We are IntechOpen, the world's leading publisher of Open Access books
Built by scientists, for scientists

6,300
Open access books available

170,000
International authors and editors

185M
Downloads

154
Countries delivered to

Our authors are among the

TOP 1%
most cited scientists

12.2%
Contributors from top 500 universities

BOOK CITATION INDEX
CLARIVATE ANALYTICS
INDEXED

WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com

Chapter

Perspective Chapter: Microorganisms and Their Relationship with Tree Health

Rodrigo F. Ramos, Lisiane Sobucki, Estéfany Pawlowski, Janaina S. Sarzi, Jessica E. Rabuske, Lucas G. Savian, Tiago E. Kaspary and Cristiano Bellé

Abstract

The health of plants depends on numerous environmental factors. All plants, including trees, live in close relationship with microorganisms. Plants harbor microbial communities in above- and below-ground tissues, where plant-associated microbial communities are influenced by environmental conditions and host genotype. The microbiome of trees is composed of mutualistic, commensal, and pathogenic microorganisms. Mutualistic microorganisms can help trees obtain nutrients (e.g., phosphorus and nitrogen) and defend against plant pathogens. Ecological interactions between different microbial groups directly influence host health, and endophytic microorganisms can inhibit pathogen growth or induce the expression of genes related to tree defense against these adverse organisms. Hence, understanding host-microbiome-environment interactions are crucial for modulating tree health.

Keywords: plant holobiont, microbial ecology, bacteria, ectomycorrhizas, arbuscular mycorrhizae

1. Introduction

Trees, including those outside of forests (i.e., orchards, gardens, trees in urban environments), are terrestrial plants that provide several ecosystem services essential to life and the economy. Trees contribute to carbon sequestration, animal and insect biodiversity maintenance, lignocellulosic biomass production for the industry, food supply (i.e., fruits and seeds), tourism (i.e., forest nature trails), air filtration in urban areas, and wood production for construction. Given their importance and the benefits trees provide, understanding the factors related to their health is pivotal for proper human intervention in forests, woodlands, and orchards.

Tree health depends on numerous factors, and it is now understood that their health, as well as other multicellular organisms, is closely related to the structure of the microbial community of the holobiont (the host and its associated microorganisms) [1]. The theory of plant holobiont seeks to shed more light on the plant as a meta-organism,

in which plant growth, health, and productivity are closely related to the composition and functions of the microbiota inhabiting different niches in the plant [2]. Within this perspective, trees are not autonomous entities, and their health can be considered a function of the plant microbiota (set of all associated microorganisms) or the plant microbiome (set of all associated microbial genomes) [3–4].

Trees establish different symbiotic relationships with a plethora of microorganisms. Therefore, the plant microbiome, also known as a phytobiome, is composed of commensal, mutualistic, and pathogenic microorganisms [5]. The diverse microbial composition contributes to host-microbial homeostasis, meaning the microbial community structure can modulate and maintain tree health over time. It is now known that the colonization of plant tissues by a pathogenic microorganism and disease development may be related to an imbalance of host-microbial homeostasis. In some cases, this imbalance results from atypical environmental conditions or the loss of partner microbes or ancestor microorganisms that are key to tree health.

The microorganisms that are part of the phytobiome include a wide diversity of prokaryotes distributed in different phyla (Proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes, etc.), in addition to fungi (including mycorrhizae), protozoa, nematodes, and viruses. In general, the rhizospheric soil and endosphere are the environments most densely populated by microorganisms; nevertheless, the phylloplane is also an important environment for tree-associated microbial communities. Partner microorganisms can contribute directly and indirectly to tree health through nutrient provision (i.e., phosphorus solubilization and nitrogen fixation), plant hormone production (i.e., gibberellins, auxins), pathogen inhibition via competition, and the inhibition of systemic host resistance.

2. The ecological community of microorganisms

Symbiotic relationships are common to all organisms. Trees establish three main symbiotic relationships with microorganisms: commensalism, mutualism, and parasitism (pathogenic microorganisms). Commensals represent a wide diversity of microorganisms that internally and externally inhabit plant tissues; they benefit from the resources made available by the host tree (contact surface, space, moisture, mucilage, cellular debris, etc.) and do not cause any harm to the host. In contrast, the benefits of commensal microorganisms are considered "neutral" to their host [6]. Although the classical definition of commensalism defines the absence of benefits to the host, this may not be truly applicable to the networks of microbial interactions that develop in plants. The development of a community of commensal microorganisms results in the occupation of a niche that, in their absence, would be held by other groups of microorganisms, including pathogens. Hence, these microorganisms' survival strategies, including cooperation with other commensal microorganisms, pose an obstacle to the pathogen colonization and development in these niches. From this perspective, the benefit of a single commensal species may be neutral, although the gains from the presence of a commensal microbial community are positive to the host, despite not being straightforward to establish the actual gains from the commensal relationship between microorganisms and plants.

While the community of commensal microorganisms can act as an obstacle to establishing primary pathogens, this community can harbor opportunistic pathogens. Factors related to this phenomenon include unusual environmental conditions (i.e., long drought periods or excess water), physical damage to plant tissues (i.e.,

mechanical damage to the roots, stems, leaves, and fruits), extreme temperatures, and other factors that can affect key components of plants' "innate immunity" [7]. For instance, acute oak decline (AOD) has been a recurring problem in European forests and is associated with opportunistic pathogens, as in the case of the fungus *Armillaria gallica* Marxm. & Romagn (Agaricales: Physalacriaceae). This fungus is an important saprophytic species in wood decay in forests, and it can develop a wide network of hyphae in the subterranean soil and is unable to colonize vigorously growing hosts [8]. Nevertheless, *A. gallica* invades oak trees weakened by insect defoliation or drought, colonizing the root system and causing root rot [9]. The transition from saprophytic to pathogenic lifestyle indicates that a microorganism can alter its relationship with the host depending on environmental conditions and the plant's immune status [9].

The symbiotic mutualistic relationship is a key survival strategy between plants and microorganisms. It is now recognized that mycorrhizal fungi were undoubtedly the most important microorganisms for the successful terrestrial colonization by plants. The evolution of symbiosis with mycorrhizal fungi occurred simultaneously with the establishment of plants on land 450 million years ago [10]. Arbuscular mycorrhizal fungi (AMF—phylum Glomeromycota) were the first fungi to establish a mutualistic symbiosis with plants, and, currently, this group is associated with the roots of over 85% of all plant species [11]. However, the establishment of plants on land also occurred concomitantly with the diversification of other mutualistic symbioses. In forest environments, symbiosis with ectomycorrhizae (ECM—phyla Basidiomycota and Ascomycota) is found in various gymnosperm and angiosperm lineages [12]. Both mycorrhizae groups contribute to the nutrition of their hosts by making scarce nutrients available (i.e., phosphorus and nitrogen), as well as increasing the tolerance of their hosts to abiotic (salinity and water stress) and biotic (pathogen attack) stress. The biogeographical distribution of these symbionts is influenced by climatic factors, such as temperature and rainfall regime. In tropical forests, mutualistic symbiotic association with AMF is more common, whereas ECM fungi are more diverse in temperate and boreal ecosystems [13, 14].

Another important association that may have contributed to the plants' successful terrestrial colonization is symbiosis with nitrogen-fixing bacteria. Association with nitrogen-fixing, nodule-forming bacteria, termed root nodule symbiosis (RNS), is restricted to four angiosperm orders: Fabales, Fagales, Cucurbitales, and Rosales [15]. Most leguminous tree species in tropical forests are capable of forming root nodules and fixing atmospheric nitrogen [16]. In some situations, trees can establish a mutualistic symbiotic association with rhizobia in conjunction with mycorrhizal fungi. The synergistic interaction between these two types of mutualism can improve plant performance, especially in soils nutritionally poor in phosphorus and nitrogen or saline soils. For instance, co-inoculation of the AMF *Rhizophagus fasciculatus* (Thaxt.) Gerd. & Trappe (Glomerales: Glomeraceae) and the actinobacterium Frankia (root nodule symbiont) improved the tolerance to salt stress of the tree species *Casuarina equisetifolia* and *C. obesai* (Fagales) [17].

Unlike RNS, nitrogen fixation through plant-cyanobacteria association is widely distributed in terrestrial plants [18]. Association with nitrogen-fixing cyanobacteria can occur in below-ground (rhizosphere) and above-ground (phyllosphere) environments. These microorganisms can live with mosses growing on the soil, be associated with bryophytes and arboreal epiphytes, or grow in the leaf cavities of plants [18–20]. In fact, evidence has shown that nitrogen fixation by cyanobacteria is associated with "feather moss" (i.e., *Hylocomium splendens*, *Ptilium crista-castrensis*, *Pleurozium*

schreberi, and *Sphagnum caprifolium*), an important source of nitrogen input into boreal forest ecosystems [21–22].

The phytobiome also harbors pathogenic microorganisms (symbiotic parasitism relationship). Forest pathogens include fungi, oomycetes, bacteria, phytoplasmas, parasitic higher plants, viruses, and nematodes [23]. Despite a plethora of causative agents, the diseases of forest trees are primarily caused by fungal and oomycete pathogens [24]. The development of some tree diseases has been correlated with changes in the phytobiome. Thus, it is believed that the population growth of a particular pathogen may be related to the decline in the population of beneficial microorganisms. For example, one study reported that pine plants with pine wilt disease (PWD) caused by the nematode *Bursaphelenchus xylophilus* had a lower diversity of beneficial fungi and bacteria in the rhizosphere compared to the rhizosphere of healthy pines [25]. Recent studies have focused on analyzing the microbiome of diseased trees in an attempt to map unknown pathogen groups. Research on the microbiome of oak trees with AOD has reported that this concerning disease is caused by a polymicrobial complex, that is, the onset of AOD is related to the interaction of different bacterial species (*Brenneria goodwinii*, *Gibbsiella quercinecans*, and *Rahnella victoriana*) that work synergistically to develop the disease [26–28]. Some studies suggest that the physiological state of the host can influence the abundance and diversity of pathogenic microorganisms. For example, a recent study evaluated the diversity of foliar endophytes in *Platycladus orientalis* and *Styphnolobium japonicum* trees with different ages (individuals ranging from 10 to 5000 years old for *P. orientalis* and 10 to 1700 years old for *S. japonicum*) [29]. The authors demonstrated that the abundance of latent pathogens (fungi) increased as the trees aged. Thus, the abundance of pathogens *Collectotrichum gloeosporioides* and *Botryosphaeria dothidea* in *S. japonicum* and *Pestalotiopsis funerea* and *Amyloporia subxantha* in *P. orientalis* increased linearly with tree age, indicating that tree age is also an important structuring factor for host communities [29].

Although forest pathology is a recent science, it has been growing rapidly in recent decades mainly due to recent tree death events in forest ecosystems throughout Europe and North America. Forest decline diseases have concerned scientists and government bodies and are becoming increasingly problematic for tree health worldwide [28, 30]. Hence, shedding more light on the role of the tree microbiome will be crucial for properly managing forest environments.

3. Plants as microbial habitats

The plant microbiome is highly dynamic and diverse. Plant-associated microbial communities are deeply influenced by environmental conditions (pH, moisture, temperature, and nutrient availability) and host genotypes. Plants harbor microbial communities in above- and below-ground tissues (**Figure 1**). Below ground, the rhizosphere (soil region in intimate contact with roots) is the environment most densely populated by microorganisms [31]. The root endosphere is another important below-ground region that hosts a vast diversity of microbial communities. The endosphere is the region encompassing the apoplastic spaces in the root cortex (inside the roots). The host genotype strongly influences the microbial communities of the rhizosphere and endosphere, and this can be considered an "extended root phenotype" (i.e., a manifestation of the effects of plant genes on their environment inside and/or outside the organism) [32].
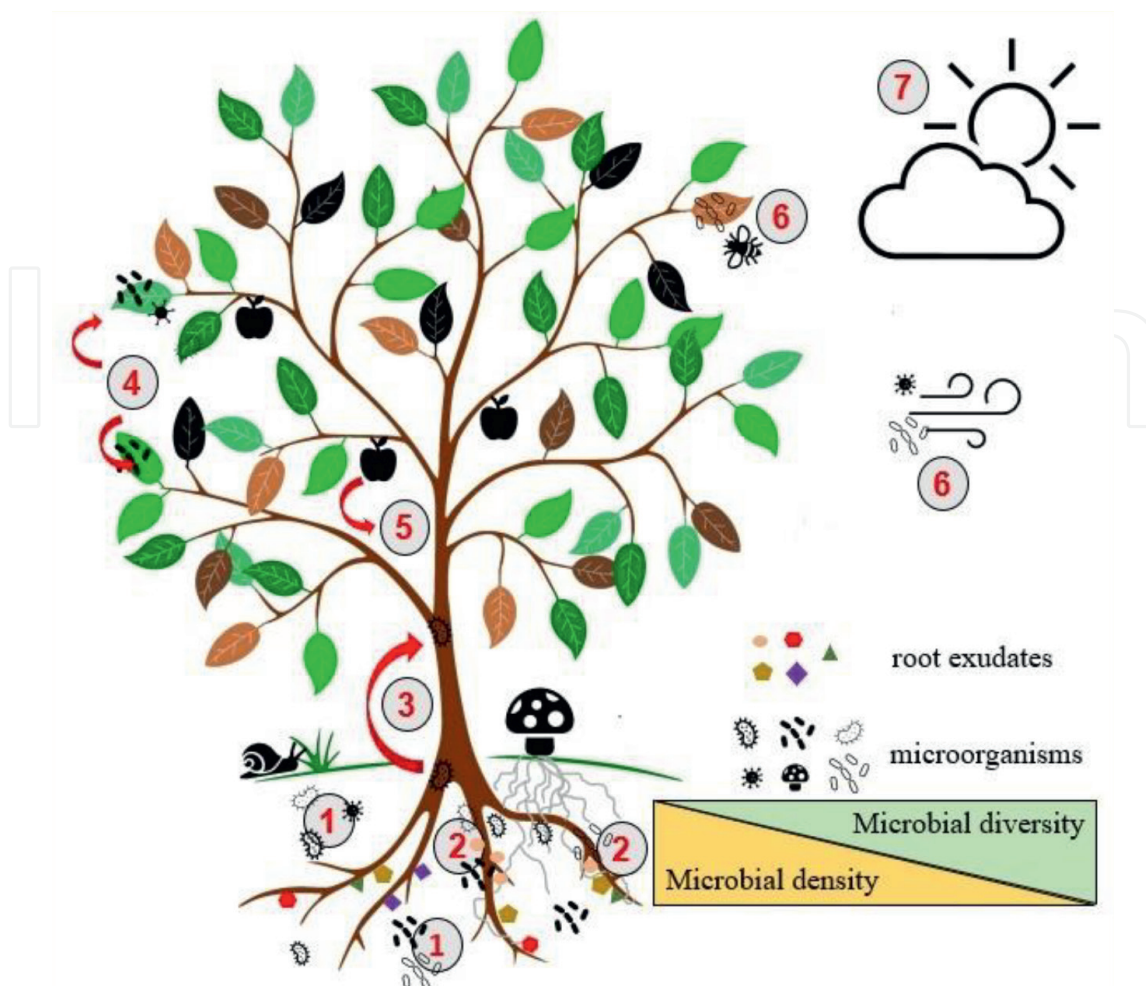
Figure 1.
Interactions between microorganisms and trees. Microorganisms present in the bulk soil that roots can recruit via organic molecule exudation (1). Microorganisms in the rhizosphere and endosphere. The presence of root exudates (sugars, lipids, proteins, and secondary metabolites) stimulates the recruitment of specific microbial taxa. The rhizosphere microbiota is strongly influenced by the physicochemical profile of the exudates of this niche (2). Endophytic microorganisms can inhabit internal regions of the plant without causing disease. Bacteria that inhabit the root endosphere can be translocated via the xylem to other regions of the plant above ground (3). The phyllosphere is the compartment that houses associated microorganisms above ground, and this niche is mainly represented by the leaves (4). Other above-ground compartments may harbor associated microorganisms, such as the outer surface of fruits (carposphere), flowers (anthosphere), and the stem (caulosphere) (5). Microorganisms can be dispersed from one plant to another or from the soil to the phyllosphere by wind, rain, insects, and animals (6). The composition of the microbial community of the phyllosphere is significantly influenced by environmental factors, including solar radiation, temperature, and humidity (7).

Between the volume of soil not occupied by roots and the endosphere region, there is a selection degree of microorganisms. Various studies have demonstrated that microbial species richness is the highest in the bulk soil and that it decreases in the rhizosphere and endosphere (**Figure 1**). In contrast, the population density of specific microorganisms increases from the soil toward the root surface, indicating favorable conditions for the selected microbial species [5]. This phenomenon is called the rhizospheric effect, that is, the composition of root exudates (sugars, oligosaccharides, vitamins, nucleotides, flavones, auxins, and secondary metabolites) modulates the physicochemical conditions of the rhizosphere region and, thus, the plant can recruit and select groups of microorganisms that can proliferate in the specific physicochemical conditions of the root zone [33]. Estimates have indicated that up to 40% of the carbon reserves fixed by photosynthesis are provided in

the rhizosphere, indicating the active role of plants in recruiting microbial communities. Although the root zone harbors a wealth of biodiversity, the rhizosphere and endosphere microbial communities are dominated by four bacterial phyla: Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria [5, 34]. In the bulk forest soil, the dominant fungal group is Basidiomycota, while Ascomycota is the most prevalent group in plant tissues [9].

Evidence suggests that plants adapt to biotic stress by altering their root exudate chemistry to assemble health-promoting microbiomes [35]. This phenomenon is termed the "cry-for-help" hypothesis, and it posits that plants modulate the chemistry of root exudates to recruit partner microorganisms capable of increasing the plants tolerance to a given stress condition, such as insect herbivory, pathogen attack, or nutrient shortage. Therefore, the chemical composition of root exudates influences the metabolism of rhizosphere microbial taxa while the recruited microbiota assists plant homeostasis by encoding functionalities that extend the plant genome [36]. For example, a study with the model plant *Arabidopsis thaliana* and inoculated with the Gram-negative pathogen *Pseudomonas syringae* demonstrated that subsequent generations of *A. thaliana* subjected to inoculation with the pathogen were able to modulate the root exudation profile, alter the composition of the rhizosphere microbial community, and increase the disease suppressive response [37].

Above ground, there is also an important plant compartment that hosts microorganisms; it is called the phyllosphere and refers mainly to the leaves. However, there are also other important plant sub-compartments above ground, such as the anthosphere (external environment of flowers), caulosphere (environment of the plant stem), carposphere (external surface of fruits), and spicosphere (niche formed in plants with spikes) [38–39]. The phyllosphere is an oligotrophic environment subject to severe modifications in a short period of time (temperature, humidity, and radiation fluctuations); despite being disconnected from the soil, this environment indirectly influences the phyllosphere. Dust particles from the soil can be dispersed by the wind and deposited in the above-ground plant compartments and thus provide nutrients for the microbial communities of the phyllosphere. In addition, microorganisms can be dispersed from the soil to the above-ground part of the plant by wind or colonize the phyllosphere after being recruited in the rhizosphere and systematically translocated to the above-ground part via the xylem. Microorganisms that can colonize plant tissues internally or translocate via the xylem to different tissues of the plant above ground without causing disease are called endophytes. These microorganisms may live part of their life cycle associated with the root endosphere region or translocated to plant tissues above ground. Furthermore, as in the rhizosphere, the bacterial communities of the phyllosphere are dominated by the taxa Actinobacteria, Bacteroidetes, Firmicutes, and Proteobacteria [40].

The phyllosphere is an open environment where the arrival and departure of taxa are constant [41]. The phyllosphere generally consists of microorganisms that are dispersed mainly from the soil and reach the surface of leaves and stem through rain, wind, and insects **(Figure 1)**. The survivability and colonization of these microorganisms depend on several factors, such as host genotype and health (since both modulate the chemical composition of leaves), water availability, temperature fluctuation, UV exposure, chemical applications (i.e., fertilizers and pesticides), and inter- and intraspecific microbial competition [41–43]. Although several factors influence microbial communities, it is recognized that environmental conditions are the key factors that determine population structure in microbial communities of the phyllosphere. For instance, a recent study revealed that the microbial community

composition of the phyllosphere of spruce trees was influenced by seasonal changes, whereas the bacterial and fungal communities of the rhizosphere of these same trees were influenced by anthropogenic nutrient availability [44].

Because it is an environment with harsh conditions, many microorganisms have evolved and developed survival strategies to colonize the phyllosphere. Thus, to colonize niches in the phyllosphere, some microorganisms can alter the chemistry of the leaf surface or use specialized cellular structures to increase their ability to compete. For example, the bacterium *P. syringae* (an important plant pathogen) releases surfactants that increase mobility and local water availability on leaf surfaces. In addition, this microorganism has flagella that favor bacterial motility on the leaf surface. In the case of *P. syringae*, these strategies are related to its virulence [41]. Nonetheless, characteristics of the host plant's aerial part structures also influence the successful colonization of the phyllosphere. One study evaluated the bacterial functional diversity in the phyllosphere of different tree species in a Neotropical forest and found evidence suggesting an adaptive correspondence between phyllosphere microorganisms and their tree hosts [40]. The authors demonstrated that tree characteristics, such as leaf morphology and leaf metal contents (copper, manganese, and zinc), are correlated with phyllosphere microbial community composition [40].

4. Functions of the host-associated microbiota

Plant-associated microorganisms can assist the health of the host in different ways. Many endophytic microorganisms can make previously scarce nutrients available in the soil or increase host tolerance to stressors. Mycorrhizae play an important role in maintaining tree health among endophytic microorganisms. The role of these microorganisms is related not only to making phosphorus and nitrogen available to the host but also to increasing plant tolerance to water stress and pathogen attack. In one experiment, the authors evaluated the effects of inoculation of an AMF (*Glomus etunicatum*) on pistachio (*Pistacia vera*) seedlings subjected to water stress. They observed that plants inoculated with the fungus had an increased tolerance to water stress compared to the control (seedlings subjected to water stress and not inoculated) [45]. Among the mechanisms related to increased stress tolerance and possibly induced by the mycorrhizal association, the authors highlighted a greater accumulation of osmotic adjustment compounds (i.e., soluble sugar content), increased activity of antioxidant enzymes (i.e., catalase and peroxidase), secondary metabolite production (i.e., flavonoids), and nutrient accumulation (nitrogen and calcium) [45].

Further findings have also suggested that association with mycorrhizal fungi improves host resistance to pathogens [46]. For instance, a recent study used amplicon sequencing to determine the presence of a wide taxonomic range in the rhizosphere of apple (*Malus domestica* Borkh) rootstocks [47]. The authors observed that roots of the G.890 rootstock (which is tolerant to apple replant disease—ARD) harbored a significantly higher percentage of AMF species, indicating a possible active role of endophytic fungal communities in apple tree tolerance to soil pathogens (including *Rhizoctonia* spp., *Phytophthora* spp., and *Pratylenchus penetrans*) that cause ARD [47]. In another study [25], the authors evaluated the effects of inoculating ECM species (*Suillus bovinus* and *Amanita vaginata*) and dark septate endophytes (DSE, *Gaeumannomyces cylindrosporus* and *Paraphoma chrysanthemicola*) on the tolerance of pines (*Pinus tabulaeformis*) to PWD caused by the pine nematode *Bursaphelenchus xylophilus*. The authors demonstrated that inoculating pines with ECM/DSE reduced

disease severity caused by *B. xylophilus* and increased the recruitment of beneficial bacterial and fungal groups in the rhizosphere of pines [25]. In addition to improving nutrition and stimulating defense mechanisms in their hosts, ectomycorrhizal fungi can assist their host against pathogen attacks by forming a thick fungal mantle that acts as a mechanical barrier against the penetration of soil pathogens [48].

Ectomycorrhizae are known to benefit their host trees in different ways. This mutualistic symbiosis is especially useful for forest plantations intended for the production of wood, cellulose, or the recovery of degraded areas. However, mutualism between trees and ECM species can stimulate another highly profitable economic activity: truffle farming. Truffles are the reproductive structures of hypogean ectomycorrhizal fungi and are appreciated in haute cuisine [49]. A recent study evaluated the effect of mycorrhization of pecan trees under subtropical conditions in Brazil [50]. The authors demonstrated that inoculation of pecan seedlings with the ectomycorrhizal species *Tuber aestivum* and *T. brumale* increased plant growth and, in addition, ECM produced high-value edible structures (truffles) [50]. These results indicate the possibility of developing a highly profitable economic activity associated with pecan orchards in subtropical regions.

Recruitment of plant growth-promoting bacteria (PGPB) is another important strategy trees adopt to increase their resistance to pathogen attacks; PGPB is known to promote plant growth through different mechanisms, including producing or stimulating plant hormones (i.e., gibberellins, auxins, and cytokinins), nitrogen fixation, phosphate solubilization, among others. In addition, PGPB may exhibit biocontrol activity against plant pathogens; numerous mechanisms have been described as being responsible for the biocontrol ability of PGPB, such as direct competition for space, emission of volatile compounds, siderophore production, lytic enzymes (i.e., proteases, chitinases, and lipases), antibiotics (i.e., amphisin, 2,4-diacetylphloroglucinol, and oomycin A), and induction of systemic resistance of the host plant [51–53].

The ability of the plant to recruit partner microorganisms indicates that the rhizosphere is a reservoir of beneficial microorganisms amenable to selecting and applying disease biocontrol programs. For example, an endophytic PGPB (*Bacillus velezensis* OEE1) was isolated from olive (*Olea europaea*) roots, and its disease biocontrol ability was tested against fungal (*Fusarium solani*, *Botrytis cinera*, etc.) and oomycete (*Phytophthora* spp.) pathogens [54]. The authors observed that the biocontrol ability of fungal pathogens and oomycetes by the isolate *B. velezensis* OEE1 was related to a wide range of competitive characteristics, including phosphate solubilization and producing siderophores, extracellular hydrolytic enzymes (amylases, cellulases, and pectinases), biosurfactant (surfactins), and secondary metabolites [54]. In another study, bacteria were isolated from the rhizosphere of avocado trees that survived root rot infestations caused by the oomycete *Phytophthora cinnamomi* [55]. The authors evaluated the antagonistic activity of the isolates against *P. cinnamomi* and selected a potential PGPB (*Bacillus acidiceler*) that could inhibit the growth of the oomycete by producing volatile compounds, indicating the potential use of this PGPB in biocontrol programs for pathogenic oomycetes [55].

5. Conclusions

The microbial communities of the rhizosphere and phyllosphere are essential to the health of their hosts. Researchers are currently seeking to understand the active role of tree-associated microorganisms and the mechanisms related to the

recruitment of beneficial taxa. Knowledge about tree-associated microorganisms is increasingly more important in the face of the current scenario of increasing diseases of forest declines. Therefore, microbial ecology studies applied to tree-associated bacteria and fungi communities will enable researchers to bioprospect new microorganisms for use in plant growth promotion and disease control.

Acknowledgements

Conflict of interest

The authors declare no conflict of interest.

Author details

Rodrigo F. Ramos[1], Lisiane Sobucki[2], Estéfany Pawlowski[2], Janaina S. Sarzi[2], Jessica E. Rabuske[3], Lucas G. Savian[2], Tiago E. Kaspary[4] and Cristiano Bellé[1]*

1 Instituto Phytus - Staphyt Brasil, Itaara, Brazil

2 Federal University of Santa Maria, Santa Maria, Brazil

3 Regional Integrated University of Upper Uruguai and Missions, Frederico Westphalen, Brazil

4 National Institute of Agricultural Research – INIA La Estanzuela, Colonia del Sacramento, Uruguay

*Address all correspondence to: crbelle@gmail.com

InTechOpen

References

[1] Rosenberg E, Zilber-Rosenberg I. The hologenome concept of evolution after 10 years. Microbiome. 2018;**6**:78

[2] Hassani MA, Dúran P, Hacquard S. Microbial interactions within the plant holobiont. Microbiome. 2018;**6**:58

[3] Cregger MA, Veach AM, Yang ZK, Crouch MJ, Vilgalys R, Tuskan GA, et al. The *Populus* holobiont: Dissecting the effects of plant niches and genotype on the microbiome. Microbiome. 2018;**6**:31

[4] Vandenkoornhuyse P, Quaiser A, Duhamel M, Le Van A, Dufresne A. The importance of the microbiome of the plant holobiont. The New Phytologist. 2015;**206**:1196-1206

[5] Rodriguez PA, Rothballer M, Chowdhury SP, Nussbaumer T, Gutjahr C, Falter-Braun P. Systems biology of plant-microbiome interactions. Molecular Plant. 2019;**12**:804-821

[6] Terhonen E, Blumenstein K, Kovalchuk A, Asiegbu FO. Forest tree microbiomes and associated fungal endophytes: Functional roles and impact on forest health. Forests. 2019;**10**:42

[7] Charkowski AO. Opportunistic pathogens of terrestrial plants. In: Hurst CJ, editor. The Rasputin Effect: When Commensals and Symbionts Become Parasitic. Advances in Environmental Microbiology, Vol 3. Cham: Springer; 2016. p. 147-168

[8] Lee CA, Holdo RM, Muzika R-M. Feedbacks between forest structure and an opportunistic fungal pathogen. Journal of Ecology. 2021;**109**:4092-4102

[9] Marçais B, Bréda N. Role of an opportunistic pathogen in the decline of stressed oak trees. Journal of Ecology. 2006;**94**:1214-1223

[10] Brundrett MC, Tedersoo L. Evolutionary history of mycorrhizal symbioses and global host plant diversity. The New Phytologist. 2018;**220**:1108-1115

[11] Strullu-Derrien C, Selosse MA, Kenrick P, Martin FM. The origin and evolution of mycorrhizal symbioses: From palaeomycology to phylogenomics. The New Phytologist. 2018;**220**:1012-1030

[12] Radhakrishnan GV, Keller J, Rich MK, Vernié T, Mbadinga DLM, Vigneron N, et al. An ancestral signalling pathway is conserved in intracellular symbioses-forming plant lineages. Nature Plants. 2020;**6**:280-289

[13] Corrales A, Henkel TW, Smith ME. Ectomycorrhizal associations in the tropics - biogeography, diversity patterns and ecosystem roles. The New Phytologist. 2018;**220**:1076-1091

[14] Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, et al. Global diversity and geography of soil fungi. Science. 2014;**346**:1052

[15] Griesmann M, Chang Y, Liu X, Song Y, Haberer G, Crook MB, et al. Phylogenomics reveals multiple losses of nitrogen-fixing root nodule symbiosis. Science. 2018;**361**:eaat1743

[16] Chaer GM, Resende AS, Campello EFC, Faria SM, Boddey RM. Nitrogen-fixing legume tree species for the reclamation of severely degraded lands in Brazil. Tree Physiology. 2011;**31**:139-149

[17] Djighaly PI, Diagne N, Ngom D, Cooper K, Pignoly S, Hocher JMF, et al. Effect of symbiotic associations with Frankia and arbuscular mycorrhizal fungi on antioxidant activity and cell ultrastructure in *C. equisetifolia* and *C. obesa* under salt stress. Journal of Forest Research. 2022;**27**(2):117-127

[18] Delaux P-M, Radhakrishnan G, Oldroyd G. Tracing the evolutionary path to nitrogen-fixing crops. Current Opinion in Plant Biology. 2015;**26**:95-99

[19] DeLuca TH, Zackrisson O, Nilsson MC, Sun S, Crespo MA. Long-term fate of nitrogen fixation in *Pleurozium schreberi* Brid (Mit.) moss carpets in boreal forests. Applied Soil Ecology. 2022;**169**:104215

[20] Markham J, Otárola MF. Bryophyte and lichen biomass and nitrogen fixation in a high elevation cloud forest in Cerro de La Muerte. Costa Rica. Oecologia. 2021;**195**:489-497

[21] Renaudin M, Blasi C, Bradley RL, Bellenger JF. New insights into the drivers of moss-associated nitrogen fixation and cyanobacterial biomass in the eastern Canadian boreal forest. Journal of Ecology. 2022;**110**:1403-1418

[22] Ininbergs K, Bay G, Rasmussen U, Wardle DA, Nilsson MC. Composition and diversity of *nifH* genes of nitrogen-fixing cyanobacteria associated with boreal forest feather mosses. The New Phytologist. 2011;**192**:507-517

[23] Sturrock RN, Frankel SJ, Brown AV, Hennon PE, Kliejunas JT, Lewis KJ, et al. Climate change and forest diseases. Plant Pathology. 2011;**60**:133-149

[24] Desprez-Loustau M-L, Aguayo J, Dutech C, Hayden KJ, Husson C, Jakushkin B, et al. An evolutionary ecology perspective to address forest pathology challenges of today and tomorrow. Annals of Forest Science. 2016;**73**:45-67

[25] Chu H, Wang H, Zhang Y, Li Y, Wang C, Dai D, et al. Inoculation with ectomycorrhizal fungi and dark septate endophytes contributes to the resistance of *Pinus* spp. to pine wilt disease. Frontiers in Microbiology. 2021;**12**:687304

[26] Doonan JM, Broberg M, Denman S, McDonald JE. Host–microbiota–insect interactions drive emergent virulence in a complex tree disease. Proceedings of the Royal Society B: Biological Sciences. 2020;**287**:20200956

[27] Ruffner B, Schneider S, Meyer JB, Queloz V, Rigling D. First report of acute oak decline disease of native and non-native oaks in Switzerland. New Disease Reports. 2020;**41**:18

[28] Denman S, Doonan J, Ransom-Jones E, Broberg M, Plummer S, Kirk S, et al. Microbiome and infectivity studies reveal complex polyspecies tree disease in acute oak decline. The ISME Journal. 2018;**12**:386-399

[29] Yu Z, Ding H, Shen K, Bu F, Newcombe G, Liu H. Foliar endophytes in trees varying greatly in age. European Journal of Plant Pathology. 2021;**160**:375-384

[30] Pinho D, Barroso C, Froufe H, Brown N, Vanguelova E, Egas C, et al. Linking tree health, rhizosphere physicochemical properties, and microbiome in acute oak decline. Forests. 2020;**11**:1153

[31] York LM, Carminati A, Mooney SJ, Ritz K, Bennett MJ. The holistic rhizosphere: Integrating zones, processes, and semantics in the soil influenced by roots. Journal of Experimental Botany. 2016;**67**:3629-3643

[32] Cantó CF, Simonin M, King K, Moulin L, Bennett MJ, Castrillo G, et al. An extended root phenotype: the rhizosphere, its formation and impacts on plant fitness. The Plant Journal. 2020;**103**:951-964

[33] Dotaniya ML, Meena VD. Rhizosphere effect on nutrient availability in soil and its uptake by plants: A review. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences. 2015;**85**:1-12

[34] Soussi A, Ferjani R, Marasco R, Guesmi A, Cherif H, Rolli E, et al. Plant-associated microbiomes in arid lands: Diversity, ecology and biotechnological potential. Plant and Soil. 2016;**405**:357-370

[35] Rolfe SA, Griffiths J, Ton J. Crying out for help with root exudates: Adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. Current Opinion in Microbiology. 2019;**49**:73-82

[36] Rolli E, Vergani L, Ghitti E, Patania G, Mapelli F, Borin S. 'Cry-for-help' in contaminated soil: A dialogue among plants and soil microbiome to survive in hostile conditions. Environmental Microbiology. 2021;**23**:5690-5703

[37] Yuan J, Zhao J, Wen T, Zhao M, Li R, Goossens P, et al. Root exudates drive the soil-borne legacy of aboveground pathogen infection. Microbiome. 2018;**6**:156

[38] Kavamura VN, Mendes R, Bargaz A, Mauchline TH. Defining the wheat microbiome: Towards microbiome-facilitated crop production. Computational and Structural Biotechnology Journal. 2021;**19**:1200-1213

[39] Compant S, Samad A, Faist H, Sessitsch A. A review on the plant microbiome: Ecology, functions, and emerging trends in microbial application. Journal of Advanced Research. 2019;**19**:29-37

[40] Lajoie G, Maglione R, Kembel SW. Adaptive matching between phyllosphere bacteria and their tree hosts in a neotropical forest. Microbiome. 2020;**8**:1-10

[41] Koskella B. The phyllosphere. Current Biology. 2020;**30**:R1143

[42] Liu H, Brettell LE, Singh B. Linking the phyllosphere microbiome to plant health. Trends in Plant Science. 2020;**25**:841-844

[43] Vorholt JA. Microbial life in the phyllosphere. Nature Reviews. Microbiology. 2012;**10**:828-840

[44] Haas JC, Street NR, Sjödin A, Lee NM, Högberg MN, Näsholm T, et al. Microbial community response to growing season and plant nutrient optimisation in a boreal Norway spruce forest. Soil Biology and Biochemistry. 2018;**125**:197-209

[45] Abbaspour H, Saeidi-Sar S, Afshari H, Abdel-Wahhab MA. Tolerance of mycorrhiza infected Pistachio (*Pistacia vera* L.) seedling to drought stress under glasshouse conditions. Journal of Plant Physiology. 2012;**169**:704-709

[46] Cowan JA, Gehring CA, Ilstedt U, Grady KC. Host identity and neighborhood trees affect belowground microbial communities in a tropical rainforest. Tropical Ecology. 2021;**63**:216-228

[47] Van Horn C, Somera TS, Mazzola M. Comparative analysis of the rhizosphere and endophytic microbiomes

across apple rootstock genotypes in replant orchard soils. Phytobiomes. 2021;**5**:231-243

[48] Khullar S, Reddy MS. Ectomycorrhizal Diversity and Tree Sustainability. In: Satyanarayana T, Das SK, Johri BN, editors. Microbial Diversity in Ecosystem Sustainability and Biotechnological Applications. Singapore: Springer; 2019. pp. 145-166

[49] Sulzbacher MA, Hamann JJ, Fronza D, Jacques RJS, Giachini AJ, Grebenc G, et al. Ectomycorrhizal fungi in pecan orchards and the potential of truffle cultivation in Brazil. Ciência Florestal. 2019;**29**:975-987

[50] Freiberg JA, Sulzbacher MA, Grebenc T, Santana NA, Schardong IS, Mazorri G, et al. Mycorrhization of pecans with European truffles (*Tuber* spp., Tuberaceae) under southern subtropical conditions. Applied Soil Ecology. 2021;**168**:104108

[51] Orozco-Mosqueda MC, Rocha-Granados MC, Glick BR, Santoyo G. Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. Microbiological Research. 2018;**208**:25-31

[52] Olanrewaju OS, Glick BR, Babalola OO. Mechanisms of action of plant growth promoting bacteria. World Journal of Microbiology and Biotechnology. 2017;**33**:197

[53] Compant S, Duffy B, Nowak J, Clément C, Barka EA. Use of plant growth-promoting bacteria for biocontrol of plant diseases: Principles, mechanisms of action, and future prospects. Applied and Environmental Microbiology. 2005;**71**:4951-4959

[54] Cheffi M, Bouket AC, Alenezi FN, Luptakova L, Belka M, Vallat A, et al.

Root endophyte *Bacillus velezensis* OEE1 counteracts oomycete and fungal harmful pathogens and harbours a large repertoire of secreted and volatile metabolites and beneficial functional genes. Microorganisms. 2019;**7**:314

[55] Méndez-BravoA,Cortazar-MurilloEM, Guevara-Avendaño E, Ceballos-Luna O, Rodríguez-Haas B, Kiel-Martínez AL, et al. Plant growth-promoting rhizobacteria associated with avocado display antagonistic activity against *Phytophthora cinnamomi* through volatile emissions. PLoS One. 2018;**13**:e0194665