioides*, *Talaromyces funiculosus*, *Aspergillus flavus*, *Trichoderma aureoviride*, *Trichoderma harzianum*, *Penicillium janthinellum*, *Fusarium proliferatum*, *Fusarium equiseti*, and *Aspergillus stellatus* from wheat plant.

Dhayanithy et al. (2019) isolated twenty endophytic fungi from the leaves and stem of *Catharanthus roseus*, among them *Colletotrichum*, *Alternaria*, and *Chaetomium* were the dominant genera. Many of them make endophytic association begin with epiphytic initiation (Rodriguez et al. 2009; Porras-Alfaro and Bayman 2011), and some endophytes later turned to pathogens. The olive tree phyllosphere is found to be highly diverse having more than 149 genera and 68 families of fungi (Martins et al. 2016) in a Mediterranean ecosystem (Portugal), but Abdelfattah et al. (2015) reported only 13 endophytic fungal taxa in the leaves and twigs of olive trees. There has been a discrepancy to understand the phyllosphere fungi as endophytic or epiphytic, occasionally it is uncertain, for the reason that some can reside both epiphytic and endophytic modes of association. In general, phyllosphere endophytic fungi are the epiphytic habitats and are penetrated into the plant tissues to form an endophytic association (Kharwar et al. 2010; Porras-Alfaro and Bayman 2011). Though they are phyllospheric, the soil has acted as a reserve for these potential endophytic inoculums of the above-ground organs (Zarraonaindia et al. 2015). For example, *Ascochyta* sp. and *Fagus crenata* B1 (Osono 2006), *Colletotrichum gloeosporioides* and *Phomopsis* sp. (Rivera-Vargas et al. 2006; Twizeyimana et al. 2013), and Table 5.1 listed some examples of phyllosphere fungal endophytes.

Osono (2008) reported that endophytic *Colletotrichum gloeosporioides* and *C. acutatum*, and epiphytes *Pestalotiopsis* sp., *Aureobasidium pullulans*, *Phoma* sp., and *Ramichloridium* sp. are the phyllosphere fungi in the plant *Camellia japonica*. However, the abundance and diversity of the fungi differ in plant species as well as in different eco-climatic conditions. Moreover, seasonal and leaf age-dependent variations also occur in the epiphytic and endophytic phyllosphere fungal assembly, for example, *Geniculosporium* sp. is varied in leaf age, and *Cladosporium cladosporioides* has been varied in both season and leaf age of the plant *Camellia japonica* (Osona 2008). Phyllosphere fungi play an important function in mineral absorption and mineral recycling process, specifically carbon, nitrogen, and phosphorus recycling in the forest ecosystem. Therefore, the study about the phyllosphere fungi and its physiology with host plant is important.

### 5.4.3 Actinomycetes Diversity in Phyllosphere

In addition to bacterial diversity, actinobacteria share a considerable interest in epiphytic and endophytic life forms in the phyllosphere. They are soil-inhabiting saprophytic microbes and have been extensively studied for their therapeutic secondary metabolites. This versatile group of gram-positive bacteria has adapted to diverse environments including the phyllosphere of the plant (Singh et al. 2018). Some actinobacteria form symbiotic association residing in plant tissues have generated

**Table 5.1** Phyllosphere fungal endophytes

Endophytic fungi	Host plant	Type	References
<i>Aspergillus</i> , <i>Phomopsis</i> , <i>Wardomyces</i> , <i>Penicillium</i>	<i>Euterpe oleracea</i> (palm)	Palm	Rodrigues (1994)
<i>Ramularia</i> spp.	<i>Vitis riparia</i> (grapevine)	Wild	Kernaghan et al. (2007)
<i>Absidia</i> sp., <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Cunninghamella</i> sp., <i>Fusarium</i> sp., <i>Nigrospora</i> sp., <i>Paecilomyces</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp.,	<i>Meyna spinosa</i> Roxb.	Medicinal plant	Bhattacharyya et al. (2017)
<i>Penicillium chrysogenum</i> , and <i>Penicillium crustosum</i>	<i>Teucrium polium</i>	Medicinal plant	El-Din Hassan (2017)
<i>Alternaria alternata</i> , <i>Setosphaeria</i> sp., <i>Cochliobolus</i> sp., <i>Alternaria</i> sp. <i>Phoma herbarum</i> , <i>Davidiella tassiana</i> , <i>Botryosphaeria dothidea</i> , <i>Ulocladium alternariae</i> , <i>Phoma macrostoma</i> var. <i>incolorata</i> , <i>Phoma exigua</i> var. <i>exigua</i> , <i>Cladosporium cladosporioides</i> strain, <i>Botryosphaeria</i> sp., <i>Guignardia mangiferae</i> , <i>Pyrenophora tritici-repentis</i> , <i>Guignardia alliacea</i> , <i>Rhizopus oryzae</i>	<i>Catharanthus roseus</i>	Medicinal plant	Sreekanth et al. (2017)

(continued)

enormous significance to the host and its environment through their novel metabolites. Diversity and distribution of endophytic actinobacteria have been largely documented, from medicinal plants, crop plants, and some other terrestrial plants (Qin et al. 2011; Masand et al. 2015; Dinesh et al. 2017; Nalini and Prakash 2017). Several species of actinobacteria have been reported from plants such as *Triticum aestivum*, *Lupinus termis*, *Lobelia clavatum*, *Acacia auriculiformis*, *Aquilaria crassna*, *Oryza*

**Table 5.1** (continued)

Endophytic fungi	Host plant	Type	References
Ascomycetes: <i>Trichoderma</i> , <i>Penicillium</i> , <i>Fusarium</i> , and <i>Aspergillus</i> . Non-ascomycetes: <i>Mucor</i> (Mucoromycota) and <i>Schizophyllum</i> (Basidiomycota)	<i>Stanhopea tigrina</i>	Orchid	Salazar-Cerezo et al. (2018)
<i>Trichothecium</i> sp., <i>Epicoccum nigrum</i> , <i>Alternaria alternaria</i> , <i>Alternaria arborescens</i> , <i>Nigrospora sphaerica</i> , <i>Epicoccum</i> sp., <i>Alternaria</i> sp., <i>Nigrospora</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>Fusarium oxysporum</i> , <i>Trichothecium roseum</i>	<i>Vitis vinifera</i> (Grape fruit cells)	Fruit plant	Huang et al. (2018)
<i>Aspergillus japonicus</i>	<i>Euphorbia indica</i> L.	Wild plant	Ismail et al. (2018)
<i>Alternaria</i> spp., <i>Trichophyton</i> spp., <i>Geotrichum</i> spp., <i>Candida</i> spp., <i>Aspergillus</i> spp., <i>Aureobasidium</i> spp., <i>Fusarium</i> spp., <i>Exserohilum</i> spp., <i>Curvularia</i> spp., <i>Coccidioides</i> spp., <i>Bipolaris</i> spp.	<i>Epipremnum aureum</i> , <i>Azadirachta indica</i> , <i>Piper betle</i> , <i>Catharanthus roseus</i> , <i>Ficus religiosa</i> , <i>Musa acuminata</i> , <i>Ficus Benghalensis</i> , <i>Ficus racemosa</i> , <i>Calotropis procera</i> , <i>Ocimum tenuiflorum</i>	Medicinal plant	Jariwala and Desai (2018)
<i>Nigrospora sphaerica</i> , <i>Acremonium falciforme</i> , <i>Allomyces arbuscula</i> , <i>Penicillium chrysogenum</i> , <i>Acrophialophora</i> sp., <i>Mycelia sterilia</i>	<i>Litsea cubeba</i>	Medicinal plant	Deka and Jha (2018)

(continued)

**Table 5.1** (continued)

Endophytic fungi	Host plant	Type	References
Colletotrichum gloeosporioides f. sp. camelliae and Pleosporales sp.	<i>Camellia sinensis</i>	Tea	Win et al. (2019)
Tremellales, Davidiellaceae, Basidiomycota, Rhodotorula, Tremellales, Meria, Cryptococcus, Cladosporium, Acaromycetes, Erythrobasidium, etc.	<i>Aegiceras corniculatum</i> (Myrsinaceae), <i>Avicennia marina</i> (Verbenaceae), <i>Bruguiera gymnorrhiza</i> , <i>Kandelia candel</i> and <i>Rhizophora stylosa</i> (Rhizophoraceae), and <i>Excoecaria agallocha</i> (Euphorbiaceae)	Mangrove	Yao et al. (2019)

*sativa*, *Xylocarpus granatum*, and *Elaeagnus angustifolia* from various environments like arid, semiarid, and mangrove are *Actinoplane missouriensis*, *Actinoallomurus acacia*, *Actinoallomurus coprocola*, *Actinomadura glauciflava*, *Amycolatopsis tolypomycina*, *Actinoallomurus oryzae*, *Jishengella endophytica*, *Kribbella* sp., *Microbispora mesophila*, *Microbispora* sp., *Micromonospora* sp., *Nocardioides* sp., *Nocardia alba*, *Nonomurea rubra*, *Micromonospora* sp. *Nonomurea* sp., *Pseudonocardia* sp., *Planotetraspora* sp., *Pseudonocardia endophytica*, *Pseudonocardia halophobica*, *Streptomyces* sp., and *Streptomyces javensis* (Coombs and Franco 2003; Thamchaipenet et al. 2010; Chen et al. 2011; Xie et al. 2011; Yadav 2017; Yadav and Yadav 2018). Reports revealed that the actinomycetes diversity in phyllosphere is high in the tropical and temperate ecosystem (Strobel and Daisy 2003; Yadav et al. 2018b; Yadav and Yadav 2019). Moreover, the physiology of the plant and the environment determines the actinobacterial association in plants and allows them to establish endophytic life (Du et al. 2013). Some important actinobacterial diversity in various plant sources is discussed in the following (Table 5.2).

## 5.5 Mechanism of Microbial Interaction with the Phyllosphere

The leaf physiology determines the microbial diversity and abundance on the phyllosphere. It establishes the microhabitat where the microorganisms adapt to their physiology to survive in this habitat (Staley et al. 2014; Shiraishi et al. 2015). The epiphytic microbes formed as colonial form, which gives protection to the microorganisms from this harsh microhabitat (Lindow and Brandl 2003; Remus-Emsermann

**Table 5.2** Diversity of endophytic actinobacteria

Endophytic actinobacteria	Host plant	Habitat	References
<i>Microbispora</i> sp., <i>Micromonospora</i> sp., <i>Nocardioides</i> sp., <i>Streptomyces</i> sp.,	<i>Triticum aestivum</i>	Arid	Coombs and Franco (2003)
<i>Actinoplane missouriensis</i>	<i>Lupinus termis</i>	Arid	El-Tarabily (2003)
<i>Pseudonocardia endophytica</i>	<i>Lobelia clavatum</i>	Arid	Chen et al. (2009)
<i>Actinoallomurus acaciae</i> , <i>Streptomyces</i> sp., <i>Actinoallomurus coprocola</i> , <i>Amycolatopsis tolypomycina</i> , <i>Kribbella</i> sp., <i>Microbispora</i> <i>mesophila</i>	<i>Acacia auriculiformis</i>	Arid	Thamchaipenet et al. (2010)
<i>Actinomadura glauciflava</i> , <i>Pseudonocardia halophobica</i> , <i>Nocardia alba</i> , <i>Nonomuraea</i> <i>rubra</i> , <i>Streptomyces javensis</i>	<i>Aquilaria crassna</i>	Mangrove	Nimnoi et al. (2010)
<i>Actinoallomurus oryzae</i>	<i>Oryza sativa</i>	Aquatic	Indananda et al. (2011)
<i>Jishengella endophytica</i>	<i>Xylocarpus granatum</i>	Mangrove	Xie et al. (2011)
<i>Micromonospora</i> sp., <i>Nonomuraea</i> sp., <i>Pseudonocardia</i> sp., <i>Planotetraspora</i> sp.	<i>Elaeagnus angustifolia</i>	Arid	Chen et al. (2011)
<i>Streptomyces phytohabitans</i>	<i>Curcuma phaeocaulis</i>	Arid	Bian et al. (2012)
<i>Nonomuraea solani</i>	<i>Solanum melongena</i>	Arid	Wang et al. (2013b)
<i>Actinoplanes hulinensis</i> , <i>Streptomyces harbinensi</i> , <i>Wangella harbinensis</i>	<i>Glycine max</i>	Arid	Jia et al. (2013), Liu et al. (2013), Shen et al. (2013)
<i>Micromonospora sonneratiiae</i>	<i>Sonneratia apetala</i>	Mangrove	Li et al. (2013)
<i>Modestobacter roseus</i>	<i>Salicornia europaea</i>	Saline	Qin et al. (2013)
<i>Promicromonospora endophytica</i>	<i>Eucalyptus microcarpa</i>	Arid	Kaewkla and Franco (2013)
<i>Blastococcus endophyticus</i> , <i>Plantactinospora endophytica</i>	<i>Camptotheca acuminata</i>	Arid	Zhu et al. (2013)

(continued)

**Table 5.2** (continued)

Endophytic actinobacteria	Host plant	Habitat	References
<i>Actinoplanes brasiliensis</i> , <i>Couchioplanes caeruleus</i> , <i>Gordonia otitidis</i> , <i>Micrococcus</i> <i>aloeverae</i> , <i>Streptomyces</i> <i>zhaozhouensis</i>	<i>Aloe arborescens</i>	Arid	He et al. (2014)
<i>Micromonospora</i> <i>schwarzwaldensis</i> <i>Streptomyces</i> sp., <i>Wenchangensis</i>	<i>Centella asiatica</i>	Mangrove	Ernawati et al. (2016)
<i>Glutamicibacter halophytocola</i> , <i>Kineococcus endophytica</i> , <i>Streptomyces</i> sp.,	<i>Limonium sinense</i>	Saline	Feng et al. (2017)
<i>Marmoricola endophyticus</i>	<i>Thespesia populnea</i>	Mangrove	Jiang et al. (2017)
<i>Allostreptomyces</i> <i>psammosilena</i>	<i>Psammosilene tunicoides</i>	Arid	Huang et al. (2017)
<i>Micromonospora terminaliae</i>	<i>Terminalia mucronata</i>	Mangrove	Kaewkla et al. (2017)
<i>Nocardiosis</i> sp., <i>Pseudonocardia</i> sp. <i>Streptomyces</i> sp.,	<i>Dracaena cochinchinensis</i>	Semiarid	Salam et al. (2017)
<i>Mangrovihabitans endophyticus</i>	<i>Bruguiera sexangula</i>	Mangrove	Liu et al. (2017)
<i>Actinoplanes</i> sp., <i>Agrococcus</i> sp., <i>Amnibacterium</i> sp., <i>Brachybacterium</i> sp., <i>Brevibacterium</i> sp., <i>Citricoccus</i> sp., <i>Curtobacterium</i> sp., <i>Dermacoccus</i> sp., <i>Glutamicibacter</i> sp., <i>Gordonia</i> sp., <i>Isoptricola</i> sp., <i>Janibacter</i> sp., <i>Kocuria</i> sp., <i>Leucobacter</i> sp., <i>Mycobacterium</i> sp., <i>Micrococcus</i> sp., <i>Nocardioides</i> sp., <i>Kineococcus</i> sp., <i>Kytococcus</i> sp., <i>Marmoricola</i> sp., <i>Microbacterium</i> sp. <i>Micromonospora</i> , sp., <i>Nocardia</i> sp., <i>Nocardiosis</i> sp., <i>Pseudokineococcus</i> , sp., <i>Sanguibacter</i> sp., <i>Streptomyces</i> sp., <i>Verrucosispora</i> sp.,	<i>Avicennia marina</i> , <i>Aegiceras corniculatum</i> , <i>Kandelia obovata</i> , <i>Bruguiera gymnorrhiza</i> , and <i>Thespesia populnea</i>	Mangrove	Jiang et al. (2018)
<i>Glycomyces anabasis</i>	<i>Anabasis aphylla</i>	Arid	Zhang et al. (2018)

et al. 2012). Commonly, bacteria develop larger sized colonial association on the leaf surface, especially at veins as well as the grooves of epidermal cells (Morris et al. 1997; Hirano and Upper 2000). The epidermal grooves are rich in nutrients specifically sugar and water. This region is less waxy cuticle, usually the leaf surface is fully covered with waxy cuticle which prevents the permeability and wettability of the leaf surface and regulates the colonization of the microbes on phyllosphere (Lindow and Brandl 2003; Burch et al. 2014).

The leaf surface water droplets diffuse the waxy cuticle and improve the permeability by which the compounds are diffused from the apoplast to phyllosphere surface (Schreiber 2005). These leached compounds and water on the phyllosphere are making the availability of nutrients to the microorganisms. Most commonly, the flow of water from the stomata (transpiration) is increasing the permeability and wettability of guard cells and its surface cuticles (Schönherr 2006). Hence, higher permeation of the cuticle layer permits the microbes to colonize densely (Krimm et al. 2005). Moreover, the surface bacteria are able to produce certain compounds like biosurfactants (syringafactin produced by *Pseudomonas syringae*) (Krimm et al. 2005; Burch et al. 2014) which can modify the cuticle surfaces of the leaf and establish its association. This can facilitate water availability and alter sugar availability that can improve living conditions for epiphytic bacterial growth (Lindow and Brandl 2003; Van der Wal and Leveau 2011). Epiphytes such as *Pseudomonas* sp., *Stenotrophomonas* sp., and *Achromobacter* increase the water permeability of the lipophilic cuticle present in *Hedera* and *Prunus*, which increases the availability of the compounds at the phyllosphere which will improve the epiphytic fitness on the leaf surface (Schreiber et al. 2005).

It has been experimentally proved in the bean phyllosphere containing fructose facilitates the growth of *Erwinia herbicola* and *Pantoea agglomerans* (Remus-Emsermann et al. 2013; Tecon and Leveau 2016). However, irregular distribution of fructose differentially promotes the *P. eucalypti* population on bean leaves (Mercier and Lindow 2000; Leveau and Lindow 2001; Remus-Emsermann et al. 2011). These studies suggested that the permeated carbon sources on the leaf surface are merily exploited by the epiphytic microorganisms for their growth and multiplication. At the same time, the phyllosphere microbial population can influence the modulation of the physicochemical properties of the leaf with the help of both biotic and abiotic surroundings (Bringel and Couée 2015; Ohshiro et al. 2016; Quan and Liang 2017). Soil microbial community may also influence the determination of phyllosphere microbial diversity. However, the microbes can construct the niches in the phyllosphere microhabitat wherein it can sustain and establish its population steadily (Agler et al. 2016; San Roman and Wagner 2018). Recent studies revealed the special relationships between the bacterial species in the phyllosphere community. Presence of sugars and nutrients in this environment significantly change the individual bacterial cells within the microbial aggregates (Fig. 5.2) would spatially be established with cell-to-cell interactions along with direct physical interactions (Levy et al. 2018; Tecon et al. 2018). The community structure is organized based on the driven factors such as dispersal, selection of microbes, diversification, and

ecological drift. The fitness of the community is due to internal (strain types) and external determinants (environment) of the phyllosphere (Schlechter et al. 2019).

In general, the internal factors of the community are based on the microbial relationship within the aggregates. The microbes usually have either commensal or antagonistic or mutualistic or cooperative association by which the community structure can be established. Both cooperative and mutualistic microbial interactions shape the community structure as well as to develop larger colonial association containing the maximum microbial population. While commensals have weak interactive partners in the community, they are randomly distributed in the habitat. The commensals should not influence the interactive association within the structured community (Stubbenieck et al. 2016). Besides, antagonistic microbes have a negative interaction within the community, one can outcompete the other and the sensitive microbes have been eliminated from the environment. The effect of cooperative microbial interactions on the phyllosphere community structure establishment is not demonstrated (Schlechter et al. 2019).

Bacteria can ascertain the cell-to-cell communication system and establish a larger community structure with heterogeneous populations, usually with mutualistic and cooperative partners. However, some kind of mutualistic relationship may occur between rapid growing bacteria and pathogenic fungi, which leads to cause superficial infection on the host plant which increases the nutrient accessibility of the bacteria to rich its population (Suda et al. 2009; Zeilinger et al. 2016; Amine Hassani et al. 2018). Inversely, fungal–fungal interactions seem to decrease the bacterial population, for example, oomycete species *Dioszegia* sp. and *Albugo* sp. outcompete the bacterial microbiota on *A. thaliana* leaf (Chou et al. 2000; Agler et al. 2016). Moreover, competitive interactions of microbes involve negative effects on at least one species of the habitat. Some competitive microbes produce certain toxic chemical substances (antibiotics and siderophores) as secondary metabolites which pose a negative effect on its competitor microbes. The best example of such interaction is a gram-negative *Pantoea agglomerans* bacteria which inhibit the growth of *Erwinia amylovora*, a phytopathogen of apple by antibiotic activity (Wright et al. 2001; Pusey et al. 2011).

Generally, the competition of microbes is mainly for their nutrition and space. The phyllosphere is a nutrient-limited environment, wherein the competitive partner has compromised their growth by either coexisting or excluded from the site (Saleem et al. 2017). Besides, the phyllosphere is greatly colonized by both oligotrophic and competitive microbes which play an important role in community structure formation (Schlechter et al. 2019). However, the key factors of the phyllosphere community assemblage are currently vague. Hence, more studies required to find the key factors determining the phyllosphere community structure assemblage.

## 5.6 Factors Controlling Phyllosphere Microbiomes

Once microbes arrived at the phyllosphere, a variety of factors resolve whether microbial cells are competent to colonize the leaf and become confined. Colony



establishment depends on the leaf–atmosphere environmental interaction with the residing microorganisms in the phyllosphere. At the beginning, the microbe reaches the cuticle layer, a waxy surface that protects the leaf from the pathogens. In general, cuticle restricts the microbial association due to the functions such as barrier, reducing water and solute loss, aqueous pollution, reflectance to minimize the temperature, conferring water repellent, etc. (Beattie 2002; Whipps et al. 2008). The whole-cell biosensor-based study revealed the available nutrients on the leaf surface facilitate the growth of residing microbes at a limited level (Miller et al. 2001). This was confirmed by the microscopic observation of leaf surfaces, at the low nutrient region contains less dense microbial colonization than the nutrient-rich surface (Monier and Lindow 2005). Naturally, nutrient enrichment may happen by pollen deposits and honeydew at the phyllosphere surface (Lindow and Brandl 2003), besides plant leaves release a large array of volatile organic substances into the margin layer around leaves (Jackson et al. 2006). Nutrients that include CO<sub>2</sub>, acetone, terpenoids, aldehydes, alcohols, long-chain hydrocarbons, sesquiterpenoids, and nitrogen-containing compounds (Whipps et al. 2008) are available nutrients for microbial growth. Some of the compounds may act as growth inhibitor or toxic to microbial growth (Dingman 2000; Shepherd et al. 2005). Hence, microbes establish several adaptive mechanisms for maintaining their growth in adverse conditions.

### 5.6.1 *Microbial Adaptations in Phyllosphere Environment*

Microbes like bacteria establishing colonies at the phyllosphere are limited by various factors including both biotic and abiotic. Abiotic factors such as the available nutrient (Delmotte et al. 2009), seasonal variation, rainfall, temperature, plant immunity, and competitor microbes (Rastogi et al. 2013) are influencing surveillance of microbes in the phyllosphere. Metaproteomic studies on the leaf surface communities have been identified as microbes producing vitamins and siderophores which give adaptation to the microbes at the environment. For example, phyllosphere of soybean, clover, and Arabidopsis plants largely colonized by Sphingomonas and Methylobacterium provides vitamins and siderophores to the plant (Green 2006; Delmotte et al. 2009) and it competes for other microbes. *Methylobacterium* spp. are involved in the assimilation of methanol at the phyllosphere, a by-product of demethylated pectin during the cell wall metabolism of the plant (Galbally and Kirstine 2002; Delmotte et al. 2009), and it gives epiphytic fitness to the microbes. Proteome studies revealed that some unique properties of rhizosphere bacteria have been found in the phyllosphere microbiota. For example, genes of methanol dehydrogenase and formaldehyde-activating enzyme (of Rhizosphere *Methylobacterium* spp.) and nitrogen fixation (*Rhizobium* sp.) are also reported in both phyllosphere and rhizosphere samples of rice (Knief et al. 2012). Gourion et al. (2006) observed upregulation of methylotrophic proteins such as MxaF and Fae and stress-related protein PhaA during epiphytic growth of *Methylobacterium extorquens*.

Phyllosphere colonization may occur in two different habitats, (1) the surface (epiphytic) and (2) the apoplast or leaf interior (endophytic). During the epiphytic life, many of the environmental factors regulate the growth such as solar radiation, temperature, water availability, nutrient, humidity, etc., whereas the endophytes are challenged with a plant defense mechanism. A bacteria colonizing at both habitats may differentially express their genes, for example, *P. syringae* pv. *syringae* B728a at epiphytic growth express the genes involved in motility, chemosensing, phosphate mobilization, and utilization of tryptophan which is higher than in endophytic growth (Yu et al. 2013). However, the secondary metabolite (syringomycin, syringopeptin) production was higher in the endophytic stage. One such adaptation is the production of pigments, bacteria such as *Pseudomonas*, *Sphingomonas*, and *Methylobacterium* produce pigmentation by which they give protection against UV light (Lindow and Brandl 2003). Presence of extracellular polysaccharide is another protective measure of plant-bacteria against desiccation and osmotic stress (Monier and Lindow 2004). Delmotte et al. (2009) found several stress-resistant proteins (PhyR and EcfG) from the phyllosphere of soybean, clover, and *Arabidopsis* through metaproteogenomic survey. Flagellin-like protein is high in *Pseudomonas* at the epiphytic growth which enables the bacteria to access the nutrition by the chemostatic model (Yu et al. 2013).

### 5.6.2 *Plant Immunity/Responses to Control Microbial Colonization*

The plant has its immune system which plays an important role in determining microbial assembly (Jacoby et al. 2017). Plants contain two layers of defense, the primary immunity is named pattern-triggered immunity (PTI), it has a conserved molecule named microbe/pathogen-associated molecular patterns (MAMPs/PAMPs). The PTI is a localized immunity mediated at the plasma membrane containing pattern recognition receptors (Monaghan and Zipfel 2012; Wang et al. 2019). The MAMP/PAMP limits the growth of bacterial pathogens. For example, the flagellin-sensitive receptor 2 (FLS2) is a pattern receptor which recognizes the *P. syringae* pathovar (pv.) bacterial flagellin (flg22) (Chinchilla et al. 2006; Newman et al. 2013; Trdá et al. 2015). However, the plant response to limits its defense against non-pathogenic bacteria is still unknown. The effector's protein-mediated destabilization of plant immunity and immune escape is also reported (Jones and Dangl 2006; Cui et al. 2009). Plant immunity is targeted with specific proteins, which involves the self-protection against the microbial association has been deactivated by the interaction of microbial effector proteins and it makes protein-protein networks (Bogdanove 2002; Snelders et al. 2018). Besides, plants have evolved with intracellular receptor molecules called nucleotide-binding leucine-rich repeat proteins (NLRs), which either openly or ultimately recognize effector proteins to give the second layer of plant immunity named effector-triggered immunity (ETI) (Jacob et al. 2013; Wu et al.

2014). Both PTI and ETI generate more specific and diverse immunity against phyllosphere microflora. Beneficial or the synergistic microbes interact with signaling pathways (MAMPs) of the plant to elevate the production of its immune response. However, if pathogen could interact by using MAMPs, the immune output will be higher and will restrict the colonial establishment of pathogens. Pathogens that live in host tissues use hemibiotrophs and necrotrophs mode of life (Table 5.3). Some chemicals of the plant tissues inhibit the microbial association either biotrophs (salicylic acid) or necrotrophs (jasmonic acid) type and also the reactive O<sub>2</sub> species may have an inhibitory effect on the pathogens (Lehmann et al. 2015). Plants use jasmonic acid, methyl jasmonate, ethylene, flavonoid, 12-oxo-phytodienoic acid, and salicylic acid-mediated signals for quenching pathogens on its surface (Table 5.4). Recently, pathogens with biotrophy-necrotrophy switch have been identified in fungi such as *Colletotrichum* sp, *Phytophthora capsici*, *Moniliophthora roreri*, and *Macrophomina phaseolina* in which pathogen evokes a differential response of growth in host tissues (Chowdhury et al. 2015). Some important research in the mode of immune evoke by the pathogen has been listed in Tables 5.3 and 5.4.

Phyllosphere region is usually colonized by a variety of microorganisms. Naturally, leaf epidermises are always contacted to external and internal environments and are enriched with a diverse group of bacteria, yeast, fungi, and viruses. The cuticle layer of the leaf surface plays a significant role during the contact with leaf

**Table 5.3** Mode of life cycle of pathogen established against plant immunity

Organism	Life cycle	Host	References
<i>Fusarium graminearum</i>	Hemibiotrophic	Wheat	Ding et al. (2011)
<i>Colletotrichum graminicola</i>	Biotrophic and necrotrophic	Maize	Vargas et al. (2012)
<i>Septoria tritici</i>	Hemibiotrophic	Wheat	Yang et al. (2013)
<i>Phytophthora capsici</i>	Hemibiotrophic	Tomato	Jupe et al. (2013)
<i>Colletotrichum</i> sp.	Hemibiotrophic	Plants	Gan et al (2013)
<i>Moniliophthora roreri</i>	Hemibiotrophic and necrotrophic	Cacao	Meinhardt et al. (2014)
<i>Fusarium verticillioides</i>	Biotrophic	Maize	Lanubile et al. (2014)
<i>Botrytis</i> sp	Necrotrophic	Plants	Van Kan et al. (2014)
<i>Botrytis fabae</i>	Necrotrophic	Faba bean	El-Komy (2014)
<i>Sclerotinia sclerotiorum</i>	Biotrophic, hemibiotrophic, and necrotrophic	Plants	Kabbage et al. (2015)
<i>Zymoseptoria tritici</i>	Hemibiotrophic	Wheat	Rudd et al. (2015)
<i>Phytophthora infestans</i>	Hemibiotrophic	Tomato	Zuluaga et al. (2016)
<i>Rhizoctonia solani</i>	Necrotrophic	Wheat	Foley et al. (2016)

*Note* “Hemibiotrophs” - an organism that is parasitic in living tissue for some time and then continues to live in dead tissue. “Necrotrophs” - can kill the host cells and feed on the contents

**Table 5.4** Signaling pathway inhibits pathogenic microbes in phyllosphere

Molecules/signals	Pathogen	Host	References
Flavonoid pathway	Bacterial pathogens	<i>Melampsora medusae</i>	Miranda et al. (2007)
Jasmonic acid, ethylene, and the flavonoid	<i>Phymatotrichopsis omnivora</i>	Medicago truncatula	Uppalapati et al. (2009)
Methyl jasmonate and ethylene	<i>Macrophomina phaseolina</i>	<i>Medicago truncatula</i>	Gaige et al. (2010)
Jasmonic acid and ethylene	<i>Fusarium graminearum</i>	Wheat	Sun et al. (2010)
Jasmonate and ethylene	<i>Fusarium sp</i>	Wheat	Gottwald et al. (2012)
Ethylene and jasmonate	<i>Pythium ultimum</i>	Apple	Shin et al. (2014)
Methyl jasmonate, 12-oxo-phytodienoic acid, salicylic acid, and flavonol	<i>Fusarium oxysporum</i> f.sp. <i>lycopersici</i>	Tomato	Krol et al. (2015)

microbiota (Vacher et al. 2016). Though some group of microorganism may not multiply after it reaches on the surface, many continue to survive and multiply, until they can attain maximum number (Schönherr 2006; Innerebner et al. 2011; Pusey et al. 2011). To multiply, microorganisms require carbon, nitrogen, inorganic, and organic energy sources. However, in the absence of such nutrients, phyllosphere is still usually colonized by a large number of bacteria (105–107 CFU/g of the leaf) in the presence of high relative humidity and free water at suitable environmental conditions (Schönherr 2006; Baldwin et al. 2017). This is due to the release of nutrients or leaf exudates which adequately supported the microbial growth. There are varieties of molecules leached from the plant leaves such as sugar, amino acids, organic acids, minerals, etc. (Beattie 2011; Remus-Emsermann et al. 2011; Meiners et al. 2017). These leaching materials may differ with plant species and the environmental condition (Beattie 2011; Remus-Emsermann et al. 2011; Mendes et al. 2013).

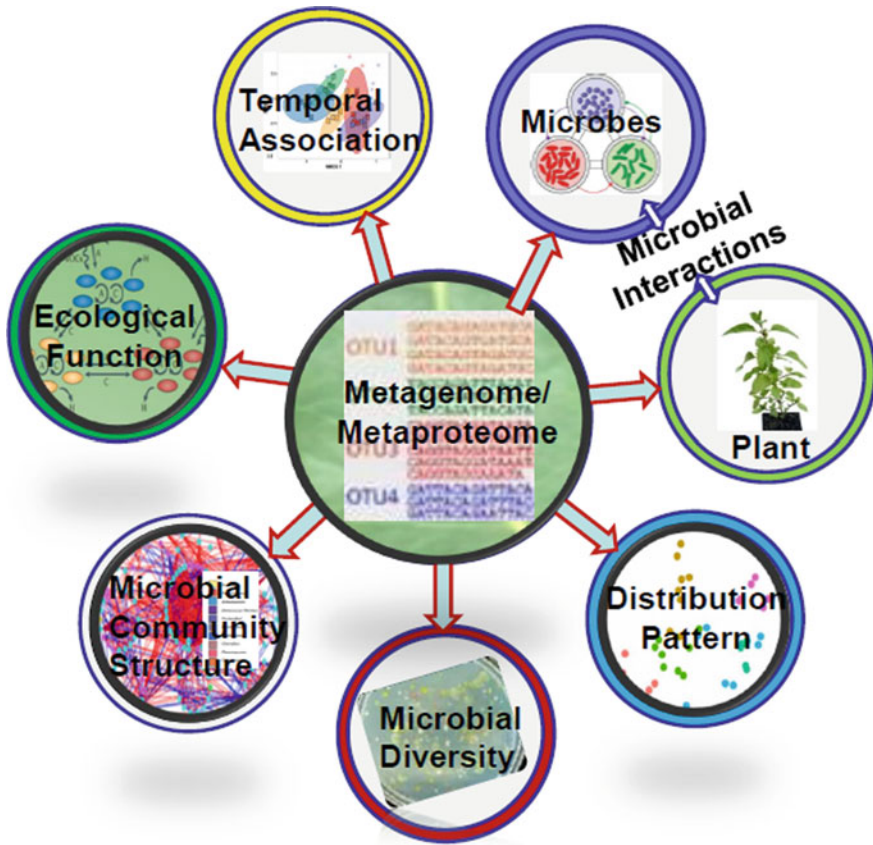
Nutrients such as sugar photosynthates from the leaf interior may be diffused through the cuticle reached the outer surface (Schreiber 2005), and are chiefly used by phyllosphere bacteria. Moreover, water droplets on a leaf surface facilitate the outward diffusion of these sugars (Van der Wal et al. 2013). Both non-pathogenic and pathogenic microorganisms establish colonization on the leaf surface. To survive and thrive, epiphytic microbes have several adaptive properties such as the production of antibiotics, extracellular polymeric substances (EPS), biosurfactant for increasing cuticle permeability, and availability of nutrients volatile organic compounds (VOCs) to the leaf surface. However, in order to avoid the entry of pathogens, plants develop defense reactions. The preliminary defense is activated by recognition of the chemical compounds released during the contact with microbes (Boller and Felix

2009). Pathogen-induced molecular patterns (PAMPs)-triggered immunity (PTI) is a broad spectrum of defenses against the pathogen invades. However, effectors produced by the pathogens often interfere with PTI activation and are recognized by specific proteins, which stimulate effector-triggered immunity (ETI) that induces a hypersensitive response (Craig et al. 2009).

## 5.7 How to Study Phyllosphere Microbiome?

The diversity and community structure of phyllosphere microbes have been intensely studied by culture-independent methods. However, this approach failed to isolate and identify the complete microbiome of the environment. Therefore, scientist used the culture-independent mass sequencing methods which have been carried out by high-throughput molecular methods, especially PCR-amplified DNA-level conserved taxonomic markers such as 16S rRNA, 18S rRNA, and internal transcribed spacer (ITS) sequences-based metagenome of phyllosphere total microbiome (Mao et al. 2012; Santhanam et al. 2014; Williams and Marco 2014; Jo et al. 2015; Copeland et al. 2015) (Fig. 5.4). The first-generation molecular techniques such as Sanger sequencing, denaturing gradient gel electrophoresis (DGGE), and terminal restriction fragment length polymorphism have been used to describe the community structure variation in plant phenotype, and geographical location (Hunter et al. 2010; Vokou et al. 2012; Izhaki et al. 2013). Those techniques are low throughput and highly expensive that can be used to detect the superficial microbial community of the environment (Rastogi and Sani 2011).

Advancements in molecular techniques, next-generation DNA sequencing is the potent method that significantly reduces the costs and allows to perform hundreds of samples in a single attempt. These techniques open up new windows of omics, specifically “environmental omics.” The 454 pyrosequencing is the first to be widely executed to study in microbial community analysis. This method comprises rRNA or ITS amplicon sequencing, whole-genome sequencing, shotgun metagenomics, and transcriptional profiling (Delmotte et al. 2009; Rastogi et al. 2012). Recently, Illumina platform has been performed better and allows ultra-high-throughput sequencing of microbial communities with high-quality reads (Degnan and Ochman 2012). Proteogenomic is another method used for the microbial community structure analysis (Delmotte et al. 2009), a combination of genomics and proteomics to a great extent makes easy the structural and functional differences of microbiota in the phyllosphere environments. Through those methods, microbial diversity of several host plants such as Arabidopsis, Apple tree, Beech, grapevine, oak, poplar, Prunus, rice, soybean, spinach, tomato wheat, etc. was documented. The metadata of the metagenomic studies helps to understand the growth behavior, colonization ability, genus-level community structure formation (or) association, low and high index of diversity, and the host genotype effects on the self-defense as well as the cell wall integrity have been reported.



**Fig. 5.4** Scope of metagenome in phyllosphere microbes and their functions

Whole microbiome analysis by environmental sequencing is popular today to explain the plant's phyllosphere containing complex microbial communities. There are many methods for mapping the diversity of microbiome which could associate with any of the living and nonliving objects. Also, the environmental sequencing approach determines the whole microbiome of the plant and it illustrates the significant association of microbes on its host under controlled conditions. Recently, studies revealed that genome-wide association (GWA) is the best method which shows potential merits for identifying the microbial communities associated with different kinds of host–microbe interactions. The high-throughput environmental sequencing approach has guided to the discoverer to find the complex microbial ecosystem of leaves. Using this strategy, many studies revealed the microbial association in the phyllosphere of different plants such as mountain shrubs (Ruiz-Pérez et al. 2016), seagrass (Fahimipour et al. 2017), subarctic grass (Uroz et al. 2016), and equatorial forest canopies (Lambais et al. 2006). The studies revealed that plant

leaves are colonized by a huge and diverse group of microorganisms, including bacteria, fungi, and viruses (Rastogi et al. 2013; Morella et al. 2018; Sapp et al. 2018; Beilsmith et al. 2019). High-throughput molecular methods or culture-independent molecular techniques have interpreted the phyllosphere microbial community today (Table 5.5). Through this technique, Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria are common microbiome of plant leaves (Bulgarelli et al. 2013), and it suggests that *Pseudomonas*, *Sphingomonas*, *Methylobacterium*, *Bacillus*, *Mas-silia*, *Arthrobacter*, and *Pantoea* are predominant genera consistently firm in the phyllosphere. Findings of the studies disclose the variation of microbial community structure mainly based on the genotypic nature of the plant species and also its geographical location. For example, Finkel et al. (2011) observed similar bacterial communities from the different species of *Tamarix* (*T. aphylla*, *T. nilotica*, and *T. tetragina*) grown in the same geographical location; however, differences in community structure of microbiota have been strongly related to its geographical distances (Rastogi et al. 2012).

Moreover, the high-throughput studies revealed the special functions/metabolism of the microbes associated with leaf surfaces, specifically carbohydrate transport, leaf litter decomposition, light-driven ATP pumps, methanol metabolism, C1 metabolism (Ottesen et al. 2013; Shade et al. 2013), and the effect of ecological factors such as climate change, temperature, seasonal variation, sporadic contact to soil, and/or anthropogenic activities such as the use of agricultural chemicals and pesticides (Ikeda et al. 2011; Shade et al. 2013; Karlsson et al. 2014; Copeland et al. 2015; Glenn et al. 2015). To attain better perceptiveness of the phyllosphere ecosystem and understand the functional relationship among plants, microbiota, and environment, metaproteome and metagenomics have been used (Rastogi et al. 2012; Bálint et al. 2013; Dees et al. 2015).

## 5.8 Impact of Phyllosphere Microbiome on Ecosystem

Phyllosphere microflora significantly influences the ecological relationship of the plants. The phyllosphere usually has bacteria, fungi, lichens, algae, and viruses that have actively participated in the adaptation, growth, resistance, and infection of the plant host (Walker et al. 2017; Verma et al. 2017; Yadav et al. 2018a). The phyllosphere microbiota has not been completely studied with their ecological significance, specifically plant and ecosystem level (Remus-Emsermann and Schlechter 2018). From seed germination to plant reproduction, studies have revealed how the phyllosphere microbiome affects the leaf functions and longevity, seed mass, apical growth, flowering, and fruit development (Jones and Dangl 2006; Sawinski et al. 2013; Kembel et al. 2014); however, the net interplay of the phyllosphere ecosystem in and around the plant is scanty. Recent scientific advancements that simplify the phyllosphere microbial life become understandable. The high-throughput genomics, such as environmental genomics and metagenomics, have greatly expanded our perceptiveness

**Table 5.5** Studies on high-throughput molecular approaches to phyllosphere communities

Method	Plant	Study	References
16S rRNA gene pyrosequencing	Soybean, clover, Arabidopsis	Epiphytic fitness of Sphingomonas and Methylobacterium	Delmotte et al. (2009)
	Pine and other trees	Phyllosphere bacteria community composition	Redford et al. (2010)
	Spinach	Genus-level communities of Proteobacteria and Firmicutes-associated spinach leaves	Lopez-Velasco et al. (2011)
	Grape	Bacterial communities on the surface of leaves and berries from grapevine	Leveau and Tech (2011)
	Lettuce	A “core” community composed of Pseudomonas, Bacillus, Massilia, Arthrobacter, and Pantoea found in lettuce foliage	Rastogi et al. (2012)
	Lettuce	Variation in phyllosphere microbiota composition. Effect of <i>E. coli</i> O157:H7 inoculation on microbiota composition	Williams et al. (2013)
	Rice	Metagenomic analysis of rice phyllospheric bacterial communities in relation to blast disease	Prasad Sahu and Kumar (2015)
	Common bean, soybean, and canola	Seasonal community succession of the phyllosphere microbiome	Copeland et al. (2015)
	Espeletia species	Microbial and functional diversity within the phyllosphere.	Ruiz-Pérez et al. (2016)
16/18S rRNA gene pyrosequencing	Oak	Fungal communities in the oak phyllosphere	Jumpponen and Jones (2009)
	<i>Tamarix aphylla</i> , <i>T. nilotica</i> , <i>T. tetragina</i>	Geographical location is a major determinant of phyllosphere bacterial communities	Finkel et al. (2011)
	Beech	Plant genotype-based fungal communities on leaf surfaces	Cordier et al. (2012)
	Balsam poplar	Plant species-based fungal community composition	Balint et al. (2013)

(continued)



**Table 5.5** (continued)

Method	Plant	Study	References
	<i>Pine</i>	Rapid microbial community changes during initial stages of pine litter decomposition	Gołębiewski et al. (2019)
Metaproteogenomics	Soybean, clover, Arabidopsis	Metabolic adaptations contribute to the epiphytic fitness of <i>Sphingomonas</i> and <i>Methylobacterium</i>	Delmotte et al. (2009)
	Rice	Several methylotrophic enzymes and their role in the carbon cycle by <i>Methylobacterium</i>	Knief et al. (2012)
	Maize	Functional genes that distinguish maize phyllosphere metagenomes in drought and well-watered conditions	Méthé et al. (2017)

and understanding on the functional life of phyllosphere microbial communities in plant–environment and the impact on the ecosystem.

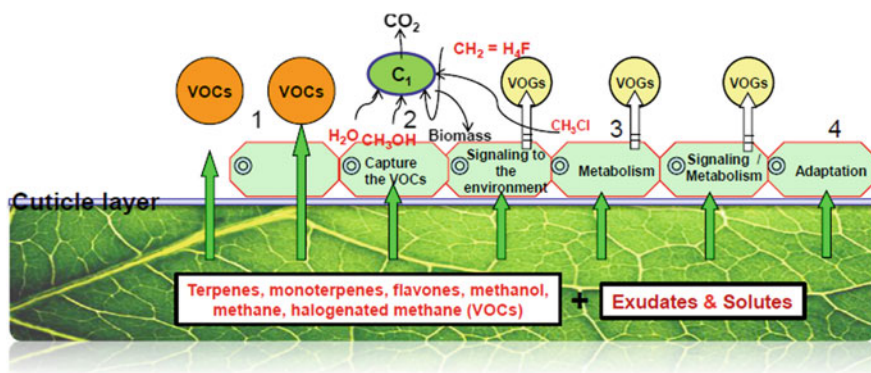
Environmental factors are drastically influencing the microbiome changes on phyllosphere. This is common to epiphytic microorganisms, exposed with heavy stress during the season cycle, the day/night cycle, and the growth, age, and anatomical dynamics of the plant. For instance, at drought condition, the epiphytic microbial community was notably increased on Holm oak (Rico et al. 2014). Similarly, at hot condition, bacterial endophytic communities are altered in lower leaves of paddy, but not in the epiphytes (Ren et al. 2014). However, the epiphytic fungal community responded well in warming seasons (Coince et al. 2014; Bálint et al. 2015). Besides, an increase of CO<sub>2</sub> at the phyllosphere region never affects the bacterial abundance (Ren et al. 2014; Vacher et al. 2016), except a few fungal genera.

Microbes have flexible metabolic adaptations, which helps them to survive in the phyllosphere microenvironment. During the metabolic functions, the plant releases carbohydrates, polyols, amino acids, amines, isoprenoids, halogenated compounds, or alcohols, as well as water and salts, which are the available nutrients for epiphytic microorganisms (Trouvelot et al. 2014). However, leaf surface commonly exhibits desolate properties such as saline or alkaline pH which generates stress in phyllosphere microbes (Finkel et al. 2012). Several alphaproteobacteria express PhyR-based stress regulation and colonization on leaf surface (Iguchi et al. 2013). Additionally, they develop multiple mode adaptation to survive in phyllosphere such as tolerance, antimicrobial, and immunity compounds against a microbial competitor (Trouvelot et al. 2014), synthesis of extracellular polysaccharides, and also synthesize phytohormonal compounds.

Besides, biotic and abiotic factors induce molecular level regulations in plants to synthesize a diverse range of phytohormones. Generally, the gaseous ethylene, jasmonate, methyl jasmonate, salicylate, and methylsalicylate are induced by bacterial pathogens (Bodenhausen et al. 2014; Horton et al. 2014). For example, many plant defense mechanisms are induced by the interaction of the biotic component of the ecosystem through signals like volatile and nonvolatile chemicals, and microbes can degrade such chemicals resulting in reduced activity (Mason et al. 2014).

The phyllosphere microbiome acts as a vital role for leaf surface environment and their surrounding ecosystem functions (Ortega et al. 2016). Phyllosphere microbes have interacted with their environment through their metabolic functions (Fig. 5.5). In general, plants release a variety of volatile organic compounds (VOCs) and its precursors on the surface of leaves (Schäfer et al. 2010), and it could regulate the microorganisms in response with the environment. Plants are the major VOCs emitter of the biosphere (>1000 Tg/year) and can release compounds such as terpenes, monoterpenes, flavones, methanol, methane, and halogenated methane (C1 compounds). The epiphytic microbes on the surface of the plant, as well as the airborne bacteria, effectively consumed the emitted VOCs through bacterial metabolism (Junker and Tholl 2013), and this effects of climate change would impact the diversity, species richness, and abundance in the phyllosphere community, and its capability on filtering of plant-emitted volatile substances.

Methane ( $\text{CH}_4$ ) is the most important greenhouse gas (~1.8 ppm), and it has been detected from the leaves, roots, and stems and is released to the atmosphere (Kepler et al. 2006). Phyllosphere microbes especially methanogens use the plant-emitted methane along with leaf exudates (Lenhart et al. 2015; Bringel and Couée 2015). Phyllospheric microbes are often rich in methylotrophic bacteria and can utilize the plant-emitted C1 compounds such as methanol, formaldehyde, and chloromethane



**Fig. 5.5** Environmental impact of phyllosphere microbes. Utilization of plant emitting volatile organic compound (VOCs) and C1 compounds by phyllosphere microbes. (1) Free diffusion of VOCs to the atmosphere; (2) Capturing the VOCs by the surface microbes, act as filters; (3) Through specialized metabolic activities microbes metabolize the VOCs; (4) Adaptive response of microbes in the specialized environment. VOGs—Volatile organic gases

(Knief et al. 2012; Jo et al. 2015). Studies proved that the C1 metabolic epiphytic bacteria such as *Methylobacterium extorquens*, *Methylobacterium radiotolerans*, and *Methylocystis* use methanol and acetate as their carbon and energy source at the phyllosphere (Belova et al. 2011; Verginer et al. 2010; Iguchi et al. 2013; Jo et al. 2015; Iguchi et al. 2015; Krishnamoorthy et al. 2018). The *Methylobacterium extorquens* contains the methanol-dehydrogenase-like protein XoxF which is expressed during the colonization on *Arabidopsis thaliana* (Schmidt et al. 2010). Besides, chloromethane metabolism (*cmu* pathway) in methylotrophs has been identified from the surface leaves of *A. thaliana* harbor (Nadalig et al. 2011; Krishnamoorthy et al. 2018). Table 5.6 shows the various phyllosphere methanogenic bacteria and its metabolism.

Chloromethane (CH<sub>3</sub>Cl) is one of the abundant chlorinated organic compounds in the atmosphere (currently ~550 ppt) and is to be responsible for the depletion of stratospheric ozone over 16% (World Meteorological Organization 2014). The fluorescence-based bacterial bioreporter study reported that phyllosphere microbes, *M. extorquens* CM4 (Roselli et al. 2013) and *Hyphomicrobium* sp. (Nadalig et al. 2011), having the genes for chloromethane utilization (*cmu*), and also volatile dimethylsulphide (DMS) and dimethylsulfoniopropionate (DMSP), considered as global climate regulator (Schäfer et al. 2010; Nevitt 2011). In the biosphere, a small number of plants like salt marsh grasses *Spartina* and sugarcanes (*Saccharum* sp.) are reported as producers of DMSP. Microbes that are associated with these plants have adaptive metabolism by which it transforms or metabolizes the DMS and DMSP (Ansele et al. 2001). Hence, the phyllosphere microbes are the major source of carbon and sulfur biogeochemical cycles, in the ecosystem and climate regulation through their active filtration or utilization of plant-related volatile compounds (DeLeon-Rodriguez et al. 2013; Šantl-Temkiv et al. 2013).

Microbial populations reside at phyllosphere as epiphytes or as endophytes, and have close contact with the rhizosphere. A microbe can be established as an epiphytic and endophytic association has the metabolic plasticity required for them to thrive. Many experimental evidences suggested that microorganisms commonly associated with plants maybe vital for nutrient accessibility and decomposition of biomass (Bernal et al. 2006; Ramírez Gómez 2011; Lizarazo-Medina and Gómez-Vásquez 2015). The functional ecology of the plant influences the composition and interaction of the phyllosphere microbes (Bodenhausen et al. 2013; Ruiz-Pérez et al. 2016). Many of the phyllosphere microbial communities share the common metabolic properties of the soil microbes. For example, the major phyllosphere bacterial communities such as *Bacillus*, *Burkholderia*, *Methylobacterium*, *Pseudomonas*, *Sphingomonas*, and *Xanthomonas* are the soil inhabitant, which have carbohydrate metabolizing genes involved in utilization of starch, hemicellulose, pectin, and cellulose, rich in humus materials (Rawat et al. 2012; Bodenhausen et al. 2013; Bulgarelli et al. 2013). The nitrogen metabolism such as ammonification, denitrification, and anammox, and the degradation of aromatic compounds are also reported in foliar microbes (Usubillaga et al. 2001; Rawat et al. 2012; Ruiz-Pérez et al. 2016).

Tropospheric microbes (aerosols) play a vital function in global carbon cycles and also metabolize the organic compounds. Some airborne Gammaproteobacteria have

**Table 5.6** Studies on Phyllospheric methylotrophic metabolism

Epiphyte	Host plant	Function	References
Methanotrophs and Methylobacteria	Linden, pine and blue spruce lilac, maple, and apple	Diversity of Methanotrophs in woody plant tissues within the winter period	Doronina et al. (2004)
<i>Methylobacterium extorquens</i>	<i>Medicago truncatula</i>	Methylotrophic metabolism is advantageous for colonization under competitive conditions	Sy et al. (2005)
<i>Methylobacterium extorquens</i>	–	A proteomic study of <i>Methylobacterium extorquens</i> reveals a response regulator essential for epiphytic growth	Gourion et al. (2006)
<i>Methylobacterium extorquens</i> AM1	–	PhyR is involved in the general stress response	Gourion et al. (2008)
<i>Methylocystis heyeri</i> H2(T) and <i>M. echinoides</i> IMET10491(T)	Peat	Acetate utilization metabolism as a survival strategy	Belova et al. (2011)
<i>Methylobacterium extorquens</i> DSM 21961	Strawberry	Monitoring the plant epiphyte <i>Methylobacterium extorquens</i> DSM 21961	Verginer et al. (2010)
<i>Methylobacterium extorquens</i>	<i>Arabidopsis thaliana</i> or <i>Medicago truncatula</i>	The influence of the factor site, host plant species, time and the presence of other phyllosphere bacteria on <i>Methylobacterium</i> community composition and population size	Knief et al. (2010)
<i>Candida boidinii</i>	<i>Arabidopsis thaliana</i>	Yeast methylotrophy and autophagy in a methanol-oscillating environment on growing leaves	Kawaguchi et al. (2011)

(continued)

**Table 5.6** (continued)

Epiphyte	Host plant	Function	References
<i>Methylobacterium</i> sp. (NC4), (NC28)	Sugarcane, pigeon pea, mustard, potato, and radish	Epiphytic pink-pigmented methylotrophic bacteria enhance germination and seedling growth of wheat ( <i>Triticum aestivum</i> ) by producing phytohormone	Meena et al. (2012)
<i>Methylobacterium</i> sp. strain OR01	Perilla plants	Dominant colonization and inheritance of <i>Methylobacterium</i> sp.	Mizuno et al. (2013)
<i>Methylosinus</i> sp. B4S	–	Stress resistance and C1 metabolism involved in plant colonization of a methanotroph Arch	Iguchi et al. (2013)
<i>Methylobacterium oryzae</i>	Rice	plant-probiotic methylotroph in the phyllosphere	Kwak et al. (2014)
<i>Methylobacterium radiotolerans</i> VRI8-A4	Groundnut	Diversity of culturable methylotrophic bacteria in different genotypes of groundnut and their potential for plant growth promotion	Krishnamoorthy et al. (2018)

ice nucleation-active (INA) property and contains specific gene (*ina*) via deposition of cloud droplets (Hill et al. 2014) on the leaf surface and mineralize the carbon compounds (Vaitilingom et al. 2013). Reports confirmed the relationship of INA bacteria and phyllosphere microbiota, combined activities of both phyllosphere microbiota and cloud microbiota actively participating carbon cycle, and strong support for climate regulation (Bringel and Cou e 2015). The above information suggested that the phyllosphere microbiome not only supports the health of its host but is also beneficial to the environment, specifically it regulates plant-derived greenhouse and other gaseous pollutants.

## 5.9 Biotechnological Potential of Phyllosphere Microbiota

The plant beneficial microbes are agriculturally important bioresources, and it can stimulate the plant growth and enhance plant nutrient uptake through solubilization and mobilization (of P, K, and Zn), nitrogen fixation, and siderophore production (microbes-mediated bio-fortification of Fe in different crops). Beneficial microbes can play an important role in increasing yields of the crop, remove contaminants, inhibit pathogens, and produce novel substances. The growth stimulation by beneficial microbes can be a consequence of biological nitrogen fixation, production of plant growth regulators such as IAA, gibberellic acids, and cytokines, and biocontrol of phytopathogens through the production of antibiotic, antifungal, or antibacterial, Fe-chelating compounds, induction of acquired host resistance, enhancing the bioavailability of minerals (Kour et al. 2019; Kumar et al. 2019b; Yadav et al. 2019a).

In this contest, the phyllosphere microbes may positively influence the growth of host plant and produce some antagonistic compound against pathogens. Phyllosphere endophytes with properties such as nitrogen fixation (Jones 1970; Freiberg 1998; Furnkranz et al. 2008), bioremediation of harmful chemicals/pollutants, and biocontrol agents against important foliar plant pathogens (Beattie and Lindow 1995; Balint-Kurti et al. 2010; De Marco et al. 2004) have been documented. Further, the microbiome of phyllosphere is a reflection of environmental conditions; they can contribute significantly to global food webs and nutrient linkages. Many beneficial microbes such as *Achromobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Flexibacterium*, *Methylobacterium*, *Micrococcus*, *Micromonospora*, *Nocardioidea*, *Pantoea*, *Penicillium*, *Planomonospora*, *Pseudomonas*, *Streptomyces*, and *Xanthomonas* have been reported from the phyllosphere environment of different crop plants (Verma et al. 2013a, b; Mukhtar et al. 2010; Meena et al. 2012; Dobrovol'skaya et al. 2017). However, compared with most other microbial habitats, the investigation of phyllosphere microbes is quite limited. Some of its important biotechnological potentials are listed below.

### 5.9.1 Biocontrol Agents

Biocontrol is the measure to control pathogens and disease-causing pest including nematodes weeds, insects, and mites by other beneficial microbes or harmless living materials. In nature, plant diseases are caused by bacterial pathogens which provide a substantial decline in the development of agricultural products. For sustainable agriculture, scientific approaches use the antagonistic properties of beneficial microbes against the harmful pathogens instead of using toxic harmful chemicals as biological control (Erwin and Ribeiro 1996; Sharma et al. 2012). Biological treatment is a desirable strategy for controlling plant diseases (You et al. 2015) and there are an increasing number of biocontrol agents (BCAs), such as *Bacillus* spp., *Pseudomonas* spp., *Trichoderma* spp., etc. being commercialized for various crops (Trabelsi and

Mhamdi 2013; Cha et al. 2016). Most of them habitat either on phyllosphere or soil and can play a significant role in killing the number of plant pathogens on the surface of the leaves by competitive principle.

Pathogenic microbial interactions in phyllosphere decrease the fitness of plants, the productivity of crops, and question the safety of horticultural products for human consumption. Phyllosphere actinomycetes have been reported to inhibit the growth and colonization of plant pathogens (Lindow and Brandl 2003). For example, the endophytic isolate *Gordonia* sp. has been reported to produce imidazole-2-yl amino acids that have antifungal properties (Mikolasch et al. 2003) and an acidic polysaccharide called Gordon as the main component in biofilms, which is considered essential for pathogenicity against plant disease (Kondo et al. 2000). Various *Streptomyces* sp. including *S. griseus* have been reported as producing various antifungal compounds such as 1-H-pyrrole-2-carboxylic acid (PCA), cycloheximide, and streptomycin which were successfully used to control fungal and bacterial diseases in plants (Leben and Keitt 1954; Nguyen et al. 2015). Wiwiek et al. (2017) studied the rice phyllosphere actinomycetes could be used as potential biocontrol agents against fungal leaf blast disease. Wang and Ma (2011) reported that exogenous actinomycete XN-1 has the potential to act as an antagonistic agent in controlling the occurrence and development of cucumber leaf spot in the greenhouse. This also confirms that phyllosphere microorganisms play an important role in combating the infection of pathogens and have a promising future in developing biocontrol products. Table 5.7 shows the plant-associated bacteria and its biological activities.

Microbes with the production of compounds like indole acetic acid and N-acyl homoserine lactone (AHL) assist the bacteria to colonize on plant surface (Lindow and Brandl 2003). Sartori et al. (2015) studied the biocontrol potential of phyllosphere microorganisms from maize against *Exserohi lumturcicum*, the causal agent of leaf blight. Shrestha et al. (2016) investigated the prospects of biological control of rice-associated *Bacillus* against sheath blight and panicle blight of rice caused by *Rhizoctonia solani* and *Burkholderia glumae*, respectively. A variety of *Bacillus* isolates were observed to inhibit the sclerotial germination of the fungus, which could be attributed to the various antimicrobial secondary metabolites produced by the bacteria. Various gram-negative bacteria also show plant protection activity. For example, *Pseudomonas graminis* isolated from the apple phyllosphere showed control against fire blight caused by *Erwinia amylovora* (Mikiciński et al. 2016), *Pseudomonas protegens* CS1 from the lemon phyllosphere are used as a biocontrol against citrus canker (Michavila et al. 2017).

Further, microbial production of siderophores quenches the phytopathogens and protects the host plant from their infection (Scavino and Pedraza 2013; Ahmed and Holmström 2014; Harsonowati et al. 2017; Sabaté et al. 2018) as a biocontrol agent. For example, the siderophore produced by *Pseudomonas syringae* pv. *syringae* 22d/93 shows biocontrol activity against *Pseudomonas syringae* pv. *glycinea* 1a/96, a plant pathogen (Wensing et al. 2010). The siderophore pyochelin produced by the endophyte control rice blast is caused by *Pyricularia oryzae* (Harsonowati et al. 2017). Plant-associated *Pseudomonas* spp. has been employed efficiently as commercial biocontrol agents (Loper and Lindow 1987; Walsh et al. 2001). Cyanogenic

**Table 5.7** Plant-associated microbial compounds and bioactivity

Compound	Source	Bioactivity	References
Blasticidin-S (VIII):	<i>Streptomyces griseochromogenes I</i>	Control the rice blast caused by <i>Pyricularia oryzae</i>	Fukunaga (1955)
Kasugamycin (IX)	<i>Streptomyces kasugaensis</i>	Rice blast caused by <i>Pyricularia oryzae</i> , leaf spot in sugar beet and celery by <i>Cercospora</i> spp., and scab in pears and apples caused by <i>Venturia</i> spp.	Umezawa et al. (1965)
Methoxyphenone	<i>Streptomyces griseolus</i>	Herbicides	Ito et al. (1974)
AM-toxin	<i>Alternaria mali</i>	phytotoxin	Park et al. (1977)
Milbemycin (XI):	<i>S. hygroscopicus</i> subsp. <i>aureolacrimosus</i>	Insecticidal and acaricidal	Mishima et al. (1983)
Diabroticin A	<i>Bacillus subtilis</i> and <i>Bacillus cereus</i>	Polar insecticide	Stierle et al. (1990)
Spinosad (X): spinosyn A and spinosyn D	<i>Saccharopolyspora spinosa</i>	Controls the caterpillar ( <i>Helicoverpa zea</i> Boddie, <i>Pieris rapae</i> (L.), <i>Keiferia lycopersicella</i> (Walsingham), thrips ( <i>Ceratitis capitata</i> (L.), <i>Thrips palmi</i> (Karny)) and beetles ( <i>Leptinotarsa decemlineata</i> (Say))	Mertz and Yao (1990)
AF-toxins	<i>Alternaria fragariae</i>	Maculosin is a cyclic dipeptide—phytotoxin	Stierle et al. (1990), Uneo (1990)
Maculosin (XVI)	<i>Phoma lingam</i>	Phytotoxin	Stierle et al. (1990)
Efrapeptins	<i>Tolypocladium</i> spp.	Pesticide and insecticide	Krasnoff and Gupta (1991), Krasnoff et al. (1991)
Abamectin	<i>Streptomyces avermitilis</i>	Insecticide and acaricide	Jansson and Dybas (1996)
Nodulisporic acid	<i>Nodulisporium</i> sp.	Insecticidal activity	Ondeyka, et al. (1997)
Pyrizadocidin (VII)	<i>Streptomyces</i> #620061	Herbicides	Gerwick et al. (1997)
Syringomycin E:	<i>Pseudomonas syringae</i> ESC 10/11	Fungicide-citrus green mold <i>Penicillium digitatum</i>	Bull et al. (1998)

(continued)



**Table 5.7** (continued)

Compound	Source	Bioactivity	References
Destruxin A and B	<i>M. anisopliae</i>	Insecticide	Strasser et al. (2000)
Oosporein	<i>Beauveria brongniartii</i>	Insecticide	Strasser et al. (2000)
Beauvericin A and B	<i>Beauveria bassiana</i> and <i>Paecilomyces</i> spp	Hexadepsipeptide—insecticide	Lane et al. (2000)
Borrelidin	<i>Streptomyces</i> species- neu-D50	Antifungal activity against <i>Phytophthora sojae</i>	Worapong et al. (2001)
Bialaphos (V)	<i>Streptomyces hygroscopicus</i> and <i>Streptomyces viridochromogenes</i>	Herbicide—weed control	Tachibana (2003)
Tartrolone C	<i>Streptomyces</i> sp. CP1130	Insecticidal macrodiolide	Lewer et al. (2003)
Coronatine	<i>Pseudomonas coronafaciens</i>	Insecticide—herbicide	Block et al. (2005)
Macrolactin A:	<i>Bacillus</i> sp. <i>sunhua</i>	Fungicide— <i>Fusarium oxysporum</i> and <i>Streptomyces scabies</i>	Han et al. (2005)
Bt-Toxins	<i>Bacillus thuringiensis</i>	Bioinsecticides endotoxins	Collier et al. (2005)
Tabtoxin	<i>Pseudomonas syringae</i> var. <i>tabaci</i>	Phytotoxic—Herbicide	Hoagland et al. (2007)
Phyllostictine A	<i>Phyllosticta cirsii</i>	Mycoherbicide	Zonno et al. (2008)
Cinnacidin (XXII):	<i>Nectria</i> sp. DA60047	Phytotoxic	Irvine et al. (2008)
Beauvericin A and B	<i>Beauveria bassiana</i> and <i>Paecilomyces</i> spp.	Hexadepsipeptide—insecticide	Miller et al. (2008)
Herbimycin (VI)	<i>Streptomyces hygroscopicus</i> AM3672	Benzaquinoid ansamycin antibiotic with potential herbicidal a	Hahn et al. (2009)
Albucidin	<i>Streptomyces albus</i> subsp. <i>chlorinus</i> NRRL B-24108	Herbicides	Hahn et al. (2009)
Zinniol	<i>Alternaria cirsioxia</i>	Phytotoxic to <i>Cirsium arvense</i> L.	Berestetskii et al. (2010)
Ascaulitoxin aglycone	<i>Ascochyta caulina</i>	Phytotoxin	Duke et al. (2011)
Antibiotic 1233A (XXIV)	<i>Cephalosporium</i> sp., <i>Fusarium</i> sp.,	Phytotoxin	Duke and Dayan (2011)

(continued)

**Table 5.7** (continued)

Compound	Source	Bioactivity	References
AK-toxin (XV):	<i>Alternaria kikuchiana</i>	Phytotoxin	Saxena (2014)
Bipolaroxin (XVIII)	<i>Bipolaris cynodontis</i>	Phytotoxic to <i>Cynodon dactylon</i>	Saxena (2014)
Bt-Toxins	<i>Bacillus thuringiensis</i>	Bioinsecticides endotoxins	Radhakrishnan et al. (2017)
Phaseolotoxin (III)	<i>Pseudomonas</i> sp.	Phytotoxins—herbicide	Aguilera et al. (2017)

fluorescent *Pseudomonas* produces siderophores in the presence of a strong chelator 8-Hydroxyquinoline which inhibits pathogens such as *Rhizoctonia solani* and *Sclerotium rolfsii* (Kotasthane et al. 2017). Table 5.8 listed some important findings as endophytes as biocontrol agents. Mostly, the biocontrol agents use either nonribosomal peptide synthetase (NRPS) gene and/or type 1 polyketide synthase gene for respective compound production.

### 5.9.2 Plant Growth-Promoting Compounds

Plant growth is regulated by the growth hormones, available nutrient, good environmental condition, and beneficial microbial interaction. Many of the microbes are the prime producers of plant growth hormones, specifically plant-associated or phyllosphere microbial communities produce IAA, gibberellic acids, and cytokines and could fix nitrogen and mobilize nutrients (Dourado et al. 2015). There are many bacteria and fungi which produce IAA, similar to those of plants (Sun et al. 2014; Venkatachalam et al. 2016; Thapa et al. 2018). Microbes use plant tryptophan to produce IAA, which can effectively improve plant growth and enhance overall health (Hayat et al. 2010; Yadav et al. 2015a, b). The genus *Methylobacterium* is among the most commonly observed leaf epiphytes and represents an abundant and stable member of the phyllosphere microbial community of a wide range of crop plants such as sugarcane (*S. officinarum* L.), pigeon pea (*Cajanus cajan* L.), mustard (*Brassica campestris* L.), potato (*Solanum tuberosum* L.), and radish (*Raphanus sativus* L.) (Meena et al. 2012), and has produced variety of growth-promoting phytohormones. The association of plant growth-promoting bacteria (PGPB), especially *Methylobacterium* sp., with plant hosts greatly benefits plant growth by production of phytohormones like auxins and cytokinins, and increased activity of enzymes such as urease and 1-aminocyclopropane-1-carboxylate deaminase (ACCD), which promotes growth and enhances the production of siderophores, thereby enhancing the uptake of essential nutrients.

The benefits associated with plant–microbe interactions are also dependent on the variety of inoculation methods such as soil, foliar, and combination of both soil

Table 5.8 Phyllosphere endophytic fungi as biocontrol agent

Endophyte	Host	Pathogen	References
<i>Fusarium proliferatum</i>	Grape	<i>Plasmopara viticola</i>	Falk et al. (1996)
<i>Acremonium zeae</i>	Maize	<i>Aspergillus flavus</i> and <i>Fusarium verticillioides</i>	Wicklow et al (2005)
<i>Trichoderma</i> sp.	Apple Tobacco, bean, iris Radish, strawberry, cucumber, potato, and tomato	<i>Nectria galligena</i> , <i>Botrytis cinerea</i> <i>Sclerotium rofskii</i> <i>Rhizoctonia solani</i> <i>Chondrostereum purpureum</i>	Reino et al. (2008)
<i>Colletotrichum gloeosporioides</i> , <i>Clonostachys rosea</i> , and <i>Botryosphaeria ribis</i>	<i>Theobroma cacao</i>	<i>Moniliophthora roreri</i> (frosty pod rot), <i>Phytophthora palmivora</i> (black pod rot), and <i>Moniliophthora perniciosa</i> (witches broom)	Mejia et al. (2008)
<i>Trichoderma martiale</i>	Cacao ( <i>Theobroma cacao</i> )	<i>Phytophthora palmivora</i>	Hanada et al. (2009)
<i>Clonostachys rosea</i>	wheat	<i>Gibberella zeae</i>	Hue et al. (2009)
<i>Cladosporium</i> , <i>Colletotrichum</i> , <i>Gibberella</i> , <i>Hypocrea</i> , and <i>Trichoderma</i>	<i>Smilanthus sonchifolius</i> (Poepp.) H. Rob.	<i>Lecytophthora</i> sp. and <i>Fusarium oxysporum</i>	Rosa et al. (2012)

(continued)

Table 5.8 (continued)

Endophyte	Host	Pathogen	References
<i>Penicillium</i> spp.	<i>Vitis vinifera</i> L.	<i>Botrytis cinerea</i>	Núñez-Trujillo et al. (2012)
<i>Colletotrichum gloeosporioides</i> , <i>Flavodon flavus</i> , <i>Diaporthe helianthi</i> , <i>Diaporthe phaeolorum</i> , <i>Aporospora</i> <i>terricola</i>	<i>Vitis labrusca</i> L.	<i>Fusarium oxysporum</i>	Brum et al. (2012)
<i>Cladosporium cladosporioides</i>	<i>Huperzia serrata</i>	<i>Colletotrichum acutatum</i> , <i>Colletotrichum fragariae</i> , <i>Colletotrichum gloeosporioides</i> , and <i>P.</i> <i>viticola</i>	Wang et al. (2013a)
<i>Bionectria ochroleuca</i> , <i>Aureobasidium</i> <i>pullulans</i> , <i>Chaetomium spirochaete</i>	<i>Vitis vinifera</i>	<i>Botrytis cinerea</i>	Cosoveanu et al. (2014)
<i>Ramularia endophylla</i>	Plant	<i>Mycosphaerella labyrinth</i>	Videira et al. (2015)

and foliar inoculations (Lee et al. 2011). A study has been conducted to investigate the inoculation of *Erwinia herbicola* on plant growth by IAA production. The test results showed that about 65% of the *E. herbicola* strain recovered from the leaves showed higher expression of the *ipdC* gene than in culture. The study indicated that physical or chemical microclimates directly influence the differential expression of *ipdC* (Brandl et al. 2001). Similarly, endophytic bacteria such as *Bacillus pumilus* E2S2 (Luo et al. 2012), *B. amyloliquefaciens* NBRI-SN13 (Nautiyal et al. 2013), *B. atrophaeus* EY6 and *B. sphaericus* B EY30, *B. subtilis* EY2, *S. kloosii* EY37, and *K. erythromyxa* EY43 (Karlidag et al. 2011) also produce PGPs.

Endophytic *Bacillus* produces phytohormones such as abscisic acid, auxins, brassinosteroids, cytokinins, ethylene, gibberellins, jasmonates, and strigolactones, and increases nutrient (nitrogen and phosphorous) accessibility to the host (Reinhold-Hurek and Hurek 2011; Brader et al. 2014; Santoyo et al. 2016; Shahzad et al. 2016; Ek-Ramos et al. 2019). Zeiller et al. (2015) reported that *C. botulinum* 2301 significantly produce PGPs in a field experiment of clover. A cold-tolerant bacterial strain *Exiguobacterium acetylicum* 1P promotes wheat seedlings growth (Selvakumar et al. 2010), *Brevibacillus brevis* improve the growth of cotton crop (Nehra et al. 2016) and *Bacillus* spp. induce phosphate solubilization more efficiently when present as endophytes in citrus (Giassi et al. 2016). The diazotrophic bacteria associated with phyllosphere gives benefits to the plant by fixing atmospheric nitrogen, solubilization of phosphorus (P), and utilization of available nutrients through its organic end product-mediated solubilization of rock phosphates (Mohammadi 2012; Kembel et al. 2014; Mwajita et al. 2013; Batool et al. 2016; Lambais et al. 2017).

### 5.9.3 Biopharmaceutical Importance

Biological activity of medicinal plants and their applications in various healing properties have been documented well. In recent years, microbes associated with plants themselves proved with high therapeutic values particularly endophytes. Endophytic microbes are known for their beneficial effects to the host, specifically phytohormones, enzymes, and stress-resistant physiology, and its biotechnological potentials (Parthasarathi et al. 2012; Singh and Dubey 2015; Gouda et al. 2016). Endophytes are known to produce bioactive metabolites, which served as a potent drug for medical and cosmetic industries (Shukla et al. 2014; Gouda et al. 2016). Secondary metabolites produced by the endophytic bacteria, actinomycetes, and fungi have economically valuable compounds such as alkaloids, flavonoids, phenolic acids, quinones, steroids, saponins, terpenoids, tetralones, xanthenes, etc. (Strobel and Daisy 2003; Joseph and Priya 2011; Godstime et al. 2014; Shukla et al. 2014; Gouda et al. 2016). For example, endophytic microbes are well-known producers of taxol, a diterpene alkaloid, and lignin such as cathartics, emetics, and cholagogue used for cancer treatment (Konuklugil 1995; Zhang et al. 2009; Nair and Padmavathy 2014; Soliman

**Table 5.9** Pharmaceutical valuable products from phyllosphere microbes

Producer	Compound	Activity against	References
<i>Hypericum perforatum</i> , <i>Diaporthe helianthi</i>	Hypericin, emodin, tyrosol	<i>Salmonella sp.</i>	Joseph and Priya (2011), Specian et al. (2012)
<i>Ganoderma boninense</i>	Rapamycin, cyclododecane, petalostemumol	<i>Bacillus subtilis</i>	Parthasarathi et al. (2012), Ismail et al. (2014)
<i>Fusarium sp.</i> <i>Cryptosporiopsis quercina</i>	Xularosides, munumbicins, Saadamycin, cryptocandin	<i>Candida albicans</i>	Jalgaonwala et al. (2011), Dutta et al. (2014)
<i>Streptomyces sp.</i> , <i>Kennedia nigricans</i>	Munumbicins	<i>Vibrio cholerae</i>	Kumar et al. (2014)
<i>Cryptosporiopsis quercina</i>	Saadamycin	<i>Campylobacter jejuni</i>	Dutta et al. (2014)
<i>Streptomyces sp.</i>	Kakadumycin A, hypericin	<i>Shigella sp.</i>	Golinska et al. (2015), Joseph and Priya (2011)
<i>Streptomyces tsusimaensis</i>	Valinomycin	<i>Corona virus</i>	Alvin et al. (2014)
<i>Fusarium proliferatum</i>	Kakadumycin, beauvericin	<i>Listeria monocytogenes</i>	Golinska et al. (2015)
<i>Boesenbergia rotunda</i> <i>Streptomyces coelicolor</i>	Munumbicins	<i>Escherichia coli</i>	Golinska et al. (2015), Singh and Dubey (2015)
<i>Grammothele lineata</i>	Paclitaxel	<i>Anticancer</i>	Das et al. (2017), Kasaei et al. (2017), Soliman and Raizada (2018)

and Raizada 2018). There are many novel metabolites with antibacterial, antifungal, antiviral, anticancer, and antihelminthic activity isolated from plant-associated microbes (Gouda et al. 2016; Kasaei et al. 2017) (Table 5.9).

### 5.9.4 Other Applications

Besides the use of phyllosphere microbes for enhanced growth as well as biocontrol agent, some plant-associated bacteria helps the plant to improve phytoremediation of toxins. For example, hydroxamate siderophores producing bacteria compact heavy metal toxicity and improve the phytoremediation property in *A. thaliana* (Grobela and Hiller 2017). Some endophytes provide additional functions to the host plant like drought tolerance, for example, endophytic *B. subtilis* strain B26 induces drought

resistance to *Brachypodium distachyon* grass. The drought resistance mechanism is due to a specific carbohydrate metabolism, the endophytic bacteria increases stress-responsive raffinose-related family carbohydrates in the host (Gagné-Bourque et al. 2015). In another example, the endophytic association increases osmotic responses of the host plant. Endophytic strains such as *Arthrobacter* sp. and *Bacillus* spp. in pepper plant increase the proline accumulation, which gives osmotic tolerance (Sziderics et al. 2007).

Further, endophytic bacterial inoculants provide abiotic stress tolerance mechanism to the host by its extracellular enzymes. For example, the endophytic association of various *Bacillus* spp. increases the superoxide dismutase, phenylalanine lyase, catalase, and peroxidase enzymes activity in gladiolus plants under sodium high concentration conditions (Damodaran et al. 2014). Little studies reported that isolation of endophytic bacteria and their enzyme production potential vary when it colonizes in the plant tissues. Moreover, Jalgaonwala et al. (2011) observed maximum proteolytic activity in *Lactobacillus fermentum* isolated from leaves of *Vinca rosea*, which is considered greater to nonendophytic isolates. Similarly, endophytic fungi isolated from *Ocimum sanctum* and *Aloe vera* has better enzymatic activity (Yadav et al. 2015a, b). Besides these mechanisms, plant-associated microorganisms improve nutrient acquisition by supplying minerals and other micro/macronutrients from the soil (Singh et al. 2017; Singh and Singh 2017). Above all merits provide new insights in the field of phyllosphere microbiome and its essentiality of interactions to host plant growth and protection and also its significant role in the ecosystem.

### 5.9.5 Conclusion and Future Prospects

The phyllosphere is a unique environment colonized by a wide variety of microorganisms including epiphytes and endophytes, beneficial and pathogenic, bacteria, fungus, viruses, etc. Understanding the phyllosphere community structure, networking, and physiology is a great challenge. However, extensive research on phyllosphere microbiota gives great potential for the applications in economic plant productivity, specifically agriculture and forestry, ecosystem cleaning, and health. Hitherto, both in vitro and in vivo experiments are required to improve the understanding of microbial aggregations in the phyllosphere and dynamic play in the ecosystem. Based on the literature understanding, further and future studies should aim to (1) study the community interplay within the closely related and distanced microbial interactions and its stimulatory response on host plant and ecosystem, (2) to know the potentials of beneficial microbes and their commercial value, (3) impact on climate change on phyllosphere microbiome, and their contribution to climate change, (4) moreover, documentation of host-specific, geographic-specific, and seasonal-specific microbial interactions—guiding host–parasite and beneficial–pathogen interactions. Besides, phyllosphere microbiome research assures to understand the current challenges highlighting the terrestrial ecosystem change and the impact of global warming, especially the dominance of pathogenesis.

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