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A Mycological Reappraisal of the Phylloplane Microbiome

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ABSTRACT:

The phylloplane is a highly varied, ecologically active microbial surface that hosts various fungal communities that can determine plant health, physiology, and ecosystem functionality. Such epiphytic fungi are both resident taxa that can potentially go through their life cycle on the leaf surface and transient species that come with environmental vectors. The heterogeneous microhabitat of the leaf that contains stomatal grooves, epidermal folds, cuticular chemistry, and nutritional hotspots created by the exudate creates selective niches that promote fungal assembly and functional differentiation. Phylloplane fungi enhance the host vitality by several mechanisms, such as nutrient absorption, hormone production, phytopathogen resistance, and systemic resistance. Some of these epiphytic fungi, such as *Trichoderma*, *Aureobasidium,* and *Pseudozyma,* are good bio-controlling agents since they are resource competitors, secrete antimicrobial chemicals, or alter the plant immunological pathways. Their ecological activities involve the control of senescence, leaf-surface interaction, decomposing processes, and influencing the nutrient cycle. The current review is a summary of the existing knowledge on phylloplane fungal diversity, colonization, ecological associations, and functional importance, through which we aim to develop the findings that will add to our knowledge of leaf-associated microbiomes.

1. Introduction

Leaves are colonized by a variety of microbes from the moment they are formed and continue to support microbial communities throughout their lives. The term phyllosphere refers to the portion of a plant that is above ground and comprises stems, buds, leaves, and flowers. F.T. Last, a plant pathologist, was the first to use the term "phyllosphere" in 1955. Among its components, the phylloplane, or the leaf surface, represents the most significant habitat. The leaf area provides a perfect place for hostile microorganisms to flourish and regulate their lives. Although bacteria are thought to be the most prevalent microbes in the phyllosphere, other microorganisms, such as yeasts, filamentous fungi, and archaea, also inhabit this environment. Fungal epiphytes settle on the plant surface and form a variety of relations with the host they associate with. According to Xu et al., (2020), these relations might be mutualistic, commensal, and pathogenic. These fungi depend on the sugars secreted by the surface of the leaf, honeydew, and the waste of fauna on leaves. The phylloplane is occupied more by yeast and sporulating species than by the filamentous fungi, which are usually the transient occupants. The composition and diversity of phylloplane microbiota are massively dependent on biotic and abiotic factors, including geographical location (Chen et al., 2020), plant species (Wellner et al., 2011), disease severity (Luo et al., 2019, pesticide applications (Chen X. et al., 2021), growth season (Ding and Melchner, 2016), and agricultural management (Karlsson et al., 2017). Surfaces of leaves offer the most favorable conditions to microbiota compared to all other tissues of plants since the nutrition, moisture, pH, and temperature requirements needed by microbiota to survive are met by the leaf exudates (Shukla & Sharma., 2016). The variability of the plant-associated microbes is not only dependent on environmental and developmental factors but also on host identity and selection pressure. Phyllosphere-associated fungi have the potential to influence plant growth, development, ecophysiological activities, and ecosystem processes. They, therefore, have a great impact on the productivity and health of plants (Kirichuk & Pivkin, 2015). Phylloplane fungi are antagonistic to pathogenic fungi and can be developed as biocontrol agents through the production of toxins. In case of colonization, microbes, in most cases, release antimicrobial phenolic compounds and can be used as bio-control agents by inhibiting the growth of microflora. Adult leaves are normally higher producers of these metabolites as compared to their younger ones, and cause microbial colonization to be extremely disproportional. There is a need to unravel the richness, ecology, and functionality of nonpathogenic fungi, which are linked to foliicolous fungalists; thus, it is only natural to utilize the benefits that could be accrued as a result of their presence to enhance the well-being of plants, productivity, and sustainability of the ecosystem. Finally, it is important to say that phytopathogens also enter plants through phylloplane, thus bypassing the plant defense mechanisms and colonizing plants, displacing native microbial communities (Bringel & Couee., 2015). The relationship between abiotic factors and microbial entities affects the ecology of the phyllosphere, thus making the study of such complex microbial communities a necessity. Although the phylloplane is a critical microbial habitat, it is still poorly researched when compared to the rhizosphere. Deep investigation in this field can help us discover unexplored ecological functions and biocontrol mechanisms in the standard rhizosphere research. With this in mind, the current review corresponds to diversity, fungi colonization, and the development of our paradigms on leaf microbial populations and their value in microbiology.

2. Leaf Surface Microhabitat

The leaf surface structure is complex and comprises epidermal elevations, stomata, hydathodes, grooves, and glandular trichomes. These microstructures, as well as the waxy cuticle, determine the permeability, wettability, and the ability of the surface to sustain microbial life. The cuticle plays a vital regulatory role in the aerial regions of the plant, as it is the primary site of interaction between plants and fungi. Most successful colonization achieved by fungal epiphytes requires the capacity of the fungus to adhere to the cuticular layer, the thickness of which, and its content, depend on the plant species, and so affect the fungal settlement. The cuticle is a layer of cross-linked polymer having exceptional mechanical strength; its modulus of elasticity has been shown to exceed 200 MPa, being 20 times stiffer than the normal rubber of a car tire. Leaves capture the fungal spores through their trichomes and waxy surfaces. Once an appropriate microhabitat is located, colonization takes place. The microtopography, nutritional distribution, and physical traits of the leaf surface are highly heterogeneous, resulting in a mosaic of possible habitats that could be inhabited. Nutrients, particularly sugar and water, would accumulate within epidermal grooves. Carbon is usually, in the form of simple sugar, the most limiting factor for the growth of epiphytes, although not all soluble sugars are readily available to the microbes (Das et al., 2022; Fones & Gurr., 2017). The radiation and wind also modify conditions on the leaf surface. The exposure to wind leads to the closure of stomata, reducing the moisture on the leaf, limiting nutrient transfer, and influencing microbial colonization. The contrasting microenvironment of upper and lower phylloplanes affects the relationships among epiphytic microorganisms inhabiting plant surfaces either by providing routes of penetration within the plant endosphere or by regulating access to nutrition coming from tissues of leaves by offering varying levels of protection from incoming sunlight (Bringel & Couée., 2015). Apart from that, anatomical differences between adaxial and abaxial leaf surfaces affect microbial dispersal. Abaxial surface stomatal grooves offer a more protected environment for microorganisms against desiccation or chemical perturbations (Yi et al., 2022; Doan et al., 2020). The composition of fungal communities varies due to the different ecological niches created by structural and chemical variations in leaf surface topography, which vary significantly between plant taxa. Selective filters, such as host traits of leaf chemistry, exudate secretion, and surface structure, predetermine which fungal taxa can successfully colonize. Such host-driven niches are further reinforced by mutualistic interactions between plants and microbes for efficient resource niche differentiation (Guo et al., 2024). Consequently, distinct fungal assemblages are commonly found to associate with different plant species, but the epiphytic community is usually more diverse and abundant compared to the endophytic ones (Gong & Xin, 2021).

3. Diversity of Phylloplane Fungi

The phyllosphere represents a microbially rich ecosystem on Earth with both endophytes residing (inside the plant tissues) and epiphytes (on the surface of plant tissue), and influences the plant through negative and positive interactions (Leveau., 2019). It is difficult to differentiate between the above two because they are quite close to each other. The phylloplane fungi are divided into two broad groups: resident and core assemblages. Fungi that can survive and complete their life cycle on healthy leaves are known as resident fungi. On the other hand, core fungi momentarily reside on the leaf surface but are unable to thrive, making their presence fleeting. Earlier studies on Arabidopsis foliar structures showed that the endophytic populations are limited to 10^2–10^3 colony-forming units (CFU)cm^2, but the epiphytic microbial load is 100 times more (Sohrabi et al., 2023). The resident communities exhibit physiological features such as production of extracellular polysaccharides and pigmentations that enable them to survive in a wide range of ecological niches (Kemler et al., 2017), frequently dominated by genera like *Alternaria* and *Cladosporium*, and their diversity tends to rise with leaf age because older leaves offer more established and resource-rich homes (Chanda et al., 2022). Transient fungi, on the other hand, are governed by abiotic and biotic variables, and their abundance is varied by humidity, growth, death, emigration, and immigration (Kemler et al., 2017). These communities even fight with core communities and pathogenic taxa for resources (Zugaib et al., 2022; Mir et al., 2022). While transient taxa enhance leaf microenvironmental change and adaptation, core communities maintain resilient and consistent plant-microbe interactions (Goswami et al., 2021). The phylogenetic group Ascomycota is the most common, which inhabit the surfaces of leaves and contribute approximately 79% of all fungal diversity, followed by Basidiomycota (approximately 11%), Chytridiomycota (approximately 5%) (Kembel & Mueller., 2014). Gomes et al., (2018) came up with the conclusion that fungi that conquered the epiphytic community are mainly the species having melanized spores and hyphae mainly belonging to the families Pleosporaceae (*Alternaria* spp., *Ulocladium* spp.), Davisiellaceae (*Cladosporium*), and Pathyrellaceae (*Coprinus spp*.). It is speculated that melanin protects against desiccation and UV radiation. Genera such as *Alternaria*, *Cladosporium*, and *Penicillium* are commonly found in a wide variety of plant genera, a fact that implies their functional significance in the phyllosphere and their wide ecological adaptability (Kembel and Mueller, 2014). Exogenous factors such as traffic pollution may alter the diversity and functional activity of phylloplane fungi, the ecological role and structure of the community. In order to correlate the activity of the aboveground microbes with broader processes in the ecosystem, Basidiomycota serve in the processing of nitrogen and leaf litter, whereas Ascomycota members typically participate in nutrient cycling (Liu et al., 2024). Chytridiomycota have an ecological significance due to their influence on the dynamics of the microbial population of leaf surfaces in general and due to their relatively low prevalence. Host phylogeny is a strong determinant of the fungal richness: in general, pathogenic fungi have narrow host selection requirements, whereas mycorrhizal or mutualistic fungi exhibit broader associations (Wang et al., 2019). Nevertheless, a large number of species are more generalists and are able to succeed under a variety of conditions, especially in tropical and subtropical settings, where microclimate and leaf exudates are the determining factors of success (Chanda et al., 2022). Taken together, these imply the regulation of ecological versatility and specialization in the phylloplane fungi. Their taxonomic and functional diversity underpins, beyond merely reflecting adaptation to diverse leaf microhabitats, their contribution to plant health and nutrient cycling.

4. Factors affecting microbial colonization

Phylloplane mycoflora does not maintain a consistent composition throughout the year because its growth and development are impaired by several factors, such as humidity, temperature, pH, wind, rainfall, UV radiation, and daylight hours. Community assembly is significantly driven by stochastic forces, including erratic timing, sequence of microbial arrival, and variable exposure to immigrant sources. Leaves from the same plant or from different individuals of the same species at the same site can support strikingly different fungal communities. Researchers observed a significant decrease in mycoflora in rainy months, probably due to the leaching of nutrients from leaf surfaces (Tanti et al., 2012). Several phyllosphere residents vary with seasonally prevailing conditions and leaf age since it may favour propagule generation. The epiphytic fungi have to invade the new leaves shortly after they emerge, when the phyllospheric taxon richness may be minimal at that time. High humidity encouraged the germination of fungal spores and growth of mycelium (Bogdanova et al., 2019). The local leaf humidity may change according to the climatic conditions of the canopy, including increased wind, and gas exchange may affect leaf surface fungi. It is essential to have water on the leaf surface for the growth, survival, and activities of phyllospheric microorganisms. When water evaporates from the leaf surface, the microbial population goes down, which makes them release osmoprotectants (Scott et al., 2017) and biofilms (Doan et al., 2020) to avoid desiccation. Seasonality influences bacterial communities more than fungal ones, but it has less effect on the formation of microbial communities than host species identity (Li et al., 2022). The most important characteristic is the content of calcium in leaves, which significantly correlates negatively with bacterial populations. This is probably because calcium helps to build cell walls and prevents bacteria from penetrating (Kembel et al., 2014). According to some reports, the genetic composition of plants influences keystone microbial groups, which then transmit these impacts to the rest of the microbial community by altering interactions between microbes and so altering the overall performance of the plant (Gupta et al., 2021).

5. Entry Points of Phylloplane Fungal Assemblage

Microorganisms can colonize plant leaves horizontally from the air, soil, insects, and vertically by seeds or pollen (Rastogi et al., 2013). The seed tissue and the germination environment are the first possible sources (Vacher et al., 2016). Seed-borne microbes are important for early plant growth and present chances to foster long-term host-microbe co-evolution. The soil is the primary source of the plant microbiome. Most fungi use a brute force approach to physically breach the plant's mechanical barriers by generating tremendous invasive pressures and enzymatically degrading the constituent parts of the barrier (Ryder et al., 2025). Research on *Arabidopsis thaliana* illustrates that the microbial communities can migrate from soil to phyllosphere, underlining the dynamic connectivity between above and below compartments (Ma et al., 2025). Although the continuous influx of airborne propagules, only a few microorganisms can survive, proliferate, and become the "true" permanent occupants of the phyllosphere due to its extreme environmental conditions. The preformed biochemicals on the leaf surface must be tolerated by the spores for phylloplane germination to be successful. While most airborne spores are transient and may even serve as nutrients for other leaf-associated organisms. Microorganisms attach to the leaf surfaces to avoid removal by environmental forces. Environmental variability is intimately related to persistence strategies. For instance, phylloplane fungal community networks become more interconnected under drought, indicating that environmental restrictions improve community cooperation and resilience. The selective forces affecting endophytic populations are very different from those affecting epiphytic fungi. Although phylloplane offers limited nutrients, a large number of microorganisms persist by exploiting microscale nutrient hotspots. Accidental sources of exogenous nutrients include pollen, honeydew, air pollution, and microbiological detritus. In rare cases, mechanical injuries caused by frost damage or insect feeding may spill plant sap, supporting microbial proliferation. Even strong plants, however, passively emit trace amounts of metabolites, such as organic acids, amino acids, and sugars, onto their leaf surfaces (Leveau & Lindow, 2001). In addition to supporting microbial growth, these exudates mediate interactions that affect the persistence and stability of communities across the phyllosphere ecosystem.

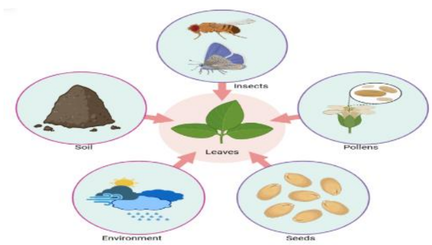

Figure1. Main Sources of phylloplane mycoflora. The sources are insects, pollens, seeds, water, soil, and air.

Certain fungi make use of naturally occurring fissures or openings in plant surfaces, such as stomata on leaves. Density of stomata and pH of the leaf surface are two significant variables affecting the makeup of microbial communities (Smets et al., 2023). Compared to the upper leaf surfaces, the undersides of the leaves (lower

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leaf surfaces) contained larger abundances of core community members but lower microbial richness (Legein et al., 2020). Phyllosphere microbial diversity is determined by host plant genetics and the availability of essential food supplies such as leaf exudates and nectar, although it is unclear that these resources are specifically designed to promote beneficial microbes (Koskella, 2020). Environmental factors such as temporal dynamics and site conditions also strongly influence microbial composition.

6. Impact on Host Plant Vitality

Plant diseases were the main focus of early research on phyllosphere microbes, but in-depth studies have shown that many of them live harmlessly on their host plant. They do release certain advantageous compounds that may aid in the promotion of plant development, resistance to pathogenic microbes, elimination of hazardous pollutants, and synthesis of secondary metabolites (Kumar et al., 2017; Sivakumar et al., 2020). Many of these fungi produce plant hormones (Ritpitakphong et al., 2016) or chemicals similar to hormones in mutualistic relationships with their host plants, thus contributing to growth and stress tolerance, improving plant health, and allowing greater stability of the environment (Kemler et al., 2017; Mir et al., 2022; Goswami et al., 2021). Mitra et al., (2019) isolated *Aspergillus niger* and *Fusarium oxysporum* from the phylloplane of tomato and barley, respectively. They found that the presence of these fungi increased the activity of carbonic anhydrase and Rubisco in the host plants, suggesting that microbial metabolites could mitigate the detrimental effects of pathogens on photosynthesis. They release antimicrobial compounds that can either directly harm pathogens or induce systemic acquired resistance (SAR) in plant cells, thereby contributing to plant defense mechanisms (Goswami et al., 2021). Phylloplane yeast, such as *Aureobasidium pullulans*, defends the same environment from UV-induced oxidative stress by producing extracellular polysaccharides as well as melanin (Liu et al., 2021). Jasmonic acid and salicylic acids are key signaling molecules that mediate the expression of many resistance genes, including PR genes and PR proteins (pathogenesis-related proteins) designed to fight infection, present in huge amounts by leaf of *Ipomoea cairica* (Convolvulaceae) of innocuous isolates of *Fusarium oxysporium* and *F. fujikuoroi* (Xu et al., 2020). These communities can either positively or negatively affect plants by conditioning metabolic processes like leaf senescence, stomatal regulation, and stress tolerance (Pajares-Murgó et al., 2025). *Diaporthe amygdali*, also known as *Fusicoccum amygdali*, generates fusicoccin, a terpenoid that causes the host plant's stomata to open permanently due to increased potassium inflow (Kembler., 2017). According to information produced by genomic, transcriptomic, proteomic, and metabolomic methods, *Trichoderma spp*. is thought to be the most thoroughly researched fungal biological agent (Chaibub et al., 2020). According to (Buxdorf et al., 2013), *Pseudozyma aphidis*, an epiphytic fungus, exhibits substantial biocontrol capability against *Botrytis cinerea*, thereby mitigating the severity of the disease. It works by inducing plant defenses as well as by showing direct antagonism to them. In addition to activating plant defense genes like PATHOGENESIS-RELATED1 (PR1) and PLANT DEFENSIN1.2 (PDF1.2), *P. aphidis* secretes antifungal compounds that inhibit a variety of phytopathogens. Even in *Arabidopsis* mutants lacking in salicylic acid (SA) or jasmonic acid (JA) signaling, it remarkably develops resistance. This suggests that other, hormone-independent mechanisms are involved. Additionally, the fungus strengthens plant defenses, improving the reaction to disease assault. Plants are protected by phylloplane microbes in two ways: directly by generating antimicrobial chemicals, or indirectly by inducing systemic acquired resistance (SAR) or induced systemic resistance (ISR). SAR is activated throughout the plant following exposure to elicitors from virulent, avirulent, or non-pathogenic microbes or synthetic chemical inducers. In contrast, ISR is typically triggered by non-pathogenic microorganisms and functions by enhancing the plant’s chemical and physical defenses, rather than directly targeting the invading pathogen. Prior inoculation with non-pathogenic microbes can induce resistance in wheat by priming the plant’s defense responses, thereby reducing the severity of subsequent pathogenic infections (Langridge, 2017). Abdelrahman et al. (2016) showed that applying *Trichoderma longibrachiatum* to onion plants increased their resistance to *Fusarium oxysporum* infection and oxidative damage by causing the buildup of metabolites linked to responses to both biotic and abiotic stimuli.

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Superoxide dismutase, peroxidase, and catalase activity all climbed in treated plants, whereas H_2O_2 and superoxide radicals in the leaves declined. Ritpitakphong et al. (2016) studied *Arabidopsis* cuticle mutants bdg (BODYGUARD) and lacs2.3 (LONG CHAIN FATTY ACID SYNTHASE 2), both initially resistant to *Botrytis cinerea*. In sterile conditions, bdg became susceptible to *Botrytis cinerea*, while lacs2.3 retained resistance when infected with *Botrytis cinerea,* but resistance was restored in bdg by its phyllosphere wash. The diurnal cycle and atmospheric exposure affect microbial epiphytes, which are impacted both directly by sunlight and indirectly by plant metabolism. These microbes, which are sometimes called endophytes, can enter the apoplast and set off a variety of plant defense mechanisms. Phyllosphere microorganisms are the leaders of the decomposition process and start the recycling of nutrients on living, recently died and senescent leaves (Gulati et al., 2022).

7. Inter-Fungal and Cross-Kingdom Communication

The leaf epidermis is not only the first physical barrier of plants, but also a site where organisms can be perceived, and plant defense reactions can be triggered. Quorum sensing (QS) is the most extensively studied method of cell-cell communication that microbes have evolved to confer benefits to their community in the environment or during infections. Farnesol-mediated control in *Candida albicans* is an example of how QS was discovered in fungi, proving its evolutionary and functional relevance beyond bacteria (Padder et al., 2018). Quorum sensing in fungi enables cell-density-dependent communication that regulates growth, morphology, and biofilm formation. Other QS molecules, such as tyrosol, phenylethanol, and tryptophol, further illustrate that QS is a common feature amongst fungal species (Albuquerque & Casadevall, 2012). Surface water allows microorganisms to move laterally, pick up nutrients that are leached from the interior of leaves, and interact with other organisms (Doan et al., 2020). Plant-fungal interactions are highly context-dependent and adaptive, but the involved molecular mechanisms are sometimes referred to as "black boxes"(Franco et al. 2022). As suggested by previous studies on plants, electrical signaling controls how plants respond to external stimuli. Better experimental design, repeatable measurements, and unambiguous proof linking electrical activity to physiological or ecological processes inside the mycelium are needed for a complete understanding of fungal electrical behavior (Blatt et al., 2024).

8. Biocontrol Agents for Sustainable Agriculture

Phylloplane fungi are promising biocontrol agents that provide environmentally benign substitutes for conventional pesticides by suppressing diseases, managing insect pests, and promoting plant growth. The most commonly used are *Trichoderma* spp., which produce metabolites and enzymes that strengthen plant defenses (Guzmán-Guzmán et al., 2023; *Beauveria* and *Metarhizium,* which target insect pests (Gohel et al., 2022). Commercial formulations are commonly used, particularly those based on *Trichoderma*; however, host specificity and environmental circumstances frequently affect how well they work.

Table1. Summary of important contributions to phyllosphere microbial studies

Serial No.	Host	Dominant microbiota	Major Findings	Reference
1.	*Ipomoea cairica* (L.)	*F. oxysporum* and *F. fujikuroi*	By neutralizing the antagonistic effects of jasmonic acid (JA) on the salicylic acid (SA) signaling pathway, *Fusarium oxysporum* contributes significantly to the development of resistance in *Ipomoea cairica* against *Colletotrichum gloeosporioides*, hence augmenting the overall resilience of	(Xu et al., 2020)

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			the plant	
2.	*Solanum lycopersicum*	*Alternaria alternate* and *Aspergillus niger*	As leaves became older, microbial colonization increased. Over time, dense populations were seen on the adaxial surface, whereas newly formed leaves' abaxial surfaces showed especially high microbial diversity	(Saleem & Paul, 2016)
3.	*Stylosanthes guianensis*, *Medicago sativa, Zea mays*, *Dactylis glomerata*	LAB, aerobic bacteria, yeasts, molds	Microbial colonization was facilitated by surface sugars and trichomes, which improved food availability and offered refuge. Conversely, LAB and aerobic bacteria were supported by surface inorganic phosphorus, whereas microbial abundance was restricted by high wax concentration	(Tang et al., 2023)
4.	*Hedera helix* L. (ivy)	Filamentous fungi, yeasts, and bacteria	Old leaves colonized by microbes showed reduced wettability and pH-dependent contact angles. Microbial colonization can mask native surface-wetting properties	(Knoll& Schreiber, 2000)
5.	*Gnetum gnemon*, *G. montanum*	Members of micromycetes	These produce biofilms and demonstrate seasonal species turnover, notably in the upper epidermis. Their reduced variety in the lower epidermis during winter implies environmental filtering and site-specific colonization	(Bogdanova et al., 2019)
6.	*Rauwolfia serpentina*	*Penicillium sublateritium, Trichoderma harzianum*	Effectively reduced conidial germination of *Alternaria alternata,* causing leaf spot disease of *Rauwolfia serpentina*, decreased disease development, and increased root biomass	(Alternata Shikhathakur, 2016)
7.	*Oryza sativa*	*Enterobacteriaceae*, *Xanthomonadaceae*	Temperature and CO_2 have a considerable impact on the structure, richness, and diversity of microflora; CO_2 alone has no effect	(Ren et al., 2015)
8.	*Sorghum vulgare*	*Engyodontium album* (strain B47-9)	Exhibited strong ability to degrade biodegradable plastic films. Facilitated film decomposition in soil and altered the local microbial community	(Koitabashi et al., 2012)

9.	*Rhizophora apiculata*	*Lasiodiplodia theobromae*, *Trichoderma harzianum*, *Nigrospora sphaerica*	Showed strong antagonistic activity against *Fusarium oxysporum* f. sp. *cubense*, with *L. theobromae* showing highest inhibition of fusarium wilt (11.11%) in banana (*Musa acuminata* L.)	(Shara & Basyuni, 2023)
10.	*Ipomoea cairica*	*Fusarium oxysporum* and *Fusarium fujikuroi*	*Fusarium species* serve as important inducers of pathogen resistance against *Colletotrichum gloeosporioides*. *F. oxysporum* played the dominant role by alleviating JA–SA antagonism and maintaining stronger resistance against *C. gloeosporioides*	(Xu et al., 2020)

Trichoderma harzianum and *Aspergillus* spp. are examples of phylloplane fungi that are crucial to integrated pest management (IPM) because they suppress pests and diseases, improve nutrient uptake, and increase plant resistance, all of which lessen the need for chemical pesticides (Das et al., 2021). In order to make sure that these fungi work in tandem with other IPM techniques rather than in opposition to them, more field-based research is necessary. Important factors include formulation, application time, and environmental conditions. Important secondary metabolites that inhibit microbial growth and survival are cyclic peptides, sesquiterpenoids, and anthraquinones, are responsible for the antibacterial activity of phylloplane fungus (Deshmukh et al., 2022). Their effective use in IPM, however, rests on compatibility with other control approaches, given that certain insecticide-fungus combinations may work while others may inhibit fungal development, thus reducing efficacy (Musso et al., 2022). Considering these, more field-based research is needed to ensure that these fungi interact positively with other IPM strategies rather than against them.

9. Commensal and Epiphytic Roles

Diverse epiphytic fungi that can act as commensals, mutualists, or antagonists are found on the leaf surface of plants. Many phylloplane dwellers form constructive interactions with their host by promoting growth, increasing nutrient absorption, often via the production of phytohormones and bioactive substances that enhance growth and tolerance against pathogens (Goswami et al., 2021; Mir et al., 2022). The surface of the leaf offers a favourable environment in which saprophytic fungi can thrive, making them obtain water and nutrients without having to pierce the host tissues. The fungi that are not pathogenic on leaves depend on the nutrients emitted by the atmosphere (Thakur., 2017). The competition between the native microbial communities determines the interaction of plants and microbes on the leaf surface of plants, which, respectively, contributes to a great part of healthy plant growth and the prevention of disease (Tanti et al., 2016). The leaf surface features, such as hair size and sculpturing, have a significant effect on the fungal diversity. Chen et al., (2021) concluded that the use of pesticides can drastically change phyllosphere communities and affect the uncommon and core microbiomes. According to this selective interference, chemical interventions could reduce the resilience and long-term health of plants in an ecosystem by disturbing the natural plant-microbe interactions, besides disturbing the microbial diversity.

10. Source of Bioactive Compounds

Phylloplane fungi are recognized as a treasure of antimicrobial agents with applications in agriculture and medicinal practices. They generate a great diversity of bioactive chemicals with a strong antimicrobial activity. Several species, e.g., *Penicillium expansum*, *Fusarium oxysporum*, and *Cladosporum herbarum*, *Trichoderma harzianum*, have antibacterial effects (Varpe., 2020).

Major secondary metabolites that play a role in the antibacterial activity of fungi are cyclic peptides, anthraquinones, and sesquiterpenoids (Deshmukh et al., 2022). Because of their distinct structures, the metabolites that phylloplane fungi produce may help to produce new antibiotics, which are crucial in the rising issue of antibiotic resistance (Deshmukh et al., 2022). Their ecological interactions with the host favor the yielding of diverse metabolites, such as phenols, terpenoids, or steroids (Hashem et al., 2023). Some yeasts and *Aspergillus niger* are examples of phylloplane fungi that play a key role in enzyme synthesis and the activation of plant defense. Goswami et al., (2019) assert that *A. niger* enhances the action of various significant defensive enzymes such as tyrosine ammonia lyase (TAL), phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and peroxidase (POX). Cutinase-like enzymes (CLEs) are secreted by *Pseudozyma* and other yeasts like *Cryptococcus*, hydrolyze cutin, which may change the environment in the phylloplane and facilitate the defense (Ueda et al., 2021). In addition, the secondary metabolites of these fungi may suppress the growth of phytopathogens, stimulate the growth of plants, and cause general resistance (Sikandar et al., 2020). Also, the phylloplane itself serves as a biochemical barrier, as the fungi that live there inhibit the germination of pathogen spores (Zugaib et al., 2022). Interestingly, it is important to note that phylloplane fungi are specialised to the breakdown of tough organic substances such as plant cuticles. Bhanot et al., (2023) employ polystyrene lids as a source of carbon; the fungus *Curvularia dactyloctenicola* VJP08 successfully invaded and broke them down. This clarifies the phylloplane fungi's capacity to biodegrade and their potential for sustainably handling plastic trash.

11. Methodological Advances and Challenges

The molecular techniques have expanded the knowledge of phylloplane fungal diversity, enabling the identification of species that are difficult to culture but ecologically significant. While there are certain pitfalls to culture-dependent approaches, including the biases imposed by growth media and incubation conditions, these methods do have considerable value for morphological studies and experimentation regarding functions. With the availability of large-scale sequencing technologies and sophisticated bioinformatics tools, a new age of plant microbiota research has begun that enables the powerful culture-independent characterization of microbial communities inhabiting plants. Molecular approaches like metaproteomics and metagenomics have been employed to investigate the functional and physiological relationships of microbes with their host and environment. For example, many species from basal lineages, such as Basidiomycota, which are poorly represented in culture-based inventories, have been identified in culture-independent studies (Rungjindamai & Jones, 2024). High-throughput technologies use transcriptomics to give complete datasets of microbial life in the phyllosphere (Remus-Emsermann & Schlechter, 2018). Li et al. (2022) illustrated the value of multi-method strategies for comprehensive analysis of the phylloplane microbiome through an integrated approach incorporating 16s rRNA metabarcoding, shotgun metagenomics, and culture-dependent techniques to investigate microbial dynamics associated with foliar fungal colonization in citrus. Over the last decade, breakthroughs in next-generation sequencing technologies and bioinformatic pipelines for phylogenomic research have resulted in tremendous gains in fungal systematics and taxonomy (Zhang et al., 2017; Chiang and Dekker, 2020). The CLSM and SEM imaging techniques are valuable to learn about the spatial organization of phylloplane fungi, as well as their contact with plant surfaces. Unlike CLSM, which allows the visualization of fungal communities in situ and the discovery of their distribution and role in the well-being of plants, SEM offers high-resolution imaging of the leaf topography and structural characteristics that affect fungal colonization. Nonetheless, the complexity of the microbes cannot be untangled by imaging only, and the combination of these methods, combined with the molecular ones, is required to gain profound knowledge of the ecological processes and dynamics within the communities. Besides allowing functional assays of antifungal activity relevant to phylloplane functioning and plant health, culturomics extends the list of cultivable species. Synthetic community tests, which have more frequently revealed nonadditive and synergistic effects on plant growth and productivity, further illustrate the impact of assembled fungal consortia on plant performance.

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Despite several advances in phylloplane fungal research, there are considerable issues concerning standardization, repeatability, and classification. Molecular methods, in particular, are required for complex groups such as *Trichoderma* and *Metarhizium,* because traditional phenotypic identification is problematic due to morphological stability, plasticity, and unculturable taxa. During the past decade, leaves from various plant species have undergone deep sequencing, thus presenting large microbial catalogs. Culturing approaches, though mostly cost-effective, are rather time-consuming and only detect less than 1% of microorganisms.

12. Phyllosphere Microbiota: Ecological Insights

Climate, farming region, host development, and agricultural practices all have an impact on the phyllosphere microbiota (Karlsson et al., 2017). The structure of the forest canopy affects fungal community growth on the leaf surfaces by changing the light, humidity, and microclimate conditions. Lower canopy leaves and those farther from the top of the stem tend to have higher levels of fungal colonization because they are more exposed and retain more moisture than upper leaves, which creates more favourable conditions for spore deposition and fungal growth. Previous studies exemplify only a few fungi from young plants, but the fungal population grows exponentially as plants mature and their leaves begin to deteriorate (Gulati et al., 2022). Plant-associated microbial populations can be significantly influenced by flooding or severe drought. The biological variables that impact the microbial populations in the plant phyllosphere include competitive microorganisms. One of the key factors affecting epiphytic colonization is the presence of carbon-containing nutrients in the leaves. A variety of factors influence the concentration of fungi on the phylloplane, including nutrition availability, humidity, leaf age, inhibitor presence, immigration (the arrival of viable propagules on the phylloplane), and emigration (the removal or physical loss of viable propagules. In addition, plants themselves evolved defense mechanisms to lessen the number of creatures that colonized their leaves. Especially in subtropical and tropical areas characterized by relatively high temperature and humidity, the phyllosphere harbours a wide range of microorganisms (Kim et al., 2012). Though microbial conservation has not gained much attention, studies of phylloplane microflora can play key roles in understanding the ecology and role of host influence on the building up of communities of the phylloplane fungi under a changing seasonal environment. According to recent research, changes in the microbiome of plants are not only a passive reaction; rather, as a result of coevolution, plants are likely to actively seek out collaboration with microorganisms to alleviate stressors. Microorganisms in the phyllosphere perform a variety of ecological tasks by affecting fruit development, seed mass, leaf functions and longevity, and host growth homeostasis.

Conclusion

The phyllosphere is one of the most vast and dynamic microbial ecosystems, supporting a varied range of fungi, bacteria, and yeasts. Previously thought to be a harsh and nutrient-poor environment, leaf surfaces have evolved into sophisticated microhabitats with variable humidity, temperature, light, and nutritional inputs. In this way, foliicolous fungi, in particular, reflect a delicate balance between ambient air conditions, leaf characteristics, and microbial interactions. Understanding fungal communities is critical because they influence plant performance via nutrient cycling, competition, and alteration of leaf surface chemistry. Resident fungi serve as stable colonizers, surviving and reproducing on leaves, whereas casual colonization contributes to short-term ecological interactions. They work together to degrade organic matter, promote microbial succession, and modulate the phyllosphere microbiome. Despite substantial advances in the study of the rhizosphere, the phylloplane is still poorly understood, with several gaps in knowledge about fungal diversity, adaptation processes, and ecological functions. With shifting worldwide climate patterns, the study of phylloplane fungi is becoming more relevant. Temperature, humidity, and atmospheric chemical variations will continue to influence colonization behavior, competition, and community stability. Improved understanding of such dynamics may support long-term plant health initiatives, such as the use of beneficial epiphytic fungi to boost plant resilience. In conclusion, the phyllosphere is an important ecological contact between plants, microorganisms, and the environment. Strengthening studies on foliicolous fungi

will advance our understanding of plant ecology and create new prospects for ecological management and agricultural innovation.

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Declaration of competing interest

None

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