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Phyllosphere Microorganisms: Sources, Drivers, and Their Interactions with Plant Hosts

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ABSTRACT: The leaves of plants are colonized by various microorganisms. In comparison to the rhizosphere, less is known about the characteristics and ecological functions of phyllosphere microorganisms. Phyllosphere microorganisms mainly originate from soil, air, and seeds. The composition of phyllosphere microorganisms is mainly affected by ecological and abiotic factors. Phyllosphere microorganisms execute multiple ecological functions by influencing leaf functions and longevity, seed mass, fruit development, and homeostasis of host growth. A plant can respond to phyllosphere microorganisms by secondary metabolite secretion and its immune system. Meanwhile, phyllosphere microorganisms play an important role in ecological stability and environmental safety assessment. However, as a result of the instability of the phyllosphere environment and the poor cultivability of phyllosphere microorganisms in the current research, there are still many limitations, such as the lack of insight into the mechanisms of plant−microorganism interactions, the roles of phyllosphere microorganisms in plant growth processes, the responses of phyllosphere microorganisms to plant metabolites, etc. This review summarizes the latest progress made in the research of the phyllosphere in recent years. This is beneficial for deepening our understanding of phyllosphere microorganisms and promoting the research of plant−atmosphere interactions, plant pathogens, and plant biological control.

KEYWORDS: *plant, phyllosphere microorganism, plant immunity, plant−microorganism interaction, ecotoxicology*

1. INTRODUCTION

Microorganisms represent a massive diversity, colonizing soil, animals, plants, and other habitats.[1−4] The development of high-throughput sequencing techniques and advanced bioinformatics tools have rapidly improved our understanding of the roles of microorganisms for hosts and ecosystems.[5,6] The interactions between plants and relevant microorganisms are crucial for host performance and resilience to ecosystem perturbations.[7,8] Plant microorganisms are defined by host species, plant endosphere compartment, and tissue location (e.g., root and leaf).[9,10] Many studies have demonstrated the role of rhizosphere microorganisms in promoting plant growth and resistance to abiotic and biotic stresses.[11−13] In the past decade or so, phyllosphere microorganism research has expanded rapidly, and there are several studies devoted to understanding phyllosphere microorganisms, especially the mechanisms by which plants control the phyllosphere microorganism assembly.[5,14−16] Furthermore, it was demonstrated that phyllosphere microorganisms influence host development, growth, immunity, nutrition, and fitness.[15,17−19]

The phyllosphere is the aerial part of the plant, harboring diverse microorganisms in both epiphytic (an organism that grows on the leaf surface) and endophytic (an organism living within a leaf) niches.[20] The phyllosphere area of the plants on Earth is estimated to be over 10^9 square kilometers and harbors up to 10^{26} bacterial cells.[21] The phyllosphere environment is complex and variable, mainly in terms of rapid changes in factors, such as water, nutrients, and temperature,[22] as well as plant species and genotypes.[23] Nonetheless, the microbial composition of the phyllosphere remains diverse and abundant.[24] Current studies show that the microorganisms in the phyllosphere are mainly bacteria, fungi and yeasts, protozoa, algae, and phages.[25,26] These microorganisms have adapted to the phyllosphere and have positive, neutral, or negative interactions with plants.[27] Relationships between microorganisms and hosts include parasitism, symbiosis, and mutualism in the phyllosphere.[28] Many communities profiling experiments using either traditional culture-dependent approaches or newly developed next-generation sequencing techniques have shown that phyllosphere-colonizing microorganisms play critical roles in multiple functions.[29] Phyllosphere microorganisms can improve plant productivity, maintain fitness by affecting host functions and life history, and play critical roles in removing contaminants.[26,30,31]

The research gaps in phyllosphere microorganisms should be addressed. As a result of the lack of studies related to the determinants of plant−microorganism interactions, the mechanisms of plant responses to pathogens and microbial symbionts remain unknown.[32] Furthermore, the principles

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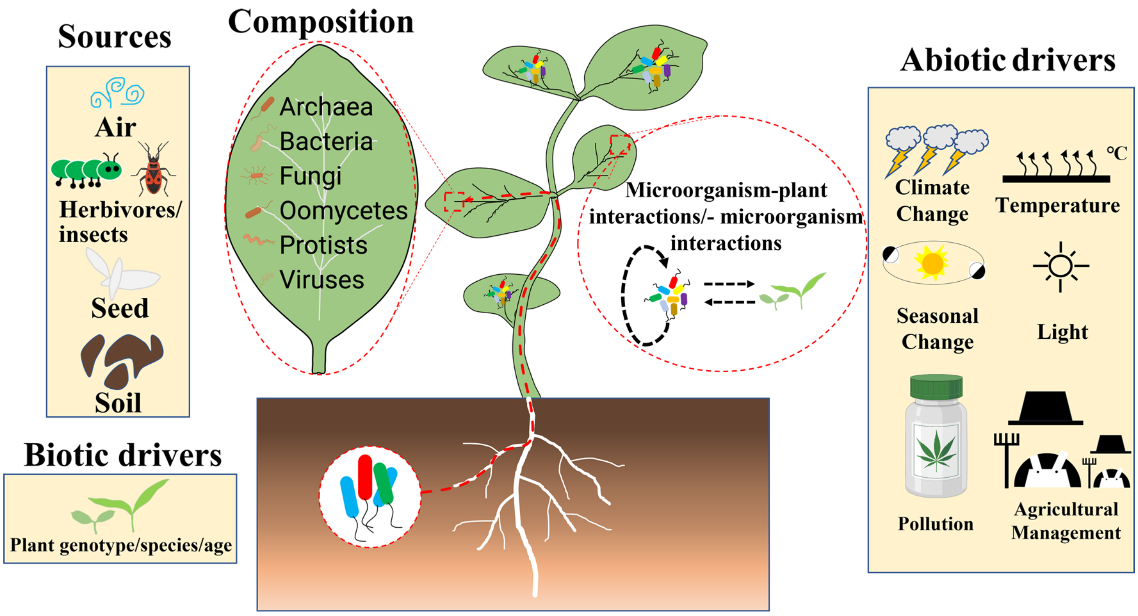

Figure 1. Main sources, composition, and drivers of phyllosphere microorganisms. The sources include soil, seeds, air, and herbivores. Phyllosphere microorganisms include archaea, bacteria, fungi, etc. The main drivers of phyllosphere microorganisms include biotic drivers (e.g., plant genotype and age), abiotic drivers (e.g., light and temperature), and plant−microorganism interactions.

governing the assembly of phyllosphere microorganisms under different environmental conditions remain elusive.[33] This review highlights recent progress related with phyllosphere microorganisms toward understanding sources, drivers, composition assembly factors, plant−microorganism interactions, ecological functions, and plant responses.

2. SOURCES AND COMPOSITION OF PHYLLOSPHERE MICROORGANISMS

The phyllosphere recruits its microorganisms either vertically or horizontally or mixed modes from neighbor microbial reservoirs.[34] In comparison to the rhizosphere, the phyllosphere environment is an open system. The relevant microorganisms are derived from multiple sources, such as soil, air, and nearby plants.[20,35] The sources and composition of microorganisms in the phyllosphere vary according to the host genotype, morphological physiology, and environmental conditions.[36] A study has revealed in depth the composition of phyllosphere microorganisms and established a set of systems to evaluate the community structure. This system involves factors such as host plant genotype, time of the year (including season), and space (e.g., the spatial position of leaves).[37] Moreover, the composition of phyllosphere communities is regular. The phyllosphere microbial communities are not randomly composed but have experienced the results of host and environmental selection.[38]

2.1. Sources of Phyllosphere Microorganisms. Soil, air, seeds, herbivores, and insects are the primary sources of phyllosphere microorganisms (Figure 1).[39−41] Many studies in different plant species, including *Arobidopsis thaliana*, grapevine, and lettuce, demonstrated that the phyllosphere and rhizosphere microorganisms can overlap substantially in key taxa, although the overall community structure and composition can differ.[42−44] These studies implied that the phyllosphere and rhizosphere microorganisms could derive from similar sources (i.e., soil and seed) or that the two microbial communities may interact with each other in natural environments through the wind, herbivores, and plant vascular tissues.[30,45,46] There was a reciprocal soil swap experiment, in which *Medicago truncatula* plants grown in one soil type were transplanted to another soil type, and the phyllosphere bacteria harbored in the transplanted plants were more like the soil microorganisms in the second soil, suggesting that soil is a major source of leaf bacterial microorganisms.[47] The soil microorganisms may enter the root tissues from emerging roots and constitute the rhizosphere microorganisms,[48] after which part of them transfer to the phyllosphere.[49] The atmospheric environment is also a source of phyllosphere microorganisms. There is a pathway by opening leaf stomata and wounds for the transformation and migration between endophytes and epiphytes. The pathway allows external microorganisms from aerosols and insects to colonize the plant, which also suggested that plants and the environment are interconnected.[50,51] Plant seeds are also the reservoir of plant microorganisms, and a study found that oak seeds transmit a large part of microorganisms to roots and leaves.[52] Moreover, seeds are involved in the vertical reproduction of microorganisms and are the most primitive source of microorganisms in plant leaves.[53] Soybean and radish differ in the microbial structure at different developmental stages, and Enterobacteriaceae and *Pseudomonas* are enriched during germination. The difference suggests that microbial communities with symbiotic-related functional shapes are likely to be selected for nutrient supply during germination.[54] In addition, microbial communities in leaves are also affected by priority effects; i.e., the order of arrival of microbial species affects the community structure.[55] When microorganisms colonizing the leaves early on form a stable community and develop some resistance, invasive species have little effect. As a result of the limitations of pure culture techniques, further studies on the sources of interleaf microorganisms are still lacking to determine the contribution of each source to the composition of the interleaf microbial community. In the future, the sources of interleaf microorganisms and the rules of their assemblage should be studied more systematically.

2.2. Composition of Phyllosphere Microorganisms. Advances in cultivation-independent methods and next-generation sequencing techniques have led to a better understanding of the composition and diversity of plant microorganisms.[56] There is a high diversity of microorganisms in the phyllosphere, especially in subtropical and tropical regions, where the temperature and humidity are relatively high.[57] Generally, the rhizosphere can provide a relatively stable environment for microorganisms, and most microorganisms can survive in the soil, while phyllosphere microorganisms face unstable growth conditions. As a result of the short life span of plant leaves and the narrow range of single leaves, the time and space provided for phyllosphere microorganisms to survive are limited and the diversity of microorganisms is inferior to that of the rhizosphere environment.[58] Even though the species composition and the number of microorganisms in the leaves are affected by plant species and the external environment, there are still dominant populations of microorganisms in the leaves.[20,55] These effects indicate that phyllosphere microorganisms have their unique composition.

The most abundant taxa of phyllosphere microorganisms are bacteria, constituting approximately 10^6-10^8 cell cm^{-2} of leaf tissue.[9,59] The phyllosphere bacteria are pathogenic, plant-growth-promoting bacteria (PGPB), endophytic, or epiphytic microorganisms.[5,13,60,61] Although phyllosphere microorganisms have different compositional structures in different species and habitats, the dominant taxa in the phyllosphere are Proteobacteria (especially α Proteobacteria and γ Proteobacteria), Bacteroidetes, Firmicutes, and Actinobacteria.[62,63] For instance, in the phyllosphere of rice, *A. thaliana* and soybean, the Proteobacteria phylum accounts for more than 70% of the community.[30,64,65]

The number of fungal communities is commonly less than the abundance of bacterial communities. The potential reason for this observation is that fungi are more sensitive to environmental variation (e.g., temperatures and elevation).[66,67] Fungi are generally saprophytic, and they may be either epiphytically or endophytically associated with the phyllosphere.[25] Some fungal epiphytes can actively enter the internal tissues or other epidermal regions through leaf stomata.[66,68] The interleaf of *Catharanthus roseus* contained 20 fungal endophytes, mostly related to the genera *Alternaria*, *Chaetomium*, and *Colletotrichum*.[69] Some fungal epiphytes can turn to pathogens inside plant tissue to induce plant diseases.[70,71] The rice blast disease is caused by the invasion of the fungal epiphyte *Magnaporthe oryzae*, which infects the leaf and destroys the leaf structure.[72] The commonly occurring genera of phyllosphere yeasts are the major phyllosphere fungal epiphytes, including *Cryptococcus*, *Sporobolomyces*, and *Rhodotorula*.[73,74] The yeast-like fungus *Aureobasidium pullulans* is usually dominant in the phyllosphere and on fruit surfaces.[66,75]

3. DRIVERS OF PHYLLOSPHERE MICROORGANISMS

The assembly of phyllosphere microorganisms is subject to multiple drivers. Like the rhizosphere, the colonization of phyllosphere microorganisms is mainly affected by the plant genotype and species,[16,23,56,77] complex and variable environmental conditions,[22,78−80] and complex interactions between organisms of multiple trophic levels,[37,55,81,82] of which the plant genotype plays a more important role.[77] The plant genotype mainly affects the microbial carrying capacity of leaves, including the type of microbial community and the scale of the whole community. In addition, abiotic environmental factors, including geographical location, solar radiation, pollution, and nutrients, affect the microbial community structure and diversity as well as biological factors, such as the leaf age and presence of other microorganisms.

3.1. Impacts of Plant Species, Genotype, and Age on Phyllosphere Microorganisms. The plant species, genotype, and age play a decisive role in the type and number of microorganisms attached to the leaves. Different plant species can provide a different microenvironment to control microbial communities, such as differences in the availability of essential nutrients, water availability, and presence of secondary metabolites.[20] The host genotypes of winter wheat, barley, oat, and rye are especially important to shape phyllosphere microorganisms.[83] A genome-wide association study using *A. thaliana* proved that plant loci associated with defense responses and cell wall integrity are likely involved in shaping phyllosphere microorganisms.[84] The leaf bacterial SynCom study showed that the *A. thaliana* cuticle mutants *lacs2* and *pec1* and the ethylene signaling mutant *ein2* displayed significant variations in the composition of phyllosphere microorganisms compared to wild-type *A. thaliana*.[85] Phyllosphere microorganisms in five dominant tree species in temperate forests of Canada were more strangely shaped by host genotype than tree location or age.[10] The genotypes of perennial mustard *Boechera stricta* and grapes also largely influence the abundance and composition of phyllosphere microorganisms.[23,43] Host genetics have a bigger influence on the structure of the endophytic fungal community than the structure of the epiphytic fungal community.[86] The genotype of the cultivar is also a crucial factor to shape the phyllosphere fungal community.[83] In addition to the plant genotype, the plant physiological stage or age was also the primary factor to drive phyllosphere microorganisms by secreting hormonal and other active substances.[43,87,88]

3.2. Impacts of Environmental Factors on Phyllosphere Microorganisms. The phyllosphere is not a closed system but is affected by ecological factors, such as the geographic location,[37,43] and abiotic factors, such as the temperature, water, light, and other anthropogenic factors.[89−93] These factors influence and shape the dynamics of plant growth, thus usually carrying different microbial groups on their leaves. These various factors are discussed below.

3.2.1. Impacts of Ecological Factors on Phyllosphere Microorganisms. There is a phenomenon in the phyllosphere microbial community that, as the geographic distance between plants increases, the microbial communities related to a single plant become more and more diverse.[94] This phenomenon could arise as a result of constraints on phyllosphere microbial dispersal, differences in leaf characteristics (structural, phenological, or physiological), or differences in climatic conditions.[95] For instance, the communities of bacteria, fungi, and oomycetes were affected by sampling season and geographic location in the *A. thaliana* phyllosphere.[37] Soil type (e.g., cities and rural areas) and local vegetation influence the composition of phyllosphere microbial communities.[96,97] The underlying reason for this observation could be that the different soil types, which serve as sources of phyllosphere microorganisms harbor distinct microbial communities in multiple meteorological conditions.[96]

3.2.2. Impacts of Abiotic Factors on Phyllosphere Microorganisms. There is a boundary layer on the leaves, which separates the environment of the leaves from the

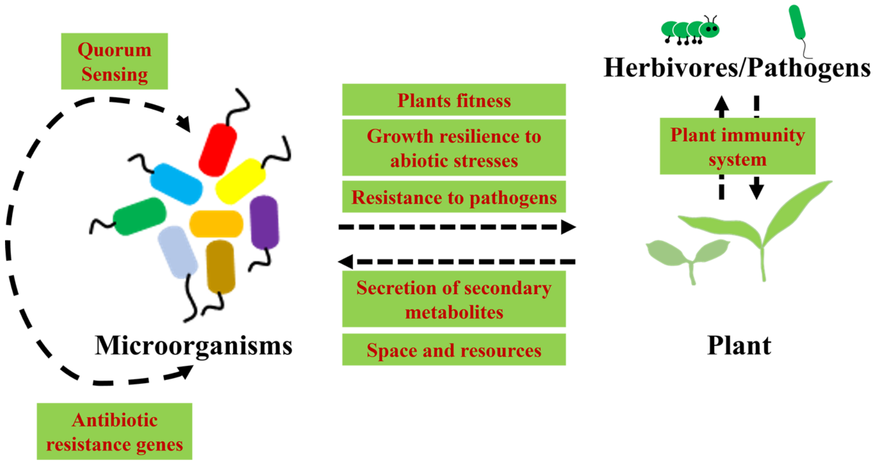

Figure 2. Interactions in the phyllosphere. There are three types of interactions in the phyllosphere: plant−microorganism, microorganism−microorganism, and microorganism−herbivore−plant.

surrounding air environment, making the leaves have a microclimate different from the surrounding environment.[98] Here, the leaf surface temperature is slightly higher than the air temperature, and the center temperature of the leaf surface is higher than that of the edge. For example, at an air temperature of 25 °C, the average canopy temperatures of adjacent trees of larch (*Larix decidua*), sessile oak (*Quercus petraea*), and hornbeam (*Carpinus betulus*) were 25, 27.5, and 30 °C, respectively,[28] which directly accelerated microorganism growth and changed their composition.[99]

The content and distribution of water in leaves are factors affecting the scale and growth of microorganisms. In general, disruption of the water status could reduce the richness and diversity of phyllosphere microorganisms.[100] The phyllosphere of a plant can recruit more active microorganisms in tropical ecosystems as a result of the higher amount of moisture of the surface on leaves.[101] In arid areas, the driving forces of microbial colonization are mainly limited by water.[102] Drought decreased the diversity of the endophytic phyllosphere but increased the richness of the epiphytic phyllosphere.[103]

Seasonal impacts on plants are mainly manifested in the temperature, solar radiation, water availability, etc.[104,105] Carbohydrates, proteins, amino acids, organic acids, and other substances produced during plant growth will change with the season.[106] The changes partially explain that phyllosphere microorganisms of *Gingko biloba*, *Pinus bungeana*, and *Sabina chinensis* differ significantly in their abundance, diversity, and metabolism of microbial nutrients between May and October.[107] It also shows that season is an important factor that affects the microorganism in the leaves, especially the metabolism of nutrients.

Light directly affects some phyllosphere microorganisms that use light as a complementary source of energy.[20] Light indirectly changes leaf surface moisture, hormone levels, secondary metabolite production, and volatile compound release. Light also ultimately affects plant−microorganism interactions and influences phyllosphere microbial lifestyle and habits as well as the composition and diversity of phyllosphere microorganisms.[108] The research focus is the influence of light treatment and circadian rhythm on phyllosphere microorganisms. Light alters the plant circadian gene expression and, thus, affects plant metabolism.[6] The phyllosphere bacteria are less responsive to light treatments, but fungi may be directly influenced by the physical properties of a particular light source.[89] Light can affect the circadian rhythm of phyllosphere fungi, which, in turn, impacts their fitness or virulence on a plant host. For example, the modification in the interaction of the pathogenic fungi *Botrytis cinerea* with *A. thaliana* was achieved by applying constant light to suppress the circadian rhythm of *Botrytis*.[109] However, the mechanisms governing these observations are not yet clear.

3.2.3. Impacts of Anthropocene Factors on Phyllosphere Microorganisms.

Anthropogenic factors, such as climate warming, air pollution, chemical pollution, application of fertilizers, etc., have universal and global impacts on leaf microorganisms.[15,22,90,92,102,110] The rising concentration of atmospheric CO_2 is a vital climate warming factor because it can significantly affect the diversity, structure, and phylogenetic composition of phyllosphere microorganisms.[90,92] Upon global warming, the beneficial bacteria in the phyllosphere were found to decrease, whereas pathogens were enriched.[22]

Because plant leaves are directly exposed to the air, air pollution directly changes the physiological characteristics of plant leaves, such as the structure of the epidermis.[111] Some airborne pollutants (e.g., toluene) can be used as carbon sources by some interstate microorganisms, thus changing the structural composition of the community.[112]

In recent years, applying chemicals in agriculture could disturb phyllosphere microorganisms.[5,15,113] The phyllosphere microorganism diversity is a more sensitive indicator related to pesticides than plants; for instance, the application of *S*-metolachlor decreased the diversity of phyllosphere microbial communities and changed their structure in a wheat study.[15] However, the microorganisms in the leaves have a certain resistance to applying agricultural antibiotics. For example, streptomycin application in apple orchards did not affect the composition of the bacterial community in the leaves for 10 years.[114] The likely reason is that exposure of antibiotics increases the abundance of phyllosphere microorganisms involved with transmission of antibiotic resistance genes (ARGs). Furthermore, the overuse of antibiotics in agriculture also enriched the abundance of ARGs in the phyllosphere.[115]

However, in comparison to pesticides and antibiotics, phyllosphere microorganisms are influenced by multiple factors under the dynamics of the open natural environment. This open natural environment may weaken the effect of fertilization on phyllosphere microorganisms.[21,116] Phyllosphere microorganisms showed more resistance to fertilization

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compared to the rhizosphere and soil.[117,118] In addition, host selection played a more important role in shaping the assembly and network complexity of phyllosphere microorganisms than fertilization when focusing on maize, wheat, and barley.[119]

3.3. Complex Interactions between Multiple Trophic Levels in the Phyllosphere. Phyllosphere microorganisms have extensive interactions with each other, including competition for nutrients and their ecological niche, direct inhibition, and indirect inhibition.[27,120] There are three types of interactions affecting the assembly of phyllosphere microorganisms: plant−microorganism, microorganism−microorganism, and microorganism−herbivore−plant (Figure 2). Many studies have shown that phyllosphere microorganisms can influence plant fitness, growth resilience to abiotic stresses, and resistance to pathogens.[17,18,121]

Microorganisms often have a large population size and high genetic variation, which translates into strong evolutionary dynamics to influence the plant−microorganism interactions.[122,123] For example, a synthetic community approach revealed that rapid evolution occurred in the nodule-forming bacterium *Ensifer meliloti* and promoted mutualism between the bacterium and the plant host *Medicago truncatula*.[124] Another factor within the microbial community dynamics are the direct or indirect interactions between multiple trophic levels in the phyllosphere. For example, microorganisms compete for limited space and resources, produce antimicrobial compounds, and may trigger plant immune responses.[125] A study found that direct inhibition of Firmicutes by Proteobacteria likely contributes to shaping the endophytic bacterial community in *A. thaliana* leaves.[126] Furthermore, phyllosphere microorganisms could be affected by insect attacks and pathogen invasion though microorganism−herbivore−plant interactions. For example, herbivorous insects are possibly mediated though plant defense activation by the herbivorous insects, which significantly alters the phyllosphere microbial community and increases the abundance of endophytic bacteria in *Cardamine cordifolia*.[127]

In addition, quorum sensing (QS) exists among phyllosphere microbial communities. Generally, bacteria secrete small signaling molecules to transmit information through the QS pathway. When the concentration of signal molecules is low, it is not enough to combine with transcriptional regulatory proteins in cells to induce the expression of target genes.[128] However, the growth of bacteria changes the environment of leaves, and the abundance of some microorganisms is dominant, while the production of EPS accelerates this process.[31] Phyllosphere microorganisms grow in the form of a biofilm to increase their ability to survive on the leaf surface. Microorganisms gather by producing extracellular polysaccharides (EPS, usually more than 1000 cells), which can assemble bacteria and fungi onto the microorganisms to maintain the microbial water balance and enhance the freezing and thawing resistance of microorganisms to a certain extent.[31,31,76] EPS synthesis is regulated by the diffusion signal and QS of polymeric microorganisms.

4. ECOLOGICAL FUNCTIONS OF PHYLLOSPHERE MICROORGANISMS

Phyllosphere microorganisms execute multiple ecological functions, such as affecting leaf functions and longevity, seed mass, fruit development, and homeostasis of host growth (Table 1).[30,31,129] Phyllosphere microorganisms could protect plants against dysbiosis, which is a disruption on the host homeostasis.[130] There are some PGPB, such as *Methylobacterium*, *Microbacterium*, and *Stenotrophomonas*, that can improve the growth and nutritional status of the host plant by producing indoleacetic acid and fixing nitrogen.[128,131] Phyllosphere microorganisms also play key roles in suppressing the overgrowth of plant pathogens.[14]

Table 1. Overview of the Ecological Functions in Phyllosphere Microorganisms

ecological function	specific response	species	reference
growth promotion	production of indoleacetic acid	*Methylobacterium* and *Microbacterium*	128
nutritional status	nitrogen fixation	*Stenotrophomonas*	130
resistance to pathogens	secretion of secondary metabolites	*Pseudomonas* sp.	129
	quorum sensing	*Pseudomonas aeruginosa*	131
reproduction	nitrogen scarcity	*Cladophora* spp.	135
transmission of antibiotic resistance genes (ARGs)			134

In addition, the signal transmission process of QS changes the behavior among bacteria, showing physiological functions that a single bacterium does not have. Bacterial QS is involved in the synthesis of bacterial antibiotics, the pathogenicity of pathogenic bacteria, the production of biosurfactants, and the expression of toxic factors.[132] For instance, pathogenic bacteria execute expression of virulence factors and biofilm formation through QS regulation, resulting in enhanced pathogenicity to host cells and immunity to antibacterial drugs.[31,133,134] QS still needs further research, which will provide a new solution for the prevention and control of pathogenic bacteria by modern molecular biotechnology.

On the other hand, some studies show negative impacts of phyllosphere microorganisms on the host. For instance, phyllosphere microorganisms involved in the transmission of ARGs in the urban green facade[135] and the reproduction of the invasive macrophyte *Hydrilla verticillata* L. under conditions of nitrogen scarcity.[136]

5. PLANT RESPONSES TO PHYLLOSPHERE MICROORGANISMS

Plants produce many secondary metabolites with antibacterial activity and possess a rich structure during their growth (Figure 3). For example, the compounds secreted by plants in rhizosphere soil are easily absorbed by other microorganisms, and plants will change their own metabolites to adjust the structure of the microbial community when they are stressed.[137] Plant leaves can also secrete metabolites, but it is still unclear whether plants can control the structure of the microbial community by changing the exudates in the leaves. Glyphosate caused a synergistic inhibitory effect on the growth and metabolism of *A. thaliana* leaves.[113] They found a correlation between the leaf exudates and phyllosphere microorganisms as the stress of addition of glyphosate decreased the fatty acid content in the leaf exudates and reduced the available nitrogen sources of microorganisms. Subsequently, the abundance of microorganisms with plant growth promotion and nutrient supplement increased in the leaf. The characteristics of leaves are particularly important to distinguish the bacterial community in the leaves, and the difference of the bacterial community is closely related to the

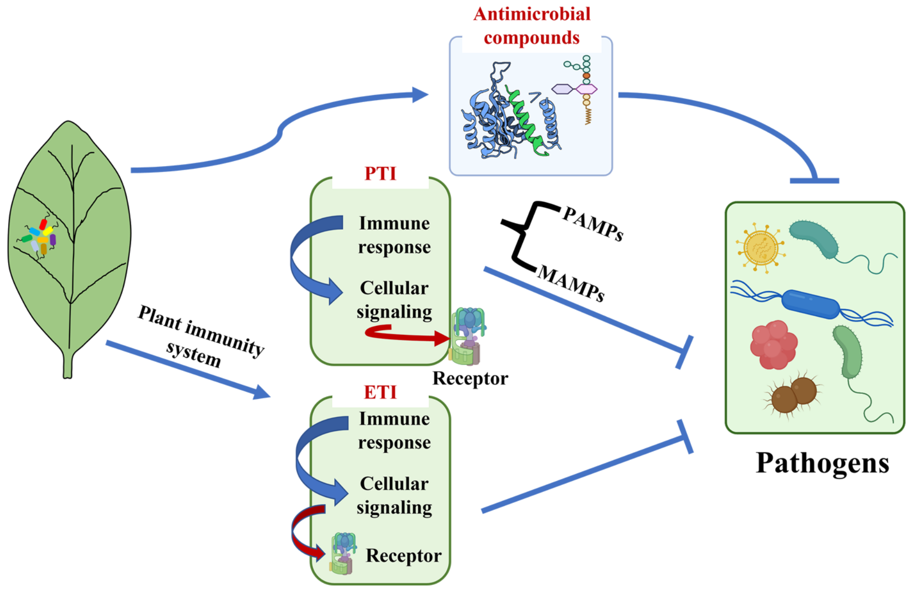

Figure 3. Plant responses to phyllosphere microorganisms. Illustration of the different ways in which phyllosphere microorganisms enhance plant resistance to pathogens. The plant immunity system includes pattern-triggered immunity (PTI) and effector-triggered immunity (ETI), and PTI, in turn, includes microorganism-associated molecular patterns (MAMPs), pathogen-associated molecular patterns (PAMPs), and damage-associated molecular patterns (DAMPs).

amount of soluble carbohydrates, the water content, and the exposure degree of leaves.

Plant responses govern phyllosphere microbial communities not only via metabolites but also by triggering the plant immune system (Figure 3).[84,138] There are two layers in the plant immune system. Pattern-triggered immunity (PTI) as the first layer of immunity is elicited by conserved molecular structures, such as microorganism- or pathogen-associated molecular patterns (MAMPs or PAMPs) or damage-associated molecular patterns (DAMPs). DAMPs are released from damaged or dying cells and activate the innate immune system by interacting with pattern recognition receptors.[139,140] Effector-triggered immunity (ETI) as the second layer of immunity directly or indirectly allows for recognition of effector proteins, which are often nucleotide-binding leucine-rich repeat proteins (NLRs).[75,141] Plants possessing two immune processes can identify the non-pathogenic microorganisms with unique transcriptional and metabolic responses.[46,142] Recently, a successive passaging study found that the potential probiotic consortia induced the plant PTI to defend against pathogenic invasions.[6] Plants can deprive the apoplast of monosaccharides upon pathogen encounter to limit pathogen growth. Plants can also supply certain availability of carbohydrates by sugar exporters to support the growth of beneficial bacteria in the phyllosphere.[143−145] These responses are likely to be spatially explicit, because the composition of phyllosphere microorganisms is heterogeneous and the same carbohydrate might promote the growth of spatially separated populations of beneficial and pathogenic bacteria.[146]

6. PERSPECTIVES

The in-depth understanding of the interlobar provides a new understanding and research direction for the field of microbial ecology. The phyllosphere involves many fields, such as air pollution, climate change, carbon and nitrogen cycles, leaf pathogens, etc. In recent years, people have paid more attention to the research of the phyllosphere. On the basis of the development of metagenomics, proteomics, next-generation sequencing, and other disciplines, the structure and function of leaf microorganisms have been linked with the function of host plants, and the interaction mechanism between them has been deeply analyzed. The environment of plant leaves is complex and variable, which makes it difficult for us to understand the phyllosphere. Even so, recent studies have focused on the steady state of leaf microorganisms, assembly mechanisms, and influencing factors, especially the interaction between multiple trophic levels in the phyllosphere.

There are still some limitations in the studies of phyllosphere microorganisms: (1) Although we have made progress in the study of pathogen−plant interactions, there is little research on the interactions between beneficial microorganisms and host plants, especially on the molecular mechanism of beneficial microorganisms to promote plant growth and stress resistance. (2) It is still unclear how leaf exudates affect the mechanism and function of microorganisms, especially how some small molecule signals of plants act like microorganisms, and what is the temporal and spatial distribution of leaf exudates? (3) There is much research on the unique patterns of the phyllosphere and the rhizosphere, but there is still little awareness of their continuity and correlation. (4) The key taxa in the phyllosphere that control or mediate plant performance are still not known. A system and novel approach, such as machine learning combined with global metadata analysis, is necessary to understand the complex interactions between phyllosphere microorganisms and host fitness and the ecological functions of these microorganisms for plant nutrition uptake, growth, and survival. The volatile substances in leaves need further study, which will provide a new perspective for the relationship and influence between plants and the atmospheric environment, surrounding plants, and surrounding microorganisms.

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Notes

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