International Journal of Agriculture and Food Science 2025; 7(1): 268-273

ISSN Print: 2664-844X
ISSN Online: 2664-8458
IJAFS 2025; 7(1): 268-273
www.agriculturaljournals.com
Received: 02-11-2024
Accepted: 06-12-2024

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Phylloplane bacteria and their role in plant disease management

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DOI: https://doi.org/10.33545/2664844X.2025.v7.i1d.267

Abstract
The phylloplane, a microbial-rich habitat on the aerial surfaces of plants, plays a crucial role in plant health and disease management. This review explores the diverse microbial communities of the phylloplane, particularly bacteria, and their significant contributions to plant growth, pathogen resistance, and ecological balance. Phylloplane microbes employ competitive strategies such as the production of antimicrobial compounds, induction of systemic resistance, and enhancement of photosynthetic efficiency. Moreover, they facilitate nutrient cycling, nitrogen fixation, and phytohormone production. Recent studies highlight their potential as biocontrol agents in sustainable agriculture, emphasizing their effectiveness in suppressing pathogens and promoting plant health. Understanding the dynamics of phylloplane microbes offers promising avenues for improving crop productivity and reducing reliance on chemical inputs.

Keywords: Phylloplane, microbial communities, plant-microbe interactions, biocontrol agents, systemic acquired resistance, induced systemic resistance, sustainable agriculture, plant growth promotion

Introduction
The term "phyllosphere" refers to the aerial or above-ground parts of plants, including leaves, stems, buds, flowers, and fruits, while the leaf surface area is specifically referred to as the phylloplane. This environment supports diverse and complex microbial communities (Inácio *et al*., 2002; Lindow & Brandl, 2003; Whipps *et al.*, 2008) [19, 25, 43]. It is primarily colonized by bacteria but also includes archaea, filamentous fungi, and yeasts. These microorganisms may exist on the plant surface as epiphytes or within plant tissues as endophytes (Arnold *et al*., 2000) [2]. The phyllosphere represents a challenging habitat, attracting significant scientific interest in its microbial inhabitants. Leaves, as a dominant aerial structure, are heavily colonized by bacteria. The bacterial population typically ranges from 10^6 to 10^7 cells/cm² and can reach up to 10^8 cells per gram of leaf tissue (Andrews & Harris, 2000) [1]. Epiphytic bacterial communities are highly dynamic, with significant variability in population size both among and within plants of the same species and across the growing season. Since the phyllosphere is directly exposed to environmental factors, it experiences considerable fluctuations in physical and nutritional conditions, leading to variations in microbial population sizes and compositions. Additionally, the specific plant species and its genetic characteristics play a crucial role in determining the microbial carrying capacity and specificity of the leaves (Kinkel *et al*., 2000) [23].
Microorganisms are found in nearly all plant tissues. The phyllosphere, encompassing the entire aerial part of the plant, and the phylloplane, specifically the leaf surface, support a vast microbial community. Microbes associated with plant surfaces are termed epiphytes, while those residing within plant tissues are known as endophytes (Arnold *et al.* 2000) [2]. Epiphytes inhabit both the upper (adaxial) and lower (abaxial) leaf surfaces (Andrews and Harris 2000) [1]. Significant research on rhizospheric microbial communities has illuminated their roles in enhancing crop productivity, protecting against pathogens, and promoting plant growth by inducing phytohormone release in host cells. For example, Caulier *et al.* (2018) [9] evaluated Bacillus and Pseudomonas spp. strains against potato pathogens and confirmed the rhizosphere's potential in biomanagement. Microorganisms such as Trichoderma spp.

Bacillus, Pseudomonas, and Streptomyces have been extensively utilized to manage fungal diseases (Toyota and Shirai 2018) [40].

The phylloplane, primarily composed of photosynthetic leaves, also hosts a highly diverse microbiota and has been a topic of considerable research interest. This diverse microbial community includes bacteria, fungi, algae, yeasts, and nematodes (Whipps *et al.* 2008) [43]. Among plant tissues, the leaf surface provides an optimal environment for microbial growth due to its exudates, which supply nutrients, moisture, and suitable pH and temperature conditions (Shukla and Sharma 2016) [38]. Interactions between plants and phylloplane microbes contribute significantly to plant growth, development, and defense (Lindow and Brandl 2003) [25]. According to Rastogi *et al.* (2012) [36] and Bulgarelli *et al.* (2013) [6], approximately 6.4 × 10^8 km² of terrestrial leaf surface is colonized by microbes. The phylloplane is a primary entry point for many phytopathogens, which can bypass plant defenses by colonizing the surface and outcompeting native microbes (Bringel and Couée 2015) [5].

Among the microbial population on the phylloplane, bacteria are the most abundant, with numbers ranging from 10^5 to 10^7 cells per gram of leaf (Yadav *et al.* 2010) [44]. Fungal spores are also present on leaves, facilitated by continuous air currents that transport them (Shukla and Sharma 2016) [38]. These spores are trapped by waxy surfaces and trichomes on leaves (Saleem and Paul 2016) [37], forming colonies in suitable microhabitats. Although fewer in number than bacteria, phylloplane fungi play essential ecophysiological roles, such as interacting with pathogenic fungi, contributing to carbon and nitrogen cycling, and initiating leaf litter decomposition (Voříšková and Baldrian 2013) [41]. Dominant phyllosphere bacteria include Methylobacterium, Sphingomonas, and Pseudomonas (Bodenhausen *et al.* 2013; Kembel *et al.* 2014) [4, 22], while fungal communities are mainly composed of Ascomycota and Basidiomycota (Jumpponen and Jones 2010) [20].

Phylloplane microbes have been recognized for their antimicrobial activities against phytopathogens, which is attributed to their competitive survival strategies (Mazinani *et al.* 2017) [28]. They produce antimicrobial compounds to suppress the growth of competing pathogens (Chaudhary *et al.* 2017) [10], and these compounds can either directly harm pathogens or trigger systemic acquired resistance (SAR) in plant cells (Lindow and Brandl 2003) [25]. Furthermore, phylloplane microbes promote plant growth by producing phytohormones such as indole acetic acid (IAA) and cytokinins. For instance, Sphingomonas spp. are known to enhance plant growth by synthesizing IAA (Enya *et al.* 2007) [15]. These microorganisms also contribute to global processes like nitrogen fixation, nitrification, and phosphate solubilization (Furnkranz *et al.* 2008; Mwajita *et al.* 2013) [6, 31]. Relationships between plant nitrogen balance and the richness of leaf epiphytic bacterial species have also been documented (Manching *et al.* 2014) [27].

Phylloplane microbes have been studied for their role in photosynthesis, a critical physiological process. Research indicates that phylloplane fungal metabolites can enhance the activity of Ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco), thus influencing photosynthesis (Mitra *et al.* 2014) [30]. However, further research is required to elucidate the molecular mechanisms and physiological impacts of phylloplane microbes. Investigating changes in the host's leaf protein profile may provide insights into these interactions, as the expression or suppression of specific proteins could reveal the effects of phylloplane microbes on the plant.

Isolation of epiphytes from phylloplane

The leaves were meticulously cleansed with sterilized water, and any incisions were treated with 70% bleach before being sealed with parafilm to avert endophyte contamination. Three grams of leaves were vigorously vortexed in 30 ml of PBS using a horizontal vortex adapter (Mobio) to optimize biomass extraction. Subsequent serial dilutions were plated on N-agar plates and incubated at 28 °C for 24–48 hours. Colony-forming units (CFU) were enumerated, and distinct colonies were isolated and purified via the quadrant-streak technique. Each isolate underwent morphological assessment, Gram staining, and tests for catalase and oxidase activity. Isolates were designated codes comprising the initial two letters indicating the wheat variety (FD for Faisalabad, SH for Sehar, and LA for Lasani), followed by "P" for phylloplane and the sampling number (1, 2, or 3) (Batool *et al.*, 2016) [3].

In the initial phyllosphere sampling of three wheat varieties, 22 distinct bacterial isolates were identified. The Faisalabad variety exhibited the highest diversity with 10 unique isolates and a bacterial load of 8 × 10^6 CFU/g. The Lasani variety followed with 7 unique isolates and 4.4 × 10^6 CFU/g, while the Sehar variety had 5 unique isolates but the highest bacterial load at 9.2 × 10^6 CFU/g. During the second sampling, the Faisalabad variety yielded 10 isolates with 4 × 10^6 CFU/g. The Sehar variety produced 9 diverse isolates and a bacterial load of 1.76 × 10^7 CFU/g. The Lasani variety had 8 distinct isolates with a bacterial load of 3.64 × 10^7 CFU/g. In the third sampling, the Faisalabad variety showed an increase to 13 diverse colonies and a bacterial load of 2.8 × 10^7 CFU/g. The Lasani variety had 12 distinct isolates with 1.12 × 10^7 CFU/g. The Sehar variety yielded 4 isolates with the highest bacterial load of 4.32 × 10^7 CFU/g across all three samplings.

Narasimhan and Banerjee (2021) [32] studied on Isolation and characterization of Phylloplane bacteria from papaya plant for the biocontrol of post - harvest diseases in papaya. Bacterial isolates from the phylloplane samples screened for dual plate assay and three isolates namely IS1, IS6 and IS7 exhibited good percentage of inhibition against fungal pathogen. IS6 was identified as Bacillus and IS7 was identified as Pseudomonas. Fruits co-inoculated with IS – 7 and the pathogens showed the maximum freshness. This shows the significant biocontrol ability of post-harvest diseases of the phylloplane bacterial isolates. From the studies conducted it is observed that bacterial isolates from the phylloplane have the ability to control fungal pathogen growth in papaya fruits. Out of 20 isolates studied, it can be concluded that IS 6 and IS 7 had maximum inhibitory activity and increased shelf life of the papaya fruits. These two isolates were found to be Grampositive rods with endospores and Gram-negative rods, respectively. The maximum inhibition was seen against Fusarium. By the Dual assay test, it was revealed that maximum antagonistic ability was revealed by IS – 6 and IS – 7. The papaya fruits treated with IS – 6 and IS– 7 showed better shelf life and appeared fresh. The isolates were morphologically and biochemically characterized and identified as Bacillus and

Pseudomonas respectively. Thus it can be concluded that Bacillus and Pseudomonas obtained from the phylloplane of the papaya plant act as potential biocontrol agents against various post-harvest diseases of papaya.
Caicedo *et al.* (2016) [8] studied on Bacteria from the citrus phylloplane can disrupt cell–cell signalling in *Xanthomonas citri* and reduce citrus canker disease severity. In this study, three bacterial strains were isolated from citrus leaves that displayed the ability to disrupt QS signalling in Xcc. Pathogenicity assays in sweet orange (*Citrus sinensis*) showed that bacteria of the genera Pseudomonas and Bacillus also have a strong ability to reduce the severity of citrus canker disease. These effects were associated with alteration in bacterial attachment and biofilm formation, factors that are known to contribute to Xcc virulence. These quorum-quenching bacteria may represent a highly valuable tool in the process of biological control and offer an alternative to the traditional copper treatment currently used to treat citrus canker disease.

Role of Phylloplane Microbes in Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR)

Systemic acquired resistance (SAR) is a plant-wide defense mechanism activated upon exposure to elicitors from various microbes - virulent, avirulent, nonpathogenic - or through artificial stimuli. In contrast, induced systemic resistance (ISR) is a defense mechanism that becomes active when a plant is infected by a pathogen.
Research by He *et al.* (2002) [17] demonstrated that nonpathogenic *Fusarium oxysporum* can trigger systemic resistance and defense responses against the pathogenic *F. oxysporum* f. sp. *asparagi* in *Asparagus officinalis*. Similarly, *Trichoderma* species produce toxic compounds with antimicrobial properties and secrete substances that stimulate plants to generate their own defense metabolites. Buxdorf *et al*. (2013) [7] found that local inoculation of *Pseudozyma aphidis* induced resistance in *Arabidopsis*, leading to reduced growth of *Botrytis cinerea* in both local and systemic leaves.
Numerous microbes inhabiting the phylloplane synthesize phytohormones like auxins, gibberellic acids, and cytokinins, and possess capabilities such as nitrogen fixation and nutrient mobilization (Dourado *et al.* 2015) [14]. The production of indole acetic acid by phyllospheric microorganisms promotes root growth, enhancing soil contact and nutrient absorption. Consequently, microbial inoculants including Bacillus, Microbacterium, Acinetobacter, Proteus, Psychrobacter, and Pseudomonas are now advocated as alternatives to chemical fertilizers (Bulgarelli *et al.* 2013) [6]. Succinate dehydrogenase (SDH) produced by Pseudomonas syringae has been shown to exhibit reduced activity. Located in the inner mitochondrial membrane, SDH influences photosynthesis, triggers fungal defense responses in plants, and regulates stomatal function and root elongation (Huang and Millar 2013) [18]. The oxidation of succinate to fumarate produces CO_2, which inhibits SDH, leading to succinate accumulation. This accumulation is toxic to plant tissues, as SDH anomalies reduce mitochondrial H_2O_2 production and increase host susceptibility to pathogens (O'Brien *et al.* 2012)] [34].

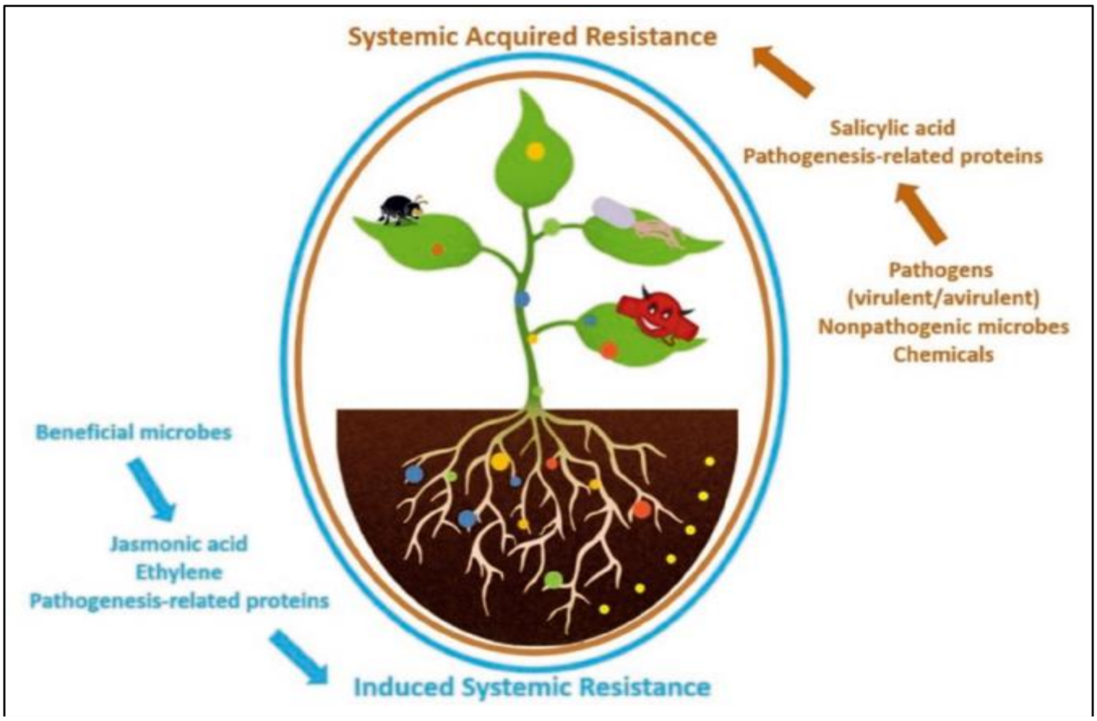

Fig 1: Microbial and bioactive soil amendments for improving strawberry crop growth, health, and fruit yields: a 2017–2018 study (Dara 2019) [12]

Microorganisms residing on leaf surfaces, known as phylloplane microbes, can adversely affect host pathogens by producing antimicrobial substances. Additionally, they may contribute to plant defense indirectly by triggering mechanisms such as induced systemic resistance (ISR) or systemic acquired resistance (SAR) (Fig. 1).

Factors affecting phylloplane microorganisms

General Microorganism populations of the leaf surface are affected by abiotic factors such as the microclimate and biotic factors such as the leaf surface itself and interactions between the microorganisms.

Abiotic factors

1. Microclimate: The boundary layer of a leaf is a thin layer of air that directly surrounds the leaf, creating a gradient from the ambient wind speed to the leaf's surface, where the wind speed is zero. This layer's thickness is influenced by factors such as the presence, absence, and density of trichomes and typically measures less than 1 mm. Often termed the phyllosphere, this microenvironment is the setting for interactions among phylloplane microorganisms. Notably, the microclimate within the leaf's boundary layer often differs significantly from the surrounding ambient climate (Dix and Webster 1995) [13].

2. Temperature: The temperature of a leaf is influenced by various factors, including ambient temperature, solar radiation, leaf position, shape, surface topography, transpiration, wind speed, and moisture levels. Within a single leaf, temperature variations can occur, typically not exceeding 2-3 °C, with the highest temperatures often found at the center. Generally, leaves are cooler at night and warmer during the day compared to the surrounding air. Temperature fluctuations are more pronounced at the periphery of the leaf than within the canopy.

3. Humidity and leaf wetness: Under typical conditions, leaves continuously transpire, leading to higher humidity in the boundary layer compared to the surrounding air. This humidity level is influenced by factors such as the boundary layer's thickness, the number and status of stomatal openings, and water availability. Generally, the abaxial (lower) leaf surface has a higher humidity than the adaxial (upper) surface, due to a greater number of stomata and reduced convection currents. Additionally, leaves located within the canopy receive less solar radiation, resulting in lower daytime temperatures and more stable humidity levels compared to those on the periphery. At night, dew commonly forms on leaves because their temperature drops below that of the ambient air. This moisture is crucial, as many phylloplane microorganisms require wet leaf surfaces or relative humidity above 95% to germinate and grow.

4. UV light: Natural ultraviolet (UV) radiation can be harmful and often lethal to many. microorganisms because it "damages DNA by causing adjacent pyrimidine bases to join up as dimers and by causing a number of other subtle changes". Some pathogenic fungi that produce long germ tubes are therefore less likely to survive on leaf surfaces than fungi that produce short germ tubes or pigmented haustoria immediately after germination.

5. Wind: The wind speed near the leaf surface is lower compared to the surrounding air. However, many microorganisms produce wind-dispersed propagules, leading to the development of spores atop structures like conidiophores, which position them in regions with higher wind velocities beyond the leaf's boundary layer. The deposition of these airborne fungal spores onto leaf surfaces occurs through wind impaction, necessitating their traversal through the boundary layer, as well as through air turbulence. Larger spores are more readily deposited than smaller ones due to their more advantageous surface area-to-mass ratio.

6. Nutrients: Various forms of debris on leaf surfaces, including pollen, honeydew, fungal spores, and other substances, supply essential nutrients that support the survival and proliferation of phylloplane microorganisms, significantly impacting their diversity and activity. Pollen grains, in particular, release sugars, amino acids, and proteins that can be utilized by germinating spores (Mercier and Lindow 2000) [29].

7. Pesticides: Applying foliar pesticides to manage plant diseases can significantly disrupt the communities of microorganisms residing on leaf surfaces, known as the phylloplane. This disruption often leads to a decrease in both the abundance and diversity of these organisms, which can adversely affect natural biological control mechanisms. Consequently, plants may become more vulnerable to other diseases and disorders (Noel *et al*., 2022) [33].

8. Pollution: Atmospheric pollutants such as lead, sulphur dioxide, ozone, and nitrogen oxides can influence the populations of microorganisms residing on leaf surfaces, known as the phylloplane. These pollutants may cause direct plant damage through high concentrations of toxic substances and indirectly by diminishing the activity of sensitive phylloplane microorganisms (Wei *et al*., 2017) [42].

Biotic factors

1. Leaf position: Heliotropism is a phenomenon where certain plant species adjust their orientation to optimize photosynthesis. For instance, sunflowers exhibit heliotropic behavior by facing east in the morning and following the sun's movement to the west throughout the day. This daily motion allows the plants to maximize sunlight exposure, enhancing their photosynthetic efficiency (Kutschera and Winslow 2016) [24]. This solar tracking behavior not only optimizes light absorption but also influences the microclimate of the leaf surface. By adjusting their orientation, plants can regulate leaf temperature and exposure to ultraviolet (UV) radiation. Elevated temperatures and increased UV exposure can inhibit the growth of certain microorganisms on the leaf surface, thereby reducing the risk of microbial infections.

2. Leaf topography: The surface characteristics of leaves, including the arrangement and form of features like veins, trichomes, stomata, glands, epidermal cells, and epicuticular waxes, define leaf topography. This topography varies across plant species, different leaf developmental stages within the same species, and distinct positions on a single plant. Variations also occur between leaves serving different functions and between the abaxial (lower) surface, which typically possesses more trichomes and stomata, and the adaxial (upper) surface of the same leaf.

3. Surface wax: The upper (adaxial) surface of leaves typically features a thicker cuticle enriched with waxes compared to the lower (abaxial) surface. This adaptation serves to reduce water loss through the cuticle and to reflect excessive sunlight, as these waxes often contain antimicrobial substances.

4. Leakage from leaf: Leaf surfaces continuously release substances into water films, which can originate from dew, rain, guttation droplets from hydathodes, and stomata, as well as through the bases of trichomes, cracks in the epidermis, and directly through the leaf cuticle. The areas along the veins leak more nutrients than other parts of the leaf surface, and this is where microbial colonies are often concentrated (Ossola and Delphine 2024) [35].

5. Antagonists and competitors: On leaf surfaces, microorganisms engage in various interactions, including competition for nutrients and space, production of antibiotics, mycoparasitism, and the stimulation of phytoalexin production in the host plant (Chaudhry *et al.*, 2021) [11].

6. Adhesion to leaves: Microorganisms inhabiting the phylloplane have evolved various strategies to adhere to leaf surfaces exposed to wind and rain. For instance, yeasts like *Aureobasidium pullulans* and other species secrete extracellular, adhesive polysaccharide slimes that help prevent their spores and cells from being washed off the leaves (Johan and Leveau 2006) [21].

7. Sources of phylloplane inoculum: The primary sources of inoculum for epiphytic bacteria, yeasts, and filamentous fungi on the phylloplane of deciduous trees include overwintering colonies in buds and on twigs. Later in the season, airborne spores settle on leaf surfaces. Other sources encompass seed, soil, orchard undergrowth, air, and shoots. Once yeasts establish themselves, their spores are primarily dispersed by water splash, deposition from the air, or by vectors such as insects, birds, and animals (Thomas *et al.*, 2024) [39].

8. Succession of establishment: In early spring, the scarcity of epiphytic nutrients and airborne inoculum allows epiphytic bacteria to dominate the phylloplane. Bacteria are more efficient at utilizing limited nutrients than fungal spores in nutrient-poor environments. They can even compete for the nutrient reserves present in fungal spores, which partially explains the very slow start observed for some fungal spores.

Conclusion

Phylloplane microbes represent a vital component of plant health and productivity. Their ability to interact with host plants and suppress pathogens through antimicrobial compounds and resistance induction underscores their ecological and agricultural significance. Studies have demonstrated the efficacy of specific bacterial strains, such as Bacillus and Pseudomonas, in managing diseases and enhancing crop yield. Leveraging these microbial communities for biocontrol offers a sustainable alternative to chemical inputs in agriculture. Future research should focus on elucidating the molecular mechanisms of these interactions to unlock their full potential for disease management and plant growth enhancement.

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