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# Rhizosphere microbiome assembly, drivers and functions in perennial ligneous plant health

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A R T I C L E   I N F O

A B S T R A C T

Plants shape and interact continuously with their rhizospheric microbiota, which play a key role in plant health and resilience. However, plant-associated microbial community can be shaped by several factors including plant phenotype and cropping system. Thus, understanding the interplay between microbiome assembly during the onset of plant-pathogen interactions and long-lasting resistance traits in ligneous plants remains a major challenge. To date, such attempts were mainly investigated in herbaceous plants, due to their phenotypic characteristics and their short life cycle. However, only few studies have focused on the microbial structure, dynamic and their drivers in perennial ligneous plants. Ligneous plants coevolved in interaction with specific fungal and bacterial communities that differ from those of annual plants. The specificities of such ligneous plants in shaping their own functional microbial communities could be dependent on their high heterozygosis, physiological and molecular status associated to seasonality and their aging processes, root system and above-ground architectures, long-lasting climatic variations, and specific cultural practices. This article provides an overview of the specific characteristics of perennial ligneous plants that are likely to modulate symbiotic interactions in the rhizosphere, thus affecting the plant's fitness and systemic immunity. Plant and microbial traits contributing to the establishment of plant-microbiome interactions and the adaptation of this holobiont are also discussed.

## 1. Perennial ligneous plant microbiome as a key to harness its full potential to promote plant health

The plant microbiota represents a reservoir of extended functions for its host and is recognized as contributing to plant growth and health. The composition of the recruited community depends largely on the initial microbial pool in the plant's surroundings, the soil being its principal reservoir. The plant exerts on these populations a filtering selection through the secretion of root exudates and the production of specific organic matter, which is highly dependent on multiple parameters such as the host's genetics and the microbial population dynamics, biotic and abiotic parameters (Trivedi et al., 2020). Despite these multiple factors, recent studies suggest the existence of core microbiomes, represented by a plant's typical assemblage of microorganisms. For example, the grapevine's rhizospheric core microbiome would be mainly composed of *Proteobacteria*, *Actinobacteria* and *Acidobacteria* (Bettenfeld et al., 2021), resembling to the poplar (Beckers et al., 2017), citrus (Xu et al., 2018; Zhang et al., 2021), oak (Uroz et al., 2010), beech and Norway spruce (Uroz et al., 2016) rhizospheric core microbiome. Moreover, the specific

recruitment of microbes by the plant is influenced by microbial traits involved in plant colonization and by the host selection pressure towards beneficial traits involved in tolerance process to biotic and abiotic stresses (Park et al., 2023). In line with the functional redundancy concept, the cumulative effect of these traits constitutes the functional core of a population and is independent on the taxonomic core, as different members of the community can perform the same functions for the plant (Lemanceau et al., 2017).

The relationship between plants, microbial communities and pathogens is still unclear (Berg et al., 2021; Ginnan et al., 2020; Lee et al., 2020). Understanding the structure and dynamic of microbial communities during the onset of plant-pathogen interaction is fundamental to determining the beneficial microbial composition to improve plant health. To date, such attempts were mainly performed on annual or biannual herbaceous plants, due to their phenotypic characteristics and their short life cycle. However, only a few studies have focused on the microbial compositions, dynamics and their drivers in ligneous perennial plants (Cazorla and Mercado-Blanco, 2016). Factors associated with longevity and aging, the presence of hardwood tissues, root and shoot

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architectures, phenology and seasonality that affect plant physiology should have a considerable impact on interactions with surrounding microbes as a potential biocontrol tool (Fig. 1) (Cazorla and Mercado-Blanco, 2016). The specificities of ligneous and perennial plants raise new problematics and perspectives in the endeavor to untangle the role played by microorganisms in plant health.

While most crops are annuals, such as rice, corn and wheat, perennials account for more than 13 % of cultivated areas worldwide (Migicovsky and Myles, 2017). Recently, a perennial rice variety was generated offering the same yield levels as elite annual varieties while integrating the benefits of sustainable crops (Zhang et al., 2022). As a perennial crop, specific problematics associated to its life cycle may arise, requiring increased attention to the functional role of microbial communities in plant health and longevity.

This article provides an overview of the specific characteristics of perennial ligneous plants that are likely to modulate their microbial communities, structure and dynamic in the rhizosphere, thus affecting plant health. Plant and microbial traits contributing to the establishment of plant-microbiome interactions and the adaptation of this holobiont are also discussed.

## 2. The ontogeny of perennial ligneous plants is accompanied by a temporal succession of rhizosphere microbiota with an enrichment of beneficial populations

Succession of plant associated microbes is a "directional change in the composition, relative abundance and spatial pattern of species comprising communities" (Frankland, 1992). Indeed, the physiological and molecular processes involved in aging are important drivers of microbial variation that could affect the recruitment and enrichment of the root and rhizospheric microbiota over time (Bond, 2000; Wagner et al., 2016). Root structural changes and root-derived exudates associated with plant aging are known to be responsible for microbial diversity and assembly in the rhizosphere (Fig. 2). Furthermore, enrichment of beneficial populations can be associated with increased pathogenic microbes. For instance, in the apple bark, age was shown to influence both pathogenic (*Alternaria, Diaporthe, Diplodia* and *Phom*) and potential beneficial microbes including fungi (*Aureobasidium, Cryptococcus, Filobasidium, Rhodotorula, Sporobolomyces*) and bacteria (*Methylobacterium, Nocardioides* and *Sphingomonas*) (Arrigoni et al., 2020). A comparison of *Eucalyptus* species at different developmental stages highlighted a decrease of the phylum WPS-2, the order of *Shingomonadales*, the *Arthrobacter* and *Sinomonas* genera, while the order GP6 increased in older plants, which may result from a reduction of root exudation and allelopathic effects limiting carbohydrate availability in the rhizosphere (Qu et al., 2020). The predictive functions also suggest a
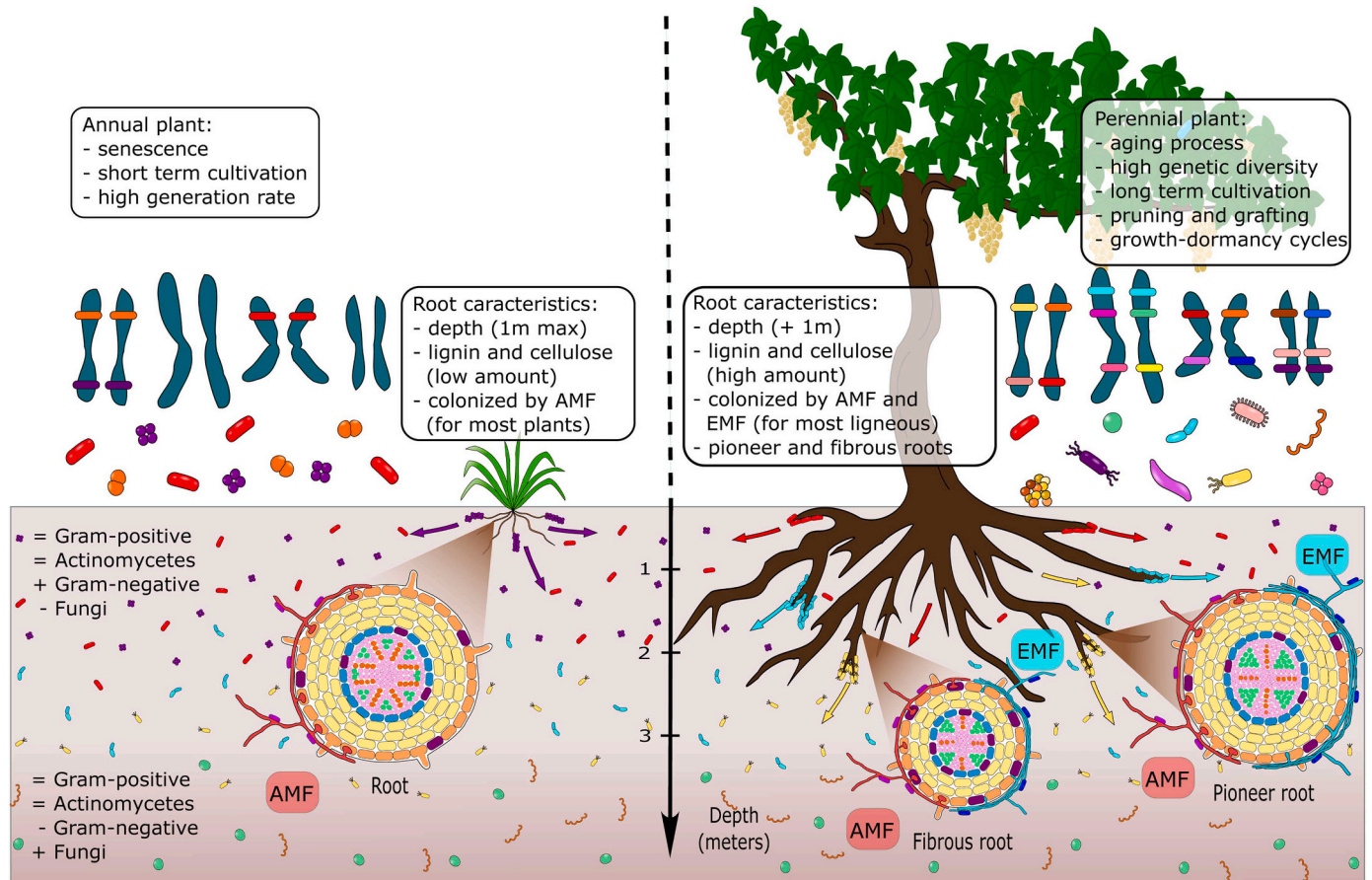


**Fig. 1.** Some characteristics differentiating annual cultivated plants from perennial ligneous at the rhizosphere level. Ligneous plants can reach different microbial populations through root depth and may exhibit specific colonization patterns due to their characteristics including higher genetic diversity or the presence of fibrous and pioneer roots with different constituents, such as defense molecules, lignin, etc. Moreover, their microbiome may also be influenced by cultural practices (pruning, grafting, long-term cultivation, etc.), the growth-dormancy cycles and aging process. These factors may also modulate plant immune responses and are not considered enough in the outcome of plant-microbiome-pathogen relationship, and in the creation of biocontrol products. -, =, +: lower, same or higher amount of microbes following the depth; AMF: arbuscular mycorrhizal fungus; EMF: ectomycorrhizal fungus; arrow: root exudates associated to recruited microbes (shared color).
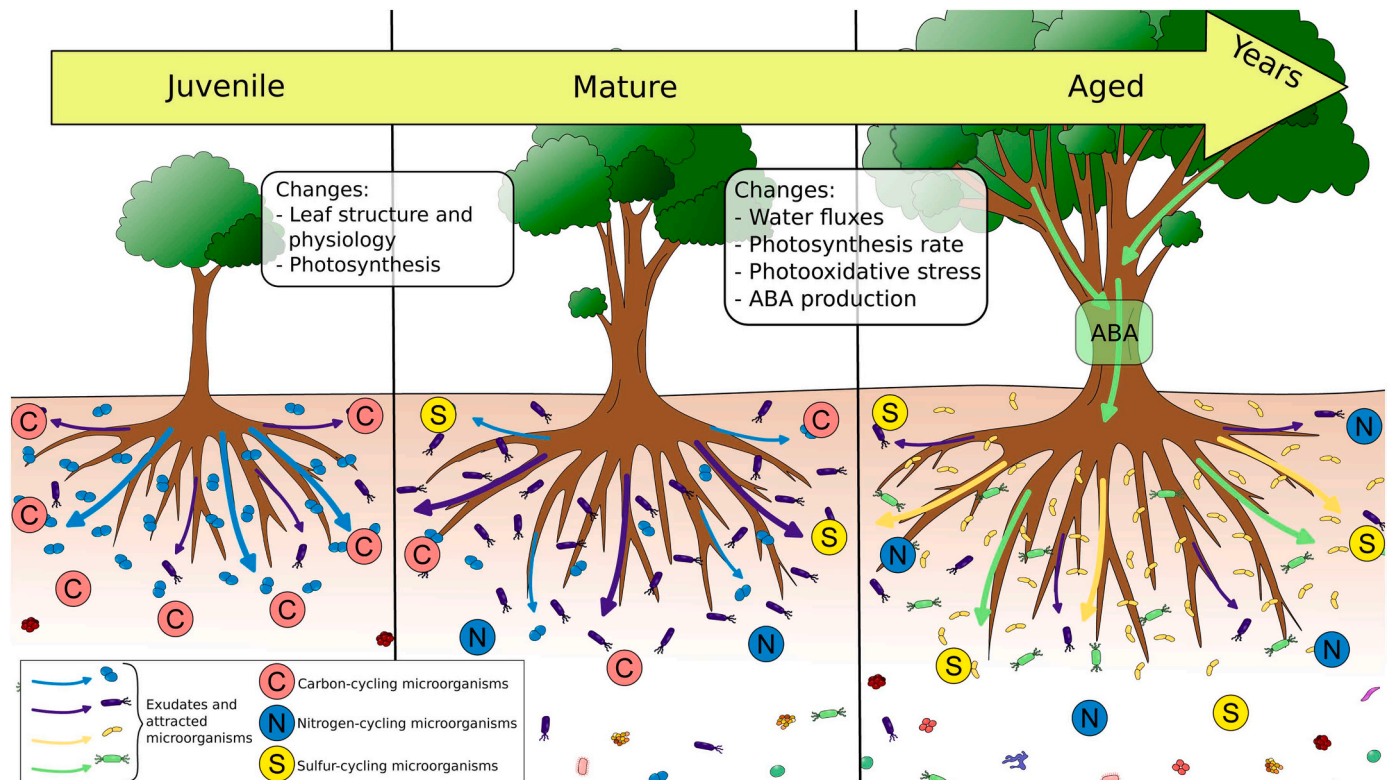
**Fig. 2.** Relationship between aging of perennial plants and the recruitment of microbes in the rhizosphere. Along the plant's growth, the physiological changes may impact the root exudates composition, thereby modifying the microbial populations attracted by the plant through the years. In particular, changes in water fluxes in aged plants have been suggested as inducing ABA production (Munné-Bosch, 2007), which is associated to the root colonization by arbuscular mycorrhizal fungi and can be perceived by specific microbial populations (ex. *Rhodococcus*, *Novosphingobium*…) (Eichmann et al., 2021). Arrows: root exudation. Each color corresponds to a specific kind and amount of exudates. These changes in microbial populations may be related to an evolution from carbon-cycling to nitrogen and sulfur-cycling metabolism (Qu et al., 2020).

metabolic shift within the microbiome during the aging process, transitioning from carbon-utilizing bacteria in younger plants to bacteria involved in nitrogen and sulfur cycling for older plants (Qu et al., 2020). The changes in nutrient acquisition strategy through plant aging, as seen in Korean pine (*Pinus koraiensis*), spruce (*Picea koraiensis*) or smelly fir (*Abies nephrolepis*) may cause this microbial metabolic shift (Ren et al., 2023). For root-associated fungi, the diversity of mycorrhizal fungi is lower in young forest stands than in older stands, as illustrated for arbuscular mycorrhizal fungal (AMF) communities associated with *Artocarpus altilis*, a long-lived perennial breadfruit (Hart et al., 2014), or ectomycorrhizal fungi (EMF) in Douglas-fir forests with fungal diversity and composition stabilizing at 26 and 65 years old, respectively (Twieg et al., 2007). However, young annual plants are shown to be more prone to forming mycorrhizal associations, although it depends on species, and are often used as bait in field studies for monitoring soil diversity (Šmilauer et al., 2021). As they age, woody perennial plants will also modify the soil parameters, such as pH and C/N ratio (Frankland, 1992; Peltoniemi et al., 2004). These modifications will strongly structure the soil microbial and rhizosphere communities, which in turn will impact plant growth and health (plant-soil feedback).

The increased changes in the microbial communities, which could be dependent on the time of conditioning of plant-soil microbe exchange, may impact their functions and effects on plant fitness (Ke et al., 2021). During the plant ontogeny, intrinsic modifications can influence its microbiota. Phytohormones play a key role in the plant aging and in the assembly of plant microbiomes, and both microbes and plants use the same hormones in different functions and adaptive strategies (Khan et al., 2013). Specific phytohormones can be exuded into the rhizosphere and exert fine-tuning selection on plant-interacting microbes in the rhizosphere (Liu et al., 2020). For example, abscisic acid was shown

to be involved in the interaction with AMF and can also be perceived by other members of the rhizosphere and even used as a carbon source by some rhizobacteria like *Rhodococcus* and *Novoshingobium* (Eichmann et al., 2021). Other phytohormones including cytokinins, gibberellic acid, strigolactones and brassinosteroids have been shown to be involved in rhizobia and AMF associations (Carvalhais et al., 2019; Liu et al., 2020; Yu et al., 2018), whereas auxins can be used as a carbon source and triggers metabolic changes in the rhizosphere promoting antimicrobial activity of some members of Streptomycetaceae (Eichmann et al., 2021). Similarly, transcriptomic analyses showed an upregulation of SA pathway-related genes in 1-year-old ginkgo (*Ginkgo biloba*) plants and a downregulation JA pathway-related genes in older ones (Wang et al., 2022). These signaling pathways, which are involved in plant defense regulation at the systemic scale, may also play an important role in the structure, assembly and recruitment of microbial communities (Carvalhais et al., 2015; Lebeis et al., 2015; Eichmann et al., 2021).

Although microbial diversity recruitment seems to be dependent on the plant age (Berlanas et al., 2019), the long-term growth legacy in grapevine plants seems more important than the aging in shaping the rhizospheric microbiota (Manici et al., 2017). The microbiota assembly in perennial plants may result from a selection pressure exerted by the plant depending on its susceptibility to environmental stresses (Kristy et al., 2022). This may be close to the soil-borne legacy hypothesis in annual plants (Bakker et al., 2018). In line with the "cry for help" strategy (Liu et al., 2024), the growth of successive plant generations subjected to the same stress can shape the recruitment of beneficial microorganisms through specific exudates, thereby priming plant for enhanced systemic resistance (Vismans et al., 2022; Yuan et al., 2018). In perennial plants, the microbiome dynamic under a long-lasting stress

period remains to be explored. One example of the prairie grass (*Andropogon gerardii*) grown under arid conditions for ten years showed significant differences in bacterial root communities, without significant change in fungal communities between different ecotypes (Sarkar et al., 2022). It is also known that young vineyards are more susceptible to black foot and Petri diseases, while Esca complex, Botryosphaeria, and Eutypa diebacks usually occur in mature vineyards (Gramaje et al., 2018). Despite a lower microbial diversity and richness in declined grapevines, symptomatic rhizosphere was enriched in beneficial microbes, which could be involved in grapevine protection against trunk diseases (Darriaut et al., 2024). Investigating plant microbiome for a long-lasting stress period could provide clues on the existence of shaped communities that could modulate the plant health and aging process.

## 3. Heterozygosis in perennial ligneous plants may provide a wide range of functions through the microbiota

In animals, it was shown that heterozygosity of the major histocompatibility complex loci, in contrast to the homozygous one, is correlated with positive diversification of the gut microbiome's functionalities and an enhancement of microbial network connectivity (Wadud Khan et al., 2019). It resulted in a functional diversification associated with an improved host health (Wadud Khan et al., 2019). In plants, surrounding microbes are detected by cognate pattern recognition receptors localized at the cell surface. Their exact role in the differentiation of beneficial from pathogenic bacteria is still under investigation in both herbaceous and ligneous plants (Héloir et al., 2019; Huang and Joosten, 2024; Zhang and Kong, 2022). We could hypothesize that plant's heterozygosity could play a critical role in tremendous diversity of plant immune receptors, thus increasing the diversity and functionality of their microbiomes.

Perennial ligneous plants have a longer juvenile period, which has limited their number of generations compared to annuals and the subsequent loss of allelic diversity through directed selection. Single nucleotide polymorphism and microsatellite analyses of grapevine and apple genomes suggest a limited erosion of genetic diversity between cultivated varieties and their wild progenitors (Cornille et al., 2012; Migicovsky and Myles, 2017; Myles et al., 2011). Compared to the annual crops, perennials are mainly heterozygous, although homozygosity and accelerated varietal selection exist in perennial crops. This heterozygosity is maintained through clonal propagation, even if this cultivation method introduces genetic homogeneity at the population scale for cultivated ligneous plants (Gaut et al., 2015). However, these genetically fixed perennial crops are more susceptible to diseases (Myles, 2013). Their heterozygotic genomes might drive higher microbial diversity and functionality of their microbiomes, despite being associated to a higher disease susceptibility in the case of clonal propagated crops. Recently, a correlation between microbial abundance in roots and heritable loci responsible for variations in PAMPs triggered immunity (PTI) was reported in switchgrass (*Panicum virgatum*) (Edwards et al., 2023). Thus, the higher genetic diversity commonly observed in perennial plants may contribute to shaping microbial diversity and presumably activating PTI through multiple signaling pathways.

## 4. Seasonality influences root colonization through plant metabolic change

Herbaceous and ligneous perennial plant are punctuated by seasonal environmental variations that affect their phenology (Friedman, 2020). These cycles induce changes in the metabolic activity of plants over the course of the seasons in response to climatic constrains. Climatic parameters and plant phenology could have a direct impact on the soil microbiome, leading to changes in the rhizospheric sub-populations. The work carried out in two *Populus* spp. from the leaf endosphere, root endosphere and rhizosphere revealed variations across seasons and

years (Argiroff et al., 2024). Together with climatic variations, specific seasonal patterns were observed each year (Argiroff et al., 2024). Similarly, Nakayama and Tateno (2023) reported important seasonal variations in the relative abundance of EMF species in a hardwood forest, with a reduced occupancy in the dormant seasons. In addition, bacterial populations in forests displayed similar abundance before and after winter, with a change in species diversity (Kubiak et al., 2018, 2017). Growth-dormancy cycles are associated with variations in carbon metabolism, affecting carbon availability for rhizospheric microbe during winter (Esperschütz et al., 2009) and symbiotic fungal partners (Nakayama and Tateno, 2023). In the beech rhizosphere, the reduction of photosynthetic activity associated to the dormancy process and subsequent rhizospheric carbon transfer correlates with an increase in microbial cyclopropyl fatty acids (Esperschütz et al., 2009). The enhanced accumulation of these fatty acids, as starvation indicators (Guckert et al., 1986), suggests a functional role of the dormancy-associated reduction in nutrient availability shaping the microbiome.

Mature ligneous plants may have more carbon to allocate as root exudate, which could in turn result in stronger effects on its rhizospheric microbiome during the dormancy process. For instance, a strong increase of belowground flux of photosynthate in boreal pine (*Pinus sylvestris*) forests between June and August was attributed to the end of the growing season (Högberg et al., 2010; Prescott, 2022). This suggests that growth-dormancy cycles could differently impact microbial communities of mature and juvenile plants. It has been reported that microbial community can tolerate changes in carbon allocations while maintaining its structure through modulation of carbon needs (Cesarz et al., 2013; Sommer et al., 2017). This is supported by the presence of intra-annual shifts in the microbiota composition, as shown with the endophytic root populations of two grapevine cultivars (Biget et al., 2023a).

The dormancy shift is often accompanied by a storage of photosynthates in parenchyma or ray cells, as well as in roots (Dominguez and Niittylä, 2022). As some roots are preserved during this process in ligneous plants, the onset of dormancy should have an impact on the rhizospheric, endophytic and epiphytic microbial populations. The chemical changes in root composition before dormancy may induce a tissue spreading of endophytes, as they require a specific chemical environment for their growth and metabolic activities (Compant et al., 2021). *De novo* colonization events could thus result in activation of new plant defense responses at the tissue level (Chuberre et al., 2018). Some microbes could spend winter in perennial roots, as the case of the endophytes in seeds (Cheplick, 2017). Roots can also host various strains, which may originate from different simultaneous or successive colonization events. For example, Olive (*Olea europaea* L.) root hairs with established populations of a *Pseudomonas* strain allows the attachment and penetration by other bacteria from the same genus (Prieto et al., 2011). An established endophytic microbiome would then initiate waves of root colonization, promoting plant immune system and interactions between colonizing microbes (Fig. 3) (Hafiz et al., 2022; Pérez-De-Luque et al., 2017). This is consistent with the fact that AMF, as a part of the endospheric microbiota, were reported to induce reprograming the root primary and secondary metabolite production (Kaur and Suseela, 2020). This could modify the issues of further symbiotic interactions (Kaur and Suseela, 2020). During growth-dormancy states, the occurring colonization events could increasingly support various ecological niches, contributing to the genotype-effect described above. Thus, exploring rhizospheric microbiome before and after dormancy could shed light on the relationships between physiological state and microbial-mediated metabolic change and plant immunity.

## 5. Specific cultural practices can contribute to microbial diversity shaping in perennial plants

The grafting of a scion on a rootstock is a common practice in ligneous crop cultivation for enhancing resistance to soil diseases and
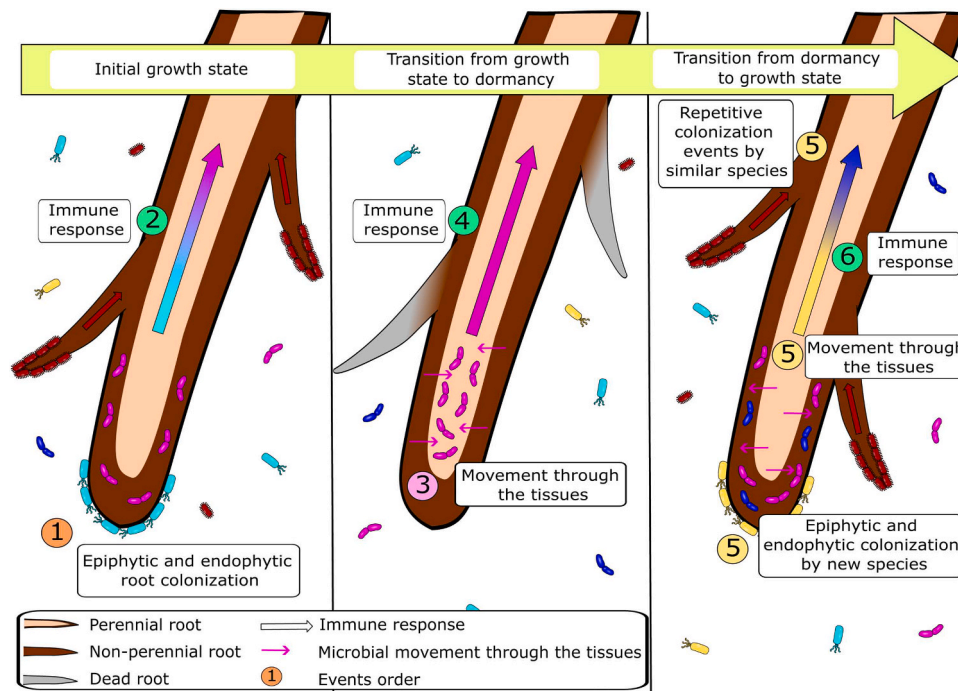
**Fig. 3.** Change in epiphytic and endophytic microbial populations through the growth-dormancy transitions. The chemical changes in root composition during growth and dormancy states may influence the epiphytic and endophytic microbial populations through different steps. Epiphytic and endophytic microbial populations may colonize the perennial and non-perennial roots during the initial growth stage (1), thus promoting plant immune system (2). Following the shift to a dormancy state, root endophytic microbes can move to different tissues (3) (Compant et al., 2021; Dominguez and Niittylä, 2022). This tissue colonization could contribute to the modulation of pant systemic immunity (4) (Chuberre et al., 2018). By the end of the dormancy state, the endophytic microbes may recolonize their initial environment (5). The presence of these established microbes may further facilitate the root colonization by other microbes (5) (Prieto et al., 2011). The appearance of new or older roots may constitute a communication network between the plants and specific populations of their microbiome (5), thus modulating plant systemic immunity (6). Big arrows: plant immune response. Small arrows: microorganisms' movement across the tissues. Each color for the arrows corresponds to specific microorganisms at their origin. Numbers: events order.

improving physiological traits (Tedesco et al., 2022; This et al., 2006; Wang et al., 2017). Grafting often combines compatible scions and rootstocks of different ages, offering the opportunity to explore the mechanisms behind the aging process in perennial plants. Grafting can influence phenotypic traits of grafted plants through various molecular signals exchanged between scion and rootstock (for a review see Wang et al., 2017). The grafting of *Pinus sp.* scions from old donors on young rootstocks impacts branching patterns, leaf morphology and growth period of dormant buds (Mencuccini et al., 2014; Velisevich et al., 2021). As shoot meristems respond to signals at a systemic scale, the scion could also modulate root system architecture and root meristem activity, thereby shaping their microbial communities. The meristematic zone of the root tip is the most active in terms of root exudate production and, as such, plays a key role in the selective process of the rhizomicrobial community (Tian et al., 2020). In addition, epigenomic and transcriptomic analyses showed that grafted plants inherited part of the rootstock's epigenomic characters, resulting in the activation of various genes at systemic level, including photosynthesis-related genes (Perrin et al., 2020). This underlines the important role of grafting process in improving photosynthetic activity, triggering root exudation and shaping microbial communities in the rhizosphere.

In grafted plants, the rootstock can modulate rhizomicrobial composition, while the effect of scion seems to be dependent on the microbial community in the rhizosphere and root compartments (Darriaut et al., 2022; Lailheugue et al., 2024). However, in grapevine, although the rootstock was shown to influence the taxonomy, structure, and network properties of the root bacterial community, their impact on microbial functional traits remains controversial (Marasco et al., 2018; Zuzolo et al., 2023). In cacao (*Theobroma cacao* L.), unlike the rootstock, the scion has shown only slight impact on the rhizomicrobiota (Schmidt et al., 2021). Some of the recruited bacterial taxa by the rootstocks might be related to the plant nutrition status (Schmidt et al., 2021). However, interactive effects of scion and rootstock genotypes resulted in different microbial diversities (ex. α- or β-diversity), suggesting that specific combinations could affect the plant's ability to recruit specific microbial functional diversity (Vink et al., 2021). The cross talks between rootstocks and scions are not well understood yet, but involve activation of phytohormone pathways, epigenetic changes, and small RNA long-distance signaling, processes that would also be involved in shaping and recruitment of microbiota (Habibi et al., 2022). Biget et al. (2023b) used several grafted grapevines to formally evaluate the hologenome concept. The authors showed that both scions and rootstocks are significant drivers of the shaped microbiome from endosphere, especially regarding the β-diversity, the rootstock effect being the stronger.

Pruning of ligneous crop plants may also contribute to shaping rhizosphere microbiota but remains poorly elucidated. If not removed, pruned shoots and leaves become a source for soil nutrients and lead to an accumulation of allelochemicals such as polyphenols, flavonoids and alkaloids, which ultimately lead to changes in soil microbial activity and biogeochemical cycling (Arafat et al., 2020; Oo et al., 2018). In tea (*Camellia sinensis*) plantations, where pruning is a common practice, it seems difficult to replant young plants, as leftover soil chemicals could negatively affect root architecture, root hair development, and apex swelling (Pham et al., 2019). Over the long term, pruning is correlated with a reduction in microbial abundance and richness (Bora et al., 2022). Nevertheless, the microbiota of pruned plants showed a higher proportion of bacteria with beneficial functions for plant growth and survival under stress conditions, like *Pseudomonas, Solibacter, Rhodopseudomonas* and *Nitrobacter* sp. In terms of functions, there was an enrichment in stress-responsive metabolic pathways, especially those related to carbohydrates and amino-acids. The stressful pruning practice

can therefore contribute to the shaping of a microbial community, which can prime plants to cope with subsequent stresses (Bora et al., 2022).

Replanting perennial plants could also have a significant impact on microbial communities in the rhizosphere. In grapevines, short-term replanting increased the abundance of beneficial bacteria and damaging fungi, while long-lasting replanting resulted in a less complex microbiota (Liu et al., 2021). This imbalance could be related to secreted autotoxins by roots into the rhizosphere, since the autotoxin ρ-hydroxybenzoic acid (4-HBA) secreted by grapevine roots can trigger mitigation of beneficial bacteria belonging to *Gemmatimonas*, *Streptomyces*, and *Bacillus* genera and spreading of pathogenic fungi, such as *Fusarium*, *Neocosmospora*, *Gibberella*, and *Fusicolla* (Guo et al., 2015; Liu et al., 2022). These effects could be due to the 4-HBA-enhanced exudation of amino acids and secondary metabolites and reduced amount of organic acids in the rhizosphere (Liu et al., 2022). Moreover, the exudation of phloridzin by apple was positively correlated with the abundance of *Actinomycetes*, *Bacillus subtilis* and *Pythium intermedium*, which are considered as indicators of apple replant disease (Hofmann et al., 2009). However, the rhizosphere of disease-tolerant rootstocks displayed an enrichment in *Burkholderia cepacia* as a beneficial bacteria, which is completely absent from the disease-susceptible rootstock environment (Laurent et al., 2010).

## 6. Root architecture, deepness and composition are key factors of microbial colonization and pathogen control

Recent review (Fleishman et al., 2022) highlighted that 92 % of 377 studies on rhizospheric microbiota did not take into account the functional properties and root architecture. Perennial plants display a more complex root architecture, with functional variation at a same root branching order i.e., pioneer roots and fibrous roots which differ in morphology, lifespan and functions (Polvergiani et al., 2011; Zadworny and Eissenstat, 2011). Pioneer roots are composed of more tracheary elements and hypodermal layers, with less passage cells than fibrous roots (Bagniewska-Zadworna et al., 2012; Zadworny and Eissenstat, 2011). They also enhance moist soil sections and are less prone to the fungal colonization involved in nutrient acquisition (Polverigiani et al., 2011; Zadworny and Eissenstat, 2011). Pioneer roots are also less susceptible to pathogen colonization than fibrous roots. This could be due to the differential microbial colonization and accumulation of antimicrobial compounds, as well as to the expression of plant defense responses, including accumulation of phenolic compounds (Emmett et al., 2014). It has been suggested that the allocation of defense molecules is different in pioneer roots, compared to first order fine-feeder roots, resulting in different outcomes against pathogens (Zadworny and Eissenstat, 2011) (Fig. 4).

The presence of additional hypodermal layers and less passage cells in pioneer roots could make them difficult to be colonized by beneficial or pathogenic microbes (Bagniewska-Zadworna et al., 2012; Emmett et al., 2014; Zadworny and Eissenstat, 2011). Nevertheless, pioneer roots could provide a perennial ecological niche for colonizing microorganisms (Polverigiani et al., 2011; Zadworny and Eissenstat, 2011). Although fibrous roots are more likely to produce higher concentrations of exudates, the attracted bacteria could only have a transient effect due to the short lifespan of the roots. However, endophytic bacteria could enter fibrous roots and then migrate through the conductive tissues towards more perennial parts. As fibrous roots have a shorter life cycle and are generated throughout a plant's lifetime, they could attract similar bacteria at each growth cycle, resulting in a priming state of plants (Conrath et al., 2015). More investigations are still needed to understand
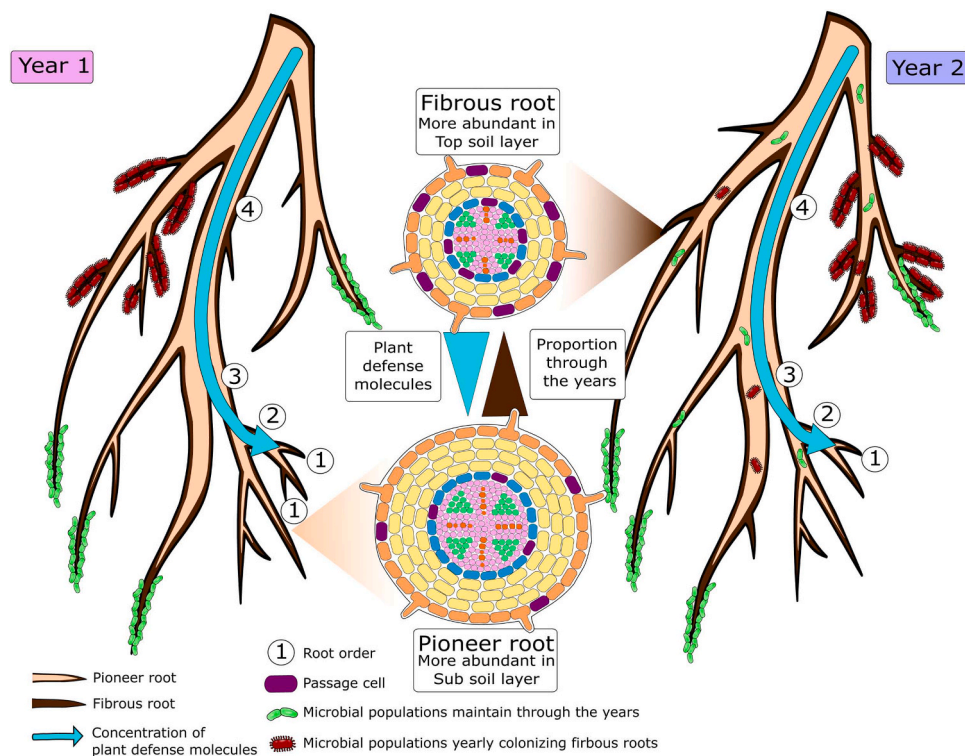


**Fig. 4.** Root characteristics of perennial plants and their potential link with root colonization by microorganisms through the years. Two kinds of roots are retrieved in woody perennial plants: the fibrous roots, more abundant in the topsoil layer, and pioneer roots, more abundant in the subsoil layer. Each root system exhibits specificities that may impact their colonization, such as a gradient of plant defense molecules (ex. phenolic compounds) (blue arrows and blue gradient), more abundant in fibrous roots and in low root order (1−4), or the presence of more passage cells (purple cells) and less tracheary elements and hypodermal layers in fibrous roots (Bagniewska-Zadworna et al., 2012; Zadworny and Eissenstat, 2011). Moreover, pioneer roots are more likely to be preserved through the years, which maintain microbial populations through the years (green microbes). The fibrous roots may be at the origin of repeated contacts with microbes (red microbes) through the years following their growth, thus resulting in the induction of plant defense responses (Polverigiani et al., 2011; Zadworny and Eissenstat, 2011).

the relationships between the root architecture of ligneous plants, their microbiota, and their immune system.

Trees and shrubs have the capacity to extend deeper in the soil than herbaceous plants (Schenk and Jackson, 2002). Microbial communities can therefore vary in size and diversity depending on the soil physico-chemical properties, which vary tremendously across soil layers (Steenwerth et al., 2008). In vineyard, when the rhizospheric soil samples from surface horizons were compared with two-meters depth, there was no significant difference in the relative abundance of Gram-positive bacteria and Actinomycetes, but a decrease in Gram-negative bacteria and an increase in fungal abundance were observed (Steenwerth et al., 2008). These shifts in soil microbial communities could be due to soil resource availability, root distribution and exudate gradient (Tückmantel et al., 2017). The fungal communities in eucalyptus (*Eucalyptus grandis*) roots were dominated by EMF at more than 4 m depth, particularly by *Pisolithus* genus, which represented 90 % of the sequences analyzed by Robin et al., (2019). This ECM genus is characterized by a mycelial structure favoring long-distance soil exploration (Agerer, 2001). The reach of deep soil layers by the roots or ECM fungi provides multiple benefits including nutrient and water uptake (Agerer, 2001). This can also be increased by hydraulic lift, with a water transfer through the roots from deep to topsoil layers (Maeght et al., 2013), thereby inducing change in microbial metabolism (Bian et al., 2022).

The deep rhizospheric microbiota may also influence the communities above through change in pattern of root exudation at the systemic level (Fig. 5). For instance, local colonization of tomato roots triggers a systemically induced root exudation of metabolites (SIREM), including acylsucrose, steroidal glycoalkaloids, lignans, hydroxycinnamic acids, which are accumulated in lateral root tips or root hairs (Korenblum et al., 2020). Glycosylated azelaic acid, known to be involved in systemic acquired resistance (SAR) signaling, was also found in SIREM of



**Fig. 5.** Root colonization waves by specific microbial species may be influenced by deeper microbial populations. The contact of plant with new microorganisms can trigger (1) a systemically induced root exudation of metabolites (SIREM) (Korenblum et al., 2020), then recruit new microorganisms at various depths (2). New colonization waves by beneficial microorganisms may occur (3). -, =, +: lower, same or higher amount of microbes following the depth. Small arrows: exudates; Big arrows: induction of SIREM. Each color corresponds to specific microorganisms and the root exudates.

tomato following a local colonization by *Bacillus* genus (Korenblum et al., 2020). However, this process has not been described so far in ligneous plants.

## 7. Root cell wall constituents are involved in microbial colonization and persistence

Root colonization by the microbiome is a critical step in establishing molecular dialogue considered as a key determinant of plant health and resilience. Due to their numerous traits, plant roots are able to selectively shape the microbiome in the rhizosphere, rhizoplane and endosphere (Edwards et al., 2015). This could have considerable impact on microbial colonization and function. Root colonization is influenced not only by their exudated chemical profile, but also by root cell wall composition (Beckers et al., 2016; Zhou et al., 2022). It has been reported that larger roots have an increased cellulose content and less lignin in Chinese pine (*Pinus tabulaeformis*), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) and European beech (*Fagus sylvatica* L.) (Thomas et al., 2014; Zhang et al., 2014).

The root's chemical composition is also dependent on the root order. *Quercus alba* and *Quercus rubra* exhibit an overall lower lignin content in the distal roots of both first and second order (Suseela et al., 2020). Still, distal roots have a higher content of guaiacyl lignin and bound phenolics which increase the intertwining of the lignocellulosic matrix, and thus ensure greater tissue integrity (Suseela et al., 2020). In peach tree (*Prunus persica* L.), fine roots, compared to medium and large ones, harbor a higher microbial diversity and a higher abundance of beneficial taxa (*Bradyrhizobium*, *Pseudomonas*, *Streptomyces*, *Burkholderia* and *Sphingomonas*), involved in soil disease suppressiveness, plant growth, nutrient fixation, solubilization and cycling (Pervaiz et al., 2020). Similar patterns have been observed with AMF and EMF associated trees by comparing five root orders (King et al., 2021). Thus, the colonization efficiency of ligneous plants could be primarily directed by the capacity of some microbes to perceive and degrade the root components and to cross their physical barriers (Debois et al., 2015; Hoff et al., 2021; Wu et al., 2015). For instance, *Bacillus velezensis* is sensing the host pectic homogalacturonans through two conserved pectinolytic enzymes, which contribute to the production of biofilm and surfactant metabolites needed to the bacterium establishment and its persistence in the roots (Beauregard et al., 2013; Boubsi et al., 2023; Wu et al., 2015). The colonization efficiency could be in favor of microorganisms with functional traits involved in the degradation of cellulose and lignocellulose in first and second root order, and of lignin in higher root orders (Suseela et al., 2020). It has also been reported that a strong colonization of *Quercus alba* fine roots by EMF under water deficit stress is associated with a decrease in ellagitannin content, and an increase of fiber-bound condensed tannins in fine root orders (Suseela et al., 2020). As ellagitannins have antimicrobial properties, their decrease could be related to an adaptive response to promote symbiotic associations.

## 8. Mycorrhizal fungi and microbial interactions in ligneous plants

Ligneous plants coevolved in interaction with specific fungal and bacterial communities that differ from those of annual plants (Brundrett, 2002; Hoeksema et al., 2018). AMF and ECM are the most common and widespread symbionts found in the rhizosphere of various ligneous plants, including wild and cultivated grapevines (Kocsis and Szałanski, 2011; Radić et al., 2018, 2021; Trouvelot et al., 2015). However, ericoid mycorrhizal fungi (ErMF) are other endosymbionts restricted to Ericaceae (Vohník et al., 2013). Besides their role in plant nutrition and plant health, EMF could provide a wider range of benefits directly, as demonstrated for AMF or through their interaction with microbial community associated with the host plant (Dreischhoff et al., 2020; Terhonen et al., 2019). It has been demonstrated that AMF inoculation resulted in a shift in the root bacterial and fungal communities
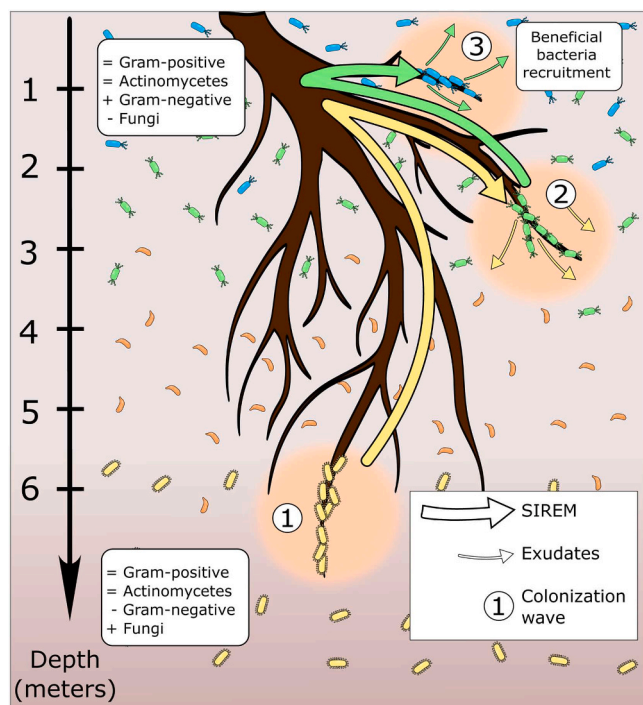
(Solís-Domínguez et al., 2011). Some bacterial genera are more associated with AMF-colonizing roots, while others are more frequent in the roots colonized by EMF. For example, the bacterial genera *Flavisolibacter* and *Phenylobacterium* are more commonly found in roots colonized by EMF, whereas *Rudrobacter* and *Gemmata* were more abundant in plants colonized by AMF (Toju et al., 2019). However, in non-mycorrhized plants *Ferrimicrobium*, *Mycobacterium* and *Nocardioides* were more abundant (Toju et al., 2019). A comparison of the bacteriome of roots and mycosphere of *Pinus sylvestris* and three ericoids revealed that the ErMF colonization is also associated to a different microbiome in the plants surrounding soil (Timonen et al., 2017). Moreover, their relative abundance increases with plant's age, as shown in rabbiteye blueberries (*Vaccinium ashei* Reade) (Che et al., 2022). Although this phenomenon can be partially explained by the influence of a mycorrhizal colonization, it also seems to be linked to specific interactions between the microbiota and mycorrhizal fungi (Liu et al., 2018; Scheublin et al., 2010). Some bacteria are able to colonize hyphae and feed on fungal-derived nutrients (Toju et al., 2019). Other bacteria are considered as mycorrhiza helpers, facilitating plant mycorrhization (Deveau and Labbé, 2016). The association of mycorrhiza with beneficial bacteria is frequently observed in AMF colonizing herbaceous plants, with a transport of the functional bacteria along the surface of their extraradical hyphae (Jiang et al., 2021). EMF could be also involved in the root recruitment of long distant beneficial bacteria through transfer of plant-derived carbon (Gorka et al., 2019) (Fig. 6). However, the soil of some AMF-associated trees is likely colonized by pathogenic microbes, which are not completely counteracted by the AMF (Kadowaki, 2024). Thus, the symbiotic AMF-tree associations are tending towards negative plant-soil feedback, while the EMF-trees are tending towards a positive one (Kadowaki, 2024).

EMF are able to build a network of intruding hyphae in the apoplast of the root cortex layers, known as Hartig net. The resulting root cracks could be used by bacteria to enter and colonize roots (Nurmiaho-Lassila et al., 2011). In addition, EMF form a dense mantle at the root surface that provides physical protection against root pathogens (Branzanti et al., 1999; Marx, 1972; Ross, 1972). The mantle also provides shelter for a number of bacteria that stimulate mycelial growth (Garbaye and Bowen, 1989). Mantle formation by EMF, as opposed to AMF, can further influence ligneous plant diversity in forests. The presence of EMF associations results in less species diversity, which could be due to an increased seedling survival promoting the spread of a dominant species (Bennett et al., 2017). Similarly, EMF dominated stands were exhibiting less prokaryotic diversity, as well as saprophytic and pathogenic fungi, compared to combined EMF-AMF stands. Moreover, the fungal communities were more homogeneous in this last condition (Edwards et al., 2024).

## 9. Concluding remarks

Microbial assembly in the rhizosphere of annual and ligneous plants is controlled by various intrinsic and environmental drivers. In this review we highlighted the specificities of ligneous plants in shaping their microbiome, including their aging processes, physiological and molecular status associated to their seasonality and their high heterozygosis, root architecture and deepness, root components and colonization process, complex microbial interactions in the rhizosphere, and cultural practices. All or part of these drivers would have a considerable impact in improving plant growth and health directly or indirectly through the recruitment and shaping functional microbiome. Furthermore, perennial plants can harbor certain populations of microorganisms exhibiting specific functions necessary to maintain the structure and role of the whole rhizomicrobiome. Furthermore, the mechanisms associated with microbial signal transduction and plant physiological state in a holobiont context remain to be elucidated. Thus, characterizing microbial assemblages in the rhizosphere to predict plant health is a fundamental issue for anticipating the outcomes of plant-microbiome interactions. To this end, research efforts should be devoted to the microbiome evolution through the years and the plants development stages by increasing sampling size. This would provide an insight into the mechanisms of the ligneous plant-microbe interactions, as a holobiont, by including deeper bacterial and fungal populations. Further investigation would also involve extended sampling site to include the mycosphere of mycorrhizal fungi. More emphasis should be placed on understanding the effects the terroir and sustainable practices (e.g., intercropping, cover crops, microbiome inoculation) on the outcome of plant-microbiome relationships, plant health and resilience to climatic events.

### CRediT authorship contribution statement

**Aziz Aziz:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Marc Buée:** Writing – review & editing, Formal analysis. **Adrian Wallner:** Writing – review & editing, Investigation, Formal analysis, Conceptualization. **Morgane Duret:** Writing – original draft, Investigation, Formal analysis, Conceptualization.

### Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.
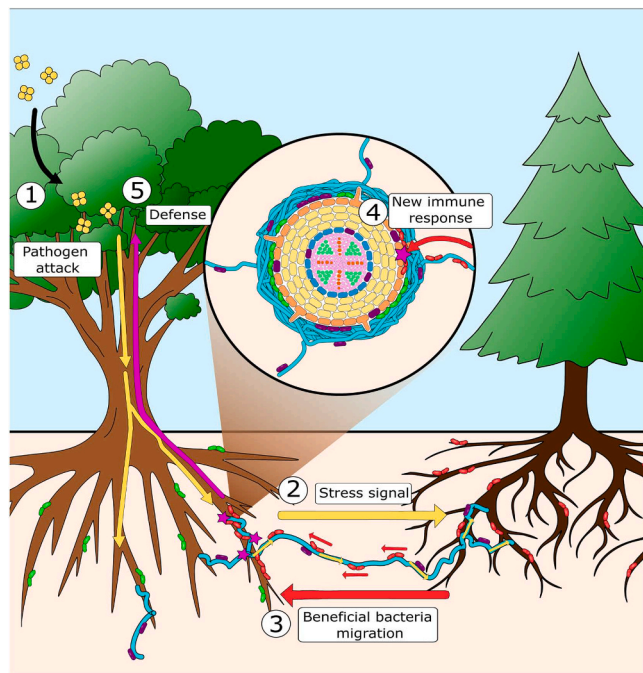


**Fig. 6.** Hypothetical changes in microbial populations during pathogen attack in mycorrhized perennial woody plants. Following pathogen attack (1; yellow dots), plant immune response (yellow arrows) is systemically expressed, and systemic signals could be transduced to neighboring plants through EMF (2) (Song et al., 2015). Some microbes are able to move along fungal hyphae (Jiang et al., 2021), and contribute to microbial transfer between the plants (3; red microbes). These microbes could then colonize roots of the attacked plants (pink stars). The enhanced immune response (4; pink arrows) could help the plant to defend itself against pathogen (5). The Hartig net can also contribute to the plant protection against soil pathogens (green microbes), while EMF themselves may provide specific beneficial microbes (purple microbes).

## Data availability

No data was used for the research described in the article.

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