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PHYLLOSPHERE MICROBES AS THE NEW PROSPECT OF PLANT-MICROBE INTERACTION

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ABSTRACT: The complete aerial plant surfaces (above-ground sections) were referred to as the phyllosphere, which served as a microorganism home. On the leaf surface, microorganisms form compositionally complex communities. Bacteria, fungus, Actinomycetes, Cyanobacteria, and viruses abound in the phyllosphere's microbiome. The physiochemistry, habitat, and immunity of the host plant all influence the variety, dispersal, and community growth on the leaf surface. A colonization process is a significant occurrence that benefits both the microorganism and the host plant. On the phyllosphere, microbes often establish either an epiphytic or an endophytic life cycle, which aids the host plant's functional communication with the surrounding environment. These communities regulate plant fitness, mediate foliar functional features, and contribute to a variety of environmental activities, including nutrient and water cycling. Beneficial microbes can be used in agriculture to improve plant growth, health, and production. Growth-promoting bacteria and biocontrol agents isolated from the phyllosphere of various plant species have thus far been underutilized compared to those isolated from the soil or rhizosphere. Successful examples include the treatment of plant diseases, pathogen reduction, and nitrogen fixation in natural and agricultural systems. Based on existing research, this review gives a fundamental overview of the microbiome in leaf structure and its physiology, microbial interactions, particularly among bacteria, fungus, and actinomycetes, and their adaptability in the phyllosphere environment. The work is the compilation of the importance of the microbiome in the phyllosphere to the host plant and its surroundings which has been collected in detail and put together here.

Keywords: Endophytic microbes; Epiphytic microbes; Microorganisms; Phyllosphere; Plant Microbe Interaction.

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1. INTRODUCTION

The term phyllosphere refers to the aerial part of the plant. Both the top and bottom of the leaves are typical, thought-about as an environment for microorganisms. The global leaf space corresponds to each higher and lower surface and has close to double as niche because of the land extent [1]. The phyllosphere is the close region for microbes to colonize and establish their association with plants typically called epiphytes. This is often an area wherever usually a range of microorganisms colonizes. The microbiome of the phyllosphere is a wealth of diversity of bacteria, fungi, Actinomycetes, true bacteria, and viruses. The variety, dispersal, and community development of microbes on the leaf surface area unit supported the physiochemistry, environment, and additionally the immunity of the host plant. This reaction results in the mutual interaction of the life cycle. Phyllosphere surroundings generally help the host plant to establish practical communication with the encircling surroundings. The type of plant and invasive microbic populations (pathogens) that are influencing the commensals and/or mutualistic relationship with their host plant[2]. Moreover, with increasing evolution stresses, the diversity and community structure of phyllosphere microflora are frequently modified.

1. Microbial Diversity In The Phyllosphere

The phyllosphere consists of various microbial communities together with bacterium, filamentous fungi, yeasts, algae, and protozoans [3,4,5,6]. The character of assorted microorganisms (epiphytic and endophytic) related to the phyllosphere is given in Fig. 1. Among the various community of microbes, bacterium per unit area of the predominant community on leaves, and its range is between 102 and 1012 g^{-1} of the leaf[7]. The standard culture-based technique has been used for the identification of various microbial communities of the leaves. Thompson[8] known seventy-eight microorganism species from the sugar beet, and Legard [9] screened eighty-eight microorganism species from thirty-seven genera. However, the culture-dependent technique primarily based identification of phyllosphere communities is likely to be incorrect and miscalculates diversity[10]. The culture-independent approaches like 16s rDNA sequences of the total microbial mass of the phyllosphere may offer the entire and complicated microbial community structure of the surroundings. Molecular studies recommended that alpha-, beta- and gamma proteobacteria and firmicutes area unit the dominant microorganism inhabitants of the phyllosphere. Frequently, lactic acid bacteria, "Actinobacteria", and true bacteria also are occurring within the phyllosphere

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications surroundings[11]. Lambais[12] detects that ninety-seven of the microorganism sequences of the phyllosphere have been new and unidentified. Yang[13] rumored massive numbers of novel bacteria from the phyllosphere of crop plants. Several studies confirmed the diversity of yeast within the phyllosphere surroundings as associate flora.



Figure 1: Epiphytic microbes on phyllosphere¹⁹⁹¹

The cultivatable yeast genera like Cryptococcus, Sporobolomyces, and Rhodotorula and their species are for the most part human within the plant leaf[8,14]. Moreover, culture-dependent methods have been used to study the abundance of filamentous fungi, starting from 102 to 108 CFU g⁻¹. Genera like *Cladosporium*, *Alternaria*, *genus Penicillium*, *Acremonium*, *Mucor*, *and Aspergillus* area unit the frequent thin fungi colonizing as epiphytes and endophytes [15,7,16]. However, the culture-independent strategy is the best to analyze the variety and distribution of specific microorganisms in terms of interest[17,18]. Aside from the 16s/18s rDNA sequences, multiplex terminal restriction fragment length polymorphism (TRFLP) has been needed to analyze many phylogenetic teams or practical genes in the micro environment[19]. Soils, water, air, tree buds, and plant trash from the previous crops area unit the sources of microbes in the phyllosphere[20]. Those microorganisms may be clad in phyllosphere either transient or residual epiphytes[21,22]. The atmospherical microflora, rainfall, humidity, wind, etc. will directly influence the transients of microorganisms to the phyllosphere[23]. During the plant growth amount, the plant life microorganism population can increase in quantity[7]. The microorganisms on the seed or roots could also be established as epiphytes or endophytes[24]. Some epiphytes could also be injected into the inner house of the leaf and colonized as endophytes. The distribution pattern of the phyllosphere microorganisms isn't even, largely bacterium colonizes at the dermal wall junctions, specifically within the grooves and also the veins or stomata or at the bottom of trichomes[25], additionally found within the cuticle layer, near hydathodes and stomatal pits[26]. The microbic load is higher at the lower leaf surface may be the lower leaf surface contains skinny cuticles, stomata,

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications and/or trichomes[27]. Mostly, all microorganisms that seem in the phyllosphere area unit capable to colonize and grow[3], and it disperses throughout the surface by rain splash, bounce-off, wash-off, water movement, or removal by insects or tormenter[28,13,12].

2. Strategies For Bacterial Colonization

Bacterial colonization occurs on the leaf's surface, and its abundance and diversity are determined by the leaf habitat's properties, as well as a variety of other host and environmental factors. Their colonization of the leaves is likewise confined, and the bacteria's metabolic activities determine how they interact with the leaf. For their growth and survival on the aerial surfaces of the plant, epiphytes generally employ two distinct fitness strategies: first, a tolerance strategy that allows the inhabitants to tolerate direct exposure to environmental stresses on the leaf surface, primarily UV radiation and low moisture conditions; and second, a survival strategy that allows the inhabitants to avoid direct exposure to environmental stresses on the leaf surface, such as UV radiation and low moisture conditions and, secondly, avoidance approach that permits epiphytes to invade areas where they are not subjected to these pressures[29]. Because saprophytes cannot survive endophytically, they must rely on tolerance techniques to survive in the foliar zone. Foliar pathogens, on the other hand, can employ both techniques to more effectively harbour plants.

2.1. Sites Of Colonization in The Phyllosphere

Bacterial colonization is most common in trichome bases, stomata, hydathodes, vein grooves, epidermal cell connections, and cuticle depressions on the leaf surface[27]. These microsites on the surface of leaves provide ideal conditions for epiphytes to thrive and propagate[30]. Large clusters of bacterial populations were found at specific places, including stomata, epidermal cell grooves along veins, and the bases of trichomes, according to analyses. The presence of trichomes, active secretory cells, and the absence of epicuticular waxes are the three key anatomical criteria that aid in the proliferation of phyllo-epiphytic communities, according to the research reviewed[31]. The cuticle is a complex hydrophobic structure formed of epicuticular wax that serves as a leaf's first line of protection (made up of long chain fatty acids or their derivatives, cutin, and polysaccharides). It is a thin layer that covers the leaf surface and varies in thickness from plant to plant or species to species. In terms of beginning pre-invasion, infection, and immune responses, cuticular components are major drivers of bacterial community structure and significant to both plants and pathogens[32]. Trichomes are epidermal appendages that aid in the regulation of leaf temperature, UV protection, and the secretion of a range of secondary compounds that discourage herbivores and prevent disease development[31]. The commonly occupied areas involved in the secretion of chemical components such as sugars, proteins, oils, secondary metabolites, and mucilage are found at the base of these glandular trichomes [33,34]. This creates favorable conditions for microbial colonization by assisting in the retention of water droplets[35], as well as influencing the epiphytic fitness of different bacteria. Baldotto and Olivares (2008) looked at the phyllosphere bacterial community of

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications 47 distinct plant species in a tropical climate and discovered that epiphytic bacteria dominated the population, with three basic distribution patterns-solitary cells, biofilms, and microcolonies. Regardless of plant species, epidermal cell wall junctions, glandular and non-glandular trichomes, veins, stomata, and epidermal cell wall surfaces were found to be the favored locations for colonization. The presence of trichomes on the leaf surface favored the formation of microbial communities, but epicuticular wax hampered their development. Using conventional microbiological procedures, a greater number of culturable bacteria are recovered from broad leaves than from grasses or waxy plants[36,37]. Nongkhlaw and Joshi (2014) used scanning electron microscopy (SEM) to investigate the epiphytic bacterial community of Rubia cordifolia, Centella asiatica, Potentilla fulgens, Acmela oleracea, and Houltuynia cordata, which are ethnomedicinal plants native to Meghalaya (India)[38]. The availability of nutrients on the leaf surface is a factor that influences epiphytic bacteria development. Tukey (1970) found that the leaching of solutes from the leaves releases a variety of organic and inorganic nutrients, with older leaves exuding more due to increased wettability [31].

2.2. Hormones and Other Chemicals

Several bacteria can boost nutrient concentrations on the leaf surface by producing plant hormones, mostly auxins (indole 3-acetic acid), which encourage cell wall loosening and improve larger levels of release even at extremely low concentrations (Fry 1989). Cytokinins are also assumed to be important in Methylobacterium colonization because they are engaged in plant cell division and expansion, causing the release of methanol from the plant cell wall, which is a source of C for their growth[39]. In some circumstances, bacteria create chemicals that increase the wettability of the leaf surface[40], enabling the solubilization and diffusion of substrates and increasing their availability to bacteria[40]. Burch et al. (2016) discovered that the phyllosphere has a higher abundance of surfactant-producing bacteria than other habitats. Trehalose is a widely utilized osmoprotectant that helps *Pseudomonas syringae* stay alive and well in the phyllosphere[41]. This has also been linked to Pseudomonas aeruginosa's behavior as an opportunistic pathogen, as it enhances nitrogen acquisition and stimulates nitrogen proliferation in the leaf apoplast. Phytotoxins are often released by phytopathogenic microorganisms, and they either cause direct harm to plant cells or contribute to increased bacterial virulence by overcoming the host barrier and exacerbating the damage caused by chlorosis and tissue rot. Toxins such syringomycins and syringopeptins are produced by Pseudomonas syringae during plant infection. Because they are amphipathic, they cause necrosis, which causes pores in the plasma membrane of plant cells[42]. These toxins are designed to impair the enzymatic machinery of amino acid biosynthesis or nitrogen metabolism, resulting in the build-up of nitrogen-containing intermediates, which infections commonly use as sustenance[43]. Some phytotoxins alter the host's metabolic and signaling processes, making pathogen invasion easier. Auxins and other plant hormones are structurally and functionally

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications identical to most of these phytotoxic compounds. *Pseudomonas syringae* produces the toxin coronatine, which mimics the plant hormone jasmonic acid isoleucine and causes several types of pathogenicity. This encourages bacterial entry through stomata and growth in the apoplast, resulting in systemic vulnerability and illness symptoms[44]. Other ways include releasing or inhibiting hormones to manipulate plant defenses and metabolism[45]. Certain phytopathogens also generate enzymes that aid in the breakdown of plant cell wall structural components or the hydrolysis of connective tissues between plant cells, supplying the pathogen with a source of carbon[31].

2.3. Exopolysaccharides

Bacteria can also grow as biofilms, changing the leaf surface by producing extracellular polysaccharide (EPS), which aids in cell anchoring and enhances bacteria's water availability. EPS protects against desiccation in low-moisture environments by retaining water in its highly hygroscopic polysaccharide matrix[46]. Freeze-thaw resistance[47], osmotic stress tolerance[48], and microbial population sustenance are all linked to EPS molecules[49]. Such organized communities, which form as biofilms, are known to govern EPS synthesis utilizing diffusible signals or quorum sensing. Due to the quenching of calcium signaling, these biofilms are often not monospecific and are made up of a complex mixture of bacteria and fungi that also assist certain phytopathogens in evading the plant immune response[50]. The gum gene cluster (gumB to gumM) encodes xanthan gum, a characteristic EPS produced by the Xanthomonasspecies, and mutant strains (unable to produce EPS) exhibit a variety of phenotypes, including altered biofilm formation, impaired survival under oxidative stress during stationary phase, and reduced epiphytic survival on citrus leaves[49,51,52].

2.4. Quorum Sensing

Bacterial development alters the leaf environment, and a succession of microorganisms in this niche leads to the dominance of various microorganisms throughout time. Quorum sensing occurs when bacteria communicate with one another via small signaling molecules known as autoinducers. Once a threshold number is reached, these are detected by other bacteria in the area, influencing gene expression. This leads to changes in the richness and variety of microbial communities in the phyllosphere due to not only distinct groupings of organisms and quantitatively different features, but also density-dependent behavior [53]. AHLs (acyl homoserine lactone) are common signaling molecules employed by phytopathogens; Pseudomonas syringae produces 3-oxo-C6-HSL (homoserine lactone), which regulates motility and EPS production[54].

2.5. Motility

Chemotaxis, or the ability of bacteria to swarm across solid surfaces like leaves, is enhanced by the expression of the flagellar gene and the activity of surfactant molecules[55]. Epiphytic pathogens use motility systems to travel towards stomata, or other ports of entry in the leaves, or to the plant's interior, to survive. Flagella-driven motility is primarily responsible for *Pseudomonas syringae*'s

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications epiphytic fitness, which aids in enhanced surface colonization and effective plant pathogenicity[56]. There is frequently a continuity between the external and internal leaf-related populations due to the phenomenon of motility[56].

3. Metabolic Dynamics Of Phyllosphere Microbiota

Flavobacteria are abundant in the *rhizosphere* and phyllosphere of terrestrial plants like A. thaliana, where they constitute one of the most dominating leaf microbiota genera (10%)[57]. According to a recent genome comparison of Flavobacteria isolated from aquatic habitats and plants, Flavobacteria may be highly adapted to plant glucose metabolism. Only Flavobacteria from terrestrial plant communities, not aquatic plant communities, had genes for glycoside hydrolase families GH78 and GH106, which are responsible for the utilization of rhamnogalacturonan, which is only found in hemicelluloses from terrestrial plants[58]. Microorganisms linked with the phyllosphere live in a light-rich environment. The photochemical conversion of this light resource into carbon and energy, which might supplement carbon resources from the host plant, could provide a significant benefit for development in nutrient-limited environments. In phyllosphere ecosystems, metagenomic data revealed the presence of bacterial rhodopsin genes[59]. It appears that some epiphytic microorganisms have retinal-dependent rhodopsin proton pumps that can be light-activated by radiations with wavelengths different from chlorophyll and carotenoids' absorption spectra, which stimulate photosynthetic processes in plants and consequently the creation of plant carbon resources that epiphytic bacteria can use[59,60] Given the importance of carbon and nitrogen resources in nutritional signaling and regulation, as well as their impact on light-dependent processes[61,62], The carbohydrate and nitrogen status of the host plant, and thus the oscillations of plant-light interactions and photoassimilate synthesis in the host plant, are expected to influence several metabolic pathways of epiphytic bacteria[63,64]. Manching[65] published a study that found global relationships between plant nitrogen balance and the diversity of leaf epiphytic bacterial species in maize. Ren[66] revealed significant changes in phyllosphere bacterial populations in rice treated to various combinations of high CO₂ and variable amounts of nitrogen fertilization in a free air CO₂ enrichment experiment. In contrast, phyllosphere microorganisms' enzymatic activities appear to act on essential plant metabolites[67], highlighting the prospect of complicated metabolic feedback loops between plant tissues and phyllosphere bacteria[68]. In a separate study, researchers looked for gene markers linked to aerobic anoxygenic phototrophic bacteria [59]. Five distinct metagenomes from phyllosphere microbiota have homologs of bchY, which encodes the Y subunit of chlorophyllide reductase, and *pufM*, which encodes the M subunit of the photosynthetic reaction center (rice, soybean, tobacco, tamarix, clover). The presence of particular pigments linked with aerobic anoxygenic phototrophic bacteria was detected using epifluorescence microscopy. The presence of the genus Methylobacterium, as well as an unknown group of bacteria that appear to be peculiar to the phyllosphere, was discovered to account for 1-7% of the overall population of

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications epiphytic bacteria, with the presence of the genus *Methylobacterium* [59]. As a result, complementary means to detect low-abundance bacterial species in the phyllosphere should be developed, particularly through microscope observation methods such as FISH or fluidic force microscope approaches[60]. Complementary techniques are also required to examine the nutritional and functional mechanisms of microbial adaptation to life in the phyllosphere, particularly by combined meta-analysis of proteomics, transcriptomics, and metabolomics data[69,70,71,72], such as auxotrophic interactions and the probable dependence of phyllosphere microbial community structure on light availability, resulting in foliage and canopy stratification[68].

4. Impact Of Phyllospheric Microorganisms On Plant-Atmosphere-Climate Interactions

Plants release a variety of volatile organic compounds (VOCs) or VOC precursors, which are transported through the phyllosphere and are thought to play a role in climate regulation[73,74,75]. Plants are the primary source of VOC emissions in the biosphere, accounting for over 1,000 Tg per year and including terpenes, monoterpenes, and C1 compounds such as methanol, methane, and halogenated methane. A thorough overview of what is known about how VOC emissions from plants interact with bacterial epiphytes at their surface was recently published[76]. It's still unclear how and to what extent VOCs released by plants could be bio-captured, absorbed, or eaten by epiphytes living directly on their surfaces through bacterial metabolism, or by transiently occurring airborne bacteria, and how climate change would affect microbial metabolism's number, diversity, and ability to filter plant-emitted VOCs[68]. Methanol, a common C1 source for epiphyte microbiota, has been shown to benefit methylotrophic epiphytes such as the Alphaproteobacteria, Methylobacterium extorquens, and the methylotrophic yeast Candida boidinii in situ[77]. In the presence of M. extorquens, Nicotiana seedlings exhaled methanol at 0.005 to 0.01 ppb, but plants not colonized by these bacteria emitted substantially more (0.4–0.7 ppb)[78]. Methane (CH4) is a major greenhouse gas and the most abundant organic trace gas in the atmosphere (with a mixing ratio of 1.8 ppm). At an initially estimated source strength of 62–236 Tg/year for living plants and 1–7 Tg/year for plant litter, both entire plants and detached leaves exhale methane[79]. In the phyllosphere of plants, methanotrophic bacteria have been discovered that use methane as a source of carbon and energy[80]. Many plant species release isoprene (2-methyl-1,3-butadiene), which has been proven to rise with greater temperatures in some circumstances[81]. Isoprene emissions to the atmosphere are comparable to methane emissions, and isoprene is a key precursor for photochemical ozone generation when nitrogen oxide levels are high[82]. Chloromethane (CH₃Cl; methyl chloride) is the most prevalent chlorinated organic chemical in the atmosphere (now 550 parts per trillion) and is thought to be responsible for over 16 percent of halogen-catalyzed stratospheric ozone depletion (World Meteorological Organization, 2014). The chloromethane utilization (cmu) pathway has been used to characterize bacterial adaptation to growth on chloromethane as the sole source of carbon and energy in *M. extorquens* CM4[83]. So far, the few cultivable chloromethane-degrading bacteria

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications obtained from plants[84] were also capable of degrading methanol, allowing them to filter a variety of C1 VOCs generated on plant leaf surfaces[68]. The volatile dimethyl sulfide (DMS) is thought to play a role in global climate regulation[85,75,86]. The oceanic sulfur cycles and phytoplanktonic production of the DMS precursor dimethylsulphoniopropionate (DMSP) are tightly linked to DMS fluxes and dynamics[85,75,86]. Some plant species[73], such as salt marsh grasses of the genus Spartina and sugar canes (Saccharum sp.), are effective providers of DMSP, which can be converted to acrylate and DMS by plant-associated microorganisms containing DMSP lyase[87]. As a result, phyllosphere microbes likely play a key role in carbon and sulfur biogeochemical cycles, ecosystemic signaling, and climate regulation via their action on plant-related volatile compounds, necessitating a better understanding of the functional ecology of phyllosphere microbes, particularly in Spartina and Saccharum species[68]. The existence of prominent bacteria that are associated with phyllosphere microbiota has been discovered in pioneering cloud microbiota research. Tropospheric microorganisms are believed to operate as water condensation or nucleation centers during cloud formation, as well as participate in global carbon cycles by metabolizing organic molecules found in clouds[83]. Furthermore, epiphytic microorganisms, notably ice nucleation-active (INA) bacteria, maybe a key source of airborne bacteria[68]. Microbial communities' combined activities in the phyllosphere, such as VOC production and interactions with plant VOCs, complicated phyllosphere-atmosphere exchanges, and ice nucleation processes, are thus potential mechanisms of large global influence on the biosphere[68].

5. Impact Of Phyllosphere Microorganisms On Plant-Plant, Plant-Insect Herbivory, And Plant-Atmosphere-Chemical Exchanges

Plants produce a wide range of volatile organic compounds (VOCs) that can either encourage or hinder specific species, influencing a wide range of biotic interactions and microbial ecosystems. Microbes, on the other hand, can intercept or change plant smell emissions, and hence plant signaling with other plants or animals[88]. Plant surface microbiota research can disclose the mechanisms that govern processes at the interface between plants, microbes, and plant-interacting creatures, or between plants, microorganisms, and the atmosphere, in both natural and anthropogenic settings[68]. Plant loci involved in defense, such as virus reproduction and cell wall integrity, trichome branching, and morphogenesis, shape the microbial species richness of the leaf microbiota, according to a genome-wide association study of the associated leaf microbial community using 196 recombinant inbred lines of field-grown *Arabidopsis thaliana* [89]. Deficiency in phytohormone jasmonic acid production had no influence on the structure of bacterial communities in another investigation focusing on tobacco plants[90]. A variety of plant defense and signaling molecules, both volatile and non-volatile, are involved in plant biotic interactions, in addition to phytohormones[91]. Plant defense compounds have been demonstrated to be degraded by plant foliage-associated bacteria, resulting in diminished protection against insect defoliators[91]. When

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications produced on plant surfaces by Colorado potato beetle larvae, bacterial symbionts of the genera Stenotrophomonas, Pseudomonas, and Enterobacter decrease the anti-herbivore defenses of tomato by boosting the microbial defense response, favoring larval growth[92]. Experimental bacterial infections of the phyllosphere revealed that individual Pseudomonas spp. strains promoted herbivore host choice and that bacterial strains exhibited variation in the way they ecologically impacted insect herbivores in a recent study of interactions between a specialist chewing insect herbivore and its sole plant host, Cardamine cordifolia[93]. Epiphytic microbes have the metabolic capability to degrade chemicals that are harmful to plants, humans, or the environment. Depollution procedures based on phyllosphere could benefit from such detoxifying capabilities[68]. Aromatic hydrocarbons (phenol, BTEX, chlorophenol, phenanthrene), s-triazines (atrazine, cyanazine), and a variety of other pesticides are all degraded by Arthrobacter species (glyphosate, phenylurea herbicides, malathion)[88]. Plants with sufficient microbial communities that digest a particular set of organic compounds could be used for processes of atmospheric depollution (clean up) in urban or industrial settings, as well as for the depletion of phytosanitary product atmospheric drifts in agricultural settings[68]. Finally, epiphytic bacteria with plant-friendly properties could be employed as probiotic agents[94].

2. CONCLUSION

The phyllosphere is an important environment for microbial ecology research, both scientifically and economically. Many phyllosphere microbial occupants are critical to plant health, a greater knowledge of microorganisms' interactions with plants and among themselves will almost certainly lead to plenty of practical applications. The phyllosphere has several characteristics that make it an ideal environment for studying microbial ecology. This new knowledge could further help us better understand the ecology of potential human pathogenic bacteria on plant surfaces, as well as bring fresh insights into the development of preventative or control techniques for enteric pathogen contamination of crops before harvest.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

HUMAN AND ANIMAL RIGHTS

No Animals/Humans were used for studies that are base of this research.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF DATA AND MATERIALS

The author confirms that the data supporting the findings of this research are available within the article.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

REFERENCES

- 1. Vorholt JA. Microbial life in the phyllosphere. Nature Reviews Microbiology. 2012 Dec;10(12):828-40.
- 2. Lindow SE, Brandl MT. Microbiology of the phyllosphere. Applied and environmental microbiology. 2003 Apr;69(4):1875-83.
- 3. Whipps JM, Hand P, Pink D, Bending GD. Phyllosphere microbiology with special reference to diversity and plant genotype. Journal of applied microbiology. 2008 Dec;105(6):1744-55.
- 4. Vaïtilingom M, Deguillaume L, Vinatier V, Sancelme M, Amato P, Chaumerliac N, Delort AM. Potential impact of microbial activity on the oxidant capacity and organic carbon budget in clouds. Proceedings of the National Academy of Sciences. 2013 Jan 8;110(2):559-64.
- 5. Verma P, Yadav AN, Khannam KS, Panjiar N, Kumar S, Saxena AK, Suman A. Assessment of genetic diversity and plant growth promoting attributes of psychrotolerant bacteria allied with wheat (Triticum aestivum) from the northern hills zone of India. Annals of microbiology. 2015 Dec;65(4):1885-99.
- 6. Verma P, Yadav AN, Khannam KS, Kumar S, Saxena AK, Suman A. Molecular diversity and multifarious plant growth promoting attributes of Bacilli associated with wheat (Triticum aestivum L.) rhizosphere from six diverse agro-ecological zones of India. Journal of Basic Microbiology. 2016 Jan;56(1):44-58.
- 7. Inácio J, Pereira P, Carvalho DM, Fonseca A, Amaral-Collaco MT, Spencer-Martins I. Estimation and diversity of phylloplane mycobiota on selected plants in a mediterranean-type ecosystem in Portugal. Microbial Ecology. 2002 Dec;44(4):344-53.
- 8. Thompson IP, Bailey MJ, Fenlon JS, Fermor TR, Lilley AK, Lynch JM, McCormack PJ, McQuilken MP, Purdy KJ, Rainey PB, Whipps JM. Quantitative and qualitative seasonal changes in the microbial community from the phyllosphere of sugar beet (Beta vulgaris). Plant and Soil. 1993 Mar;150(2):177-91.
- 9. Legard DE, McQuilken MP, Whipps JM, Fenlon JS, Fermor TR, Thompson IP, Bailey MJ, Lynch JM. Studies of seasonal changes in the microbial populations on the phyllosphere of spring wheat as a prelude to the release of a genetically modified microorganism. Agriculture, Ecosystems & Environment. 1994 Sep 1;50(2):87-101.

- Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
 10. Rasche F, Trondl R, Naglreiter C, Reichenauer TG, Sessitsch A. Chilling and cultivar type affect the diversity of bacterial endophytes colonizing sweet pepper (Capsicum anuum L.). Canadian journal of microbiology. 2006 Nov 1;52(11):1036-45.
- Kadivar H, Stapleton AE. Ultraviolet radiation alters maize phyllosphere bacterial diversity. Microbial Ecology. 2003 May 1:353-61.
- 12. Lambais MR, Crowley DE, Cury JC, Bull RC, Rodrigues RR. Bacterial diversity in tree canopies of the Atlantic forest. Science. 2006 Jun 30;312(5782):1917-.
- Yang CH, Crowley DE, Borneman J, Keen NT. Microbial phyllosphere populations are more complex than previously realized. Proceedings of the National Academy of Sciences. 2001 Mar 27;98(7):3889-94.
- Glushakova AM, Chernov IY. Seasonal dynamics in a yeast population on leaves of the common wood sorrel Oxalis acetosella L. Microbiology. 2004 Mar;73(2):184-8.
- 15. Arnold AE, Maynard Z, Gilbert GS, Coley PD, Kursar TA. Are tropical fungal endophytes hyperdiverse?. Ecology letters. 2000 Jul;3(4):267-74.
- 16. Rana KL, Kour D, Sheikh I, Yadav N, Yadav AN, Kumar V, Singh BP, Dhaliwal HS, Saxena AK. Biodiversity of endophytic fungi from diverse niches and their biotechnological applications. Advances in endophytic fungal research. 2019:105-44.
- 17. Miyamoto T, Kawahara M, Minamisawa K. Novel endophytic nitrogen-fixing clostridia from the grass Miscanthus sinensis as revealed by terminal restriction fragment length polymorphism analysis. Applied and environmental microbiology. 2004 Nov;70(11):6580-6.
- Sessitsch A, Hackl E, Wenzl P, Kilian A, Kostic T, Stralis-Pavese N, Sandjong BT, Bodrossy L. Diagnostic microbial microarrays in soil ecology. New Phytologist. 2006 Sep;171(4):719-36.
- 19. Singh BK, Nazaries L, Munro S, Anderson IC, Campbell CD. Use of multiplex terminal restriction fragment length polymorphism for rapid and simultaneous analysis of different components of the soil microbial community v. Applied and environmental microbiology. 2006 Nov;72(11):7278-85.
- 20. Manceau CR, Kasempour MN. Endophytic versus epiphytic colonization of plants: what comes first?. Phyllosphere microbiology. 2002:115-23.
- 21. Suslow TV. Production practices affecting the potential for persistent contamination of plants by microbial foodborne pathogens. Phyllosphere microbiology. 2002:241-56.
- 22. Zak JC. Implications of a leaf surface habitat for fungal community structure and function. Phyllosphere microbiology. 2002:299-315.
- Lighthart B. The ecology of bacteria in the alfresco atmosphere. FEMS Microbiology Ecology. 1997 Aug 1;23(4):263-74.

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
24. Wulff EG, Van Vuurde JW, Hockenhull J. The ability of the biological control agent Bacillus subtilis, strain BB, to colonise vegetable brassicas endophytically following seed inoculation.

- Plant and Soil. 2003 Aug;255(2):463-74.
- 25. Melotto M, Underwood W, He SY. Role of stomata in plant innate immunity and foliar bacterial diseases. Annual review of phytopathology. 2008;46:101.
- 26. Aung K, Jiang Y, He SY. The role of water in plant–microbe interactions. The Plant Journal. 2018 Feb;93(4):771-80.
- 27. Meyer KM, Leveau JH. Microbiology of the phyllosphere: a playground for testing ecological concepts. Oecologia. 2012 Mar;168(3):621-9.
- 28. Beattie GA, Lindow SE. The secret life of foliar bacterial pathogens on leaves. Annual review of phytopathology. 1995 Sep;33(1):145-72.
- 29. Monier JM, Lindow SE. Frequency, size, and localization of bacterial aggregates on bean leaf surfaces. Applied and environmental microbiology. 2004 Jan;70(1):346-55.
- 30. Thapa S, Prasanna R. Prospecting the characteristics and significance of the phyllosphere microbiome. Annals of microbiology. 2018 May;68(5):229-45.
- Aragón W, Reina-Pinto JJ, Serrano M. The intimate talk between plants and microorganisms at the leaf surface. Journal of Experimental Botany. 2017 Nov 9;68(19):5339-50.
- 32. Olson DL, Nechols JR. Effects of squash leaf trichome exudates and honey on adult feeding, survival, and fecundity of the squash bug (Heteroptera: Coreidae) egg parasitoid Gryon pennsylvanicum (Hymenoptera: Scelionidae). Environmental Entomology. 1995 Apr 1;24(2):454-8.
- 33. Ascensão L, Pais MS. The leaf capitate trichomes ofLeonotis leonurus: histochemistry, ultrastructure and secretion. Annals of Botany. 1998 Feb 1;81(2):263-71.
- 34. Brewer CA, Smith WK, Vogelmann TC. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. Plant, Cell & Environment. 1991 Dec;14(9):955-62.
- 35. Morris CE, Kinkel LL. Fifty years of phyllosphere microbiology: significant contributions to research in related fields. Phyllosphere microbiology. 2002:365-75.
- 36. Baldotto LE, Olivares FL. Phylloepiphytic interaction between bacteria and different plant species in a tropical agricultural system. Canadian Journal of Microbiology. 2008 Nov;54(11):918-31.
- 37. Nongkhlaw FM, Joshi SR. Distribution pattern analysis of epiphytic bacteria on ethnomedicinal plant surfaces: A micrographical and molecular approach. Journal of Microscopy and Ultrastructure. 2014 Mar 1;2(1):34-40.
- Kutschera U. Plant-associated methylobacteria as co-evolved phytosymbionts: a hypothesis.
 Plant signaling & behavior. 2007 Mar 1;2(2):74-8.

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
39. Georgiou G, Lin SC, Sharma MM. Surface–active compounds from microorganisms. Bio/technology. 1992 Jan;10(1):60-5.

- 40. Freeman BC, Chen C, Beattie GA. Identification of the trehalose biosynthetic loci of Pseudomonas syringae and their contribution to fitness in the phyllosphere. Environmental Microbiology. 2010 Jun;12(6):1486-97.
- 41. Melotto M, Kunkel BN. Virulence strategies of plant pathogenic bacteria. The Prokaryotes: Berlin, Heidelberg: Springer. 2013:61-82.
- 42. Arrebola E, Cazorla FM, Perez-García A, De Vicente A. Chemical and metabolic aspects of antimetabolite toxins produced by Pseudomonas syringae pathovars. Toxins. 2011 Aug 31;3(9):1089-110.
- 43. Zheng XY, Spivey NW, Zeng W, Liu PP, Fu ZQ, Klessig DF, He SY, Dong X. Coronatine promotes Pseudomonas syringae virulence in plants by activating a signaling cascade that inhibits salicylic acid accumulation. Cell host & microbe. 2012 Jun 14;11(6):587-96.
- 44. Robert-Seilaniantz A, Grant M, Jones JD. Hormone crosstalk in plant disease and defense: more than just jasmonate-salicylate antagonism. Annual review of phytopathology. 2011 Sep 8;49:317-43.
- 45. Chang WS, Van De Mortel M, Nielsen L, Nino de Guzman G, Li X, Halverson LJ. Alginate production by Pseudomonas putida creates a hydrated microenvironment and contributes to biofilm architecture and stress tolerance under water-limiting conditions.
- 46. Wu Z, Kan FW, She YM, Walker VK. Biofilm, ice recrystallization inhibition and freeze-thaw protection in an epiphyte community. Applied biochemistry and microbiology. 2012 Jul;48(4):363-70.
- 47. Freeman BC, Chen C, Yu X, Nielsen L, Peterson K, Beattie GA. Physiological and transcriptional responses to osmotic stress of two Pseudomonas syringae strains that differ in epiphytic fitness and osmotolerance. Journal of bacteriology. 2013 Oct 15;195(20):4742-52.
- 48. Dunger G, Relling VM, Tondo ML, Barreras M, Ielpi L, Orellano EG, Ottado J. Xanthan is not essential for pathogenicity in citrus canker but contributes to Xanthomonas epiphytic survival. Archives of microbiology. 2007 Aug;188(2):127-35.
- 49. Aslam SN, Newman MA, Erbs G, Morrissey KL, Chinchilla D, Boller T, Jensen TT, De Castro C, Ierano T, Molinaro A, Jackson RW. Bacterial polysaccharides suppress induced innate immunity by calcium chelation. Current Biology. 2008 Jul 22;18(14):1078-83.
- 50. Rigano LA, Siciliano F, Enrique R, Sendín L, Filippone P, Torres PS, Qüesta J, Dow JM, Castagnaro AP, Vojnov AA, Marano MR. Biofilm formation, epiphytic fitness, and canker development in Xanthomonas axonopodis pv. citri. Molecular Plant-Microbe Interactions. 2007 Oct;20(10):1222-30.

- Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
 51. Vorhölter FJ, Schneiker S, Goesmann A, Krause L, Bekel T, Kaiser O, Linke B, Patschkowski T, Rückert C, Schmid J, Sidhu VK. The genome of Xanthomonas campestris pv. campestris B100 and its use for the reconstruction of metabolic pathways involved in xanthan biosynthesis. Journal of biotechnology. 2008 Mar 20;134(1-2):33-45.
- 52. Hirano SS, Upper CD. Dynamics, spread, and persistence of a single genotype of Pseudomonas syringae relative to those of its conspecifics on populations of snap bean leaflets. Applied and environmental microbiology. 1993 Apr;59(4):1082-91.
- Quiñones B, Dulla G, Lindow SE. Quorum sensing regulates exopolysaccharide production, motility, and virulence in Pseudomonas syringae. Molecular plant-microbe interactions. 2005 Jul;18(7):682-93.
- 54. Burch AY, Shimada BK, Mullin SW, Dunlap CA, Bowman MJ, Lindow SE. Pseudomonas syringae coordinates production of a motility-enabling surfactant with flagellar assembly. Journal of bacteriology. 2012 Mar 15;194(6):1287-98.
- 55. Tans-Kersten J, Huang H, Allen C. Ralstonia solanacearum needs motility for invasive virulence on tomato. Journal of bacteriology. 2001 Jun 15;183(12):3597-605.
- 56. Beattie GA, Lindow SE. Bacterial colonization of leaves: a spectrum of strategies. Phytopathology. 1999 May;89(5):353-9.
- 57. Djonović S, Urbach JM, Drenkard E, Bush J, Feinbaum R, Ausubel JL, Traficante D, Risech M, Kocks C, Fischbach MA, Priebe GP. Trehalose biosynthesis promotes Pseudomonas aeruginosa pathogenicity in plants. PLoS pathogens. 2013 Mar 7;9(3):e1003217.
- 58. Kolton M, Sela N, Elad Y, Cytryn E. Comparative genomic analysis indicates that niche adaptation of terrestrial Flavobacteria is strongly linked to plant glycan metabolism. PloS one. 2013 Sep 26;8(9):e76704.
- 59. Atamna-Ismaeel N, Finkel OM, Glaser F, Sharon I, Schneider R, Post AF, Spudich JL, von Mering C, Vorholt JA, Iluz D, Béjà O. Microbial rhodopsins on leaf surfaces of terrestrial plants. Environmental microbiology. 2012 Jan;14(1):140-6.
- 60. Stiefel P, Zambelli T, Vorholt JA. Isolation of optically targeted single bacteria by application of fluidic force microscopy to aerobic anoxygenic phototrophs from the phyllosphere. Applied and environmental microbiology. 2013 Aug 15;79(16):4895-905.
- 61. Tolonen AC, Aach J, Lindell D, Johnson ZI, Rector T, Steen R, Church GM, Chisholm SW. Global gene expression of Prochlorococcus ecotypes in response to changes in nitrogen availability. Molecular systems biology. 2006;2(1):53.
- Moran MA, Miller WL. Resourceful heterotrophs make the most of light in the coastal ocean. Nature Reviews Microbiology. 2007 Oct;5(10):792-800.
- 63. Athanasiou K, Dyson BC, Webster RE, Johnson GN. Dynamic acclimation of photosynthesis increases plant fitness in changing environments. Plant Physiology. 2010 Jan;152(1):366-73.

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
64. Sulmon C, Gouesbet G, Ramel F, Cabello-Hurtado F, Penno C, Bechtold N, Couée I, Amrani AE. Carbon dynamics, development and stress responses in Arabidopsis: involvement of the APL4 subunit of ADP-glucose pyrophosphorylase (starch synthesis). PLoS One. 2011 Nov 3;6(11):e26855.

- 65. Manching HC, Balint-Kurti PJ, Stapleton AE. Southern leaf blight disease severity is correlated with decreased maize leaf epiphytic bacterial species richness and the phyllosphere bacterial diversity decline is enhanced by nitrogen fertilization. Frontiers in plant science. 2014 Aug 15;5:403.
- 66. Ren G, Zhang H, Lin X, Zhu J, Jia Z. Response of phyllosphere bacterial communities to elevated CO2 during rice growing season. Applied microbiology and biotechnology. 2014 Nov;98(22):9459-71.
- 67. Huang S, Zhang J, Tao Z, Lei L, Yu Y, Huang L. Enzymatic conversion from pyridoxal to pyridoxine caused by microorganisms within tobacco phyllosphere. Plant physiology and biochemistry. 2014 Dec 1;85:9-13.
- 68. Bringel F, Couée I. Pivotal roles of phyllosphere microorganisms at the interface between plant functioning and atmospheric trace gas dynamics. Frontiers in microbiology. 2015 May 22;6:486.
- 69. Delmotte N, Knief C, Chaffron S, Innerebner G, Roschitzki B, Schlapbach R, von Mering C, Vorholt JA. Community proteogenomics reveals insights into the physiology of phyllosphere bacteria. Proceedings of the National Academy of Sciences. 2009 Sep 22;106(38):16428-33.
- 70. Knief C, Delmotte N, Chaffron S, Stark M, Innerebner G, Wassmann R, Von Mering C, Vorholt JA. Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. The ISME journal. 2012 Jul;6(7):1378-90.
- Knief C, Delmotte N, Vorholt JA. Bacterial adaptation to life in association with plants–A proteomic perspective from culture to in situ conditions. Proteomics. 2011 Aug;11(15):3086-105.
- 72. Knief C, Delmotte N, Vorholt JA. Bacterial adaptation to life in association with plants–A proteomic perspective from culture to in situ conditions. Proteomics. 2011 Aug;11(15):3086-105.
- 73. Otte ML, Wilson G, Morris JT, Moran BM. Dimethylsulphoniopropionate (DMSP) and related compounds in higher plants. Journal of experimental botany. 2004 Aug 1;55(404):1919-25.
- 74. Peñuelas J, Staudt M. BVOCs and global change. Trends in plant science. 2010 Mar 1;15(3):133-44.
- 75. Schäfer H, Myronova N, Boden R. Microbial degradation of dimethylsulphide and related C1sulphur compounds: organisms and pathways controlling fluxes of sulphur in the biosphere. Journal of experimental botany. 2010 Jan 1;61(2):315-34.

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
76. Junker RR, Tholl D. Volatile organic compound mediated interactions at the plant-microbe interface. Journal of chemical ecology. 2013 Jul;39(7):810-25.

- 77. Sy A, Timmers AC, Knief C, Vorholt JA. Methylotrophic metabolism is advantageous for Methylobacterium extorquens during colonization of Medicago truncatula under competitive conditions. Applied and Environmental Microbiology. 2005 Nov;71(11):7245-52.
- 78. Abanda-Nkpwatt D, Müsch M, Tschiersch J, Boettner M, Schwab W. Molecular interaction between Methylobacterium extorquens and seedlings: growth promotion, methanol consumption, and localization of the methanol emission site. Journal of experimental botany. 2006 Dec 1;57(15):4025-32.
- Keppler F, Hamilton JT, Braß M, Röckmann T. Methane emissions from terrestrial plants under aerobic conditions. Nature. 2006 Jan;439(7073):187-91.
- 80. Iguchi H, Sato I, Sakakibara M, Yurimoto H, Sakai Y. Distribution of methanotrophs in the phyllosphere. Bioscience, biotechnology, and biochemistry. 2012:120281.
- 81. Harley PC, Loreto F, Di Marco G, Sharkey TD. Theoretical considerations when estimating the mesophyll conductance to CO2 flux by analysis of the response of photosynthesis to CO2. Plant physiology. 1992 Apr;98(4):1429-36.
- 82. Arneth A, Schurgers G, Hickler T, Miller PA. Effects of species composition, land surface cover, CO2 concentration and climate on isoprene emissions from European forests. Plant Biology. 2007;9(S 01):e87-98.
- 83. Roselli S, Nadalig T, Vuilleumier S, Bringel F. The 380 kb pCMU01 plasmid encodes chloromethane utilization genes and redundant genes for vitamin B12-and tetrahydrofolatedependent chloromethane metabolism in Methylobacterium extorquens CM4: a proteomic and bioinformatics study. PLoS One. 2013 Apr 9;8(4):e56598.
- 84. Nadalig T, Farhan Ul Haque M, Roselli S, Schaller H, Bringel F, Vuilleumier S. Detection and isolation of chloromethane-degrading bacteria from the Arabidopsis thaliana phyllosphere, and characterization of chloromethane utilization genes. FEMS microbiology ecology. 2011 Aug 1;77(2):438-48.
- 85. Charlson RJ, Lovelock JE, Andreae MO, Warren SG. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. Nature. 1987 Apr;326(6114):655-61.
- 86. Nevitt GA. The neuroecology of dimethyl sulfide: a global-climate regulator turned marine infochemical. Integrative and comparative biology. 2011 Nov 1;51(5):819-25.
- 87. Ansede JH, Friedman R, Yoch DC. Phylogenetic analysis of culturable dimethyl sulfideproducing bacteria from a Spartina-dominated salt marsh and estuarine water. Applied and Environmental Microbiology. 2001 Mar 1;67(3):1210-7.
- 88. Scheublin TR, Leveau JH. Isolation of A rthrobacter species from the phyllosphere and demonstration of their epiphytic fitness. Microbiologyopen. 2013 Feb;2(1):205-13.

Shrivastava & Ghosh RJLBPCS 2022 www.rjlbpcs.com Life Science Informatics Publications
89. Carpenter LJ, Reimann S, Burkholder JB, Clerbaux C, Hall BD, Hossaini R, Laube JC, Yvon-Lewis SA. Update on ozone-depleting substances (ODSs) and other gases of interest to the Montreal protocol. 9789966076014. 2014.

- 90. Santhanam R, Groten K, Meldau DG, Baldwin IT. Analysis of plant-bacteria interactions in their native habitat: bacterial communities associated with wild tobacco are independent of endogenous jasmonic acid levels and developmental stages. PLoS One. 2014 Apr 11;9(4):e94710.
- 91. Mason CJ, Couture JJ, Raffa KF. Plant-associated bacteria degrade defense chemicals and reduce their adverse effects on an insect defoliator. Oecologia. 2014 Jul;175(3):901-10.
- 92. Chung SH, Rosa C, Scully ED, Peiffer M, Tooker JF, Hoover K, Luthe DS, Felton GW. Herbivore exploits orally secreted bacteria to suppress plant defenses. Proceedings of the National Academy of Sciences. 2013 Sep 24;110(39):15728-33.
- 93. Humphrey PT, Nguyen TT, Villalobos MM, Whiteman NK. Diversity and abundance of phyllosphere bacteria are linked to insect herbivory. Molecular Ecology. 2014 Mar;23(6):1497-515.
- 94. Berlec A. Novel techniques and findings in the study of plant microbiota: search for plant probiotics. Plant Science. 2012 Sep 1;193:96-102.
- 95. Stadler B, Michalzik B, Müller T. Linking aphid ecology with nutrient fluxes in a coniferous forest. Ecology. 1998 Jul;79(5):1514-25.
- 96. Papen H, Geβler A, Zumbusch E, Rennenberg H. Chemolithoautotrophic nitrifiers in the phyllosphere of a spruce ecosystem receiving high atmospheric nitrogen input. Current microbiology. 2002 Jan;44(1):56-60.
- 97. Freiberg E. Microclimatic parameters influencing nitrogen fixation in the phyllosphere in a Costa Rican premontane rain forest. Oecologia. 1998 Nov;117(1):9-18.
- 98. Freiberg E. Influence of microclimate on the occurrence of cyanobacteria in the phyllosphere in a premontane rain forest of Costa Rica. Plant Biology. 1999 Mar;1(2):244-52.
- 99. Sivakumar N, Sathishkumar R, Selvakumar G, Shyamkumar R, Arjunekumar K. Phyllospheric microbiomes: diversity, ecological significance, and biotechnological applications. InPlant microbiomes for sustainable agriculture 2020 (pp. 113-172). Springer, Cham.