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Review article

Phyllosphere Microbiome in Ecosystem Management and Plant Growth Promotion for Agricultural Sustainability

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ABSTRACT
This review paper attempts to interpret the various role of phyllosphere microbiome, survival, resistant mechanisms to confront the adverse environmental conditions, production of pigment, extracellular polysaccharides, biosurfactants to promote surface attachment desiccation protection, volatile organic compounds, phytoalexins, as a defensive role to compete for space and nutrients. The beneficial phyllosphere microbes contributing to promotion of plant growth by facilitating nutrient acquisition, modulating hormonal signaling, biocontrol for plant pathogens in multi-various crops is discussed in detail. Phyllobacteria show encouraging interactions with host plants in improving plant health and biometric traits by regulating nutrient acquisition, phytohormones production, biotic and abiotic stress management. The members of genera *Bacillus, Enterobacter, Microbacterium, Methylobacterium, Stenotrophomonas, Pseudomonas, Pseudarthrobacter,* and *Kocuria* were the most dominant plant growth promoting bacteria reported in phyllosphere. The beneficial phyllosphere microorganism enhances crop yield while reducing the environmental footprint associated with synthetic fertilizers and pesticides. The review focuses and thrust on the development as well as commercialization of biostimulants derived from phyllosphere microbiomes. These biostimulants, and their metabolites, can be tapped to enhance plant growth, nutrient uptake, and overall crop performance in organic farming. Furthermore, this review paper focus on certain drawbacks that there have been few researches on phyllosphere yeast and its symbiotic association with bacteria, thereby emphasizing subsequent research in this area.

Key words: Phyllosphere, Microbiomes, Ecosystem, Plants, Biostimulants

INTRODUCTION

Phyllosphere is the aerial portion or parts of the plant that are above ground, which include leaves, stems, and flowers, and function as a habitat for a variety of microorganisms Plants provide a variety of ecosystem for endophytic and epiphytic microbial lineages that colonize plant surfaces, both below and above ground, as well as internal tissues (Whipps et al. 2008). The phyllosphere comprises the aerial or above-ground plant parts, including leaves, stems, flowers, and fruits, with leaves as the most dominant part**.** Leaves are well organized, and multi-layered organs of the plant characterized by a thin waxy cuticle layer around the upper and lower epidermis, providing a physical barrier against various biotic and abiotic stressors and therefore offer a hostile environment for microbial life**.** The survival of these microorganisms depends on their capacity to develop certain resistant mechanisms to confront the adverse environmental conditions prevalent in the phyllosphere, such as pigment production against UV radiation, production of extracellular polysaccharides (EPS) and biosurfactants to promote surface attachment and desiccation protection, chemical warfare production to compete for space and nutrients, etc., (Bashir et al. 2022).

Phyllospere microbiomes

A variety of bacteria, fungi, and yeasts colonize the phyllosphere region, followed less frequently by nematodes and protozoa. These microorganisms exhibit mutualism or amensalism, or commensalism or antagonism type of relationship on their host plants. Among the diverse community of microbes, bacterial microbiomes are predominant on leaves, with its range in between 10^2 and 10^{12} CFUg^{-1} of the leaf (Sivakumar et al. 2020). Generally, the phyllosphere contains four major bacteria such as *Proteobacteria, Firmicutes, Bacteroides,* and *Actinobacteria*. Predominant bacteria invading the phyllosphere include *Methylibium, Hyphomicrobium, Methylocella, Proteobacteria, Actinobacteria, Bacteroidetes, Flavobacterium, Massilia, Pseudomonas,* and *Rathayibacter*. Genera such as *Alternaria, Acremonium, Aspergillus, Cladosporium, Mucor, Penicillium* are the frequent epiphytic and endophytic fungal colonisers. Moreover, the abundance of filamentous fungi has been estimated to range from 10^2 to 10^8 CFU g^{-1} based on the culture-dependent methods. The cultivable yeast genera such as *Cryptococcus, Sporobolomyces, Rhodotorula,* are predominant in plant leaves.

Multifarious roles of phyllosphere microbiome

Microbiota influences productivity and plant health at different ecological scales, from individual plants to ecosystems. The process of diazotrophic nitrogen fixation, carbon-di-oxide sequestration during plant growth, subsequent conversion into plant litter upon senescence followed by decomposition impacts the global cycle of carbon and nitrogen at the ecosystem scale (Sohrabi et al. 2023).

Role of phyllosphere microorganisms in bioremediation

The technique known as "bioremediation" involves the use of microorganisms like bacteria, fungi, algae, and plants to break down, alter, remove, immobilize, or detoxify different types of chemical and physical contaminants found in the environment (Bala et al. 2022). Acetate utilization metabolism as a survival strategy of peat-inhabiting *Methylocystis heyeri* H2^T and *Methylocystis echinoides* IMET10491^T was demonstrated by Belova et al. (2011). Saikia (2024) have elaborately reviewed on the phylloplane bacteria and stated that, leaf exudates, position of leaves, leaf appendages, stomatal cavities, age and family of plant, environmental pollutants, plant protection chemicals are the factors that influence the type of microorganisms in phyllosphere. In the earlier studies of Ali et al. (2015), a culture-independent method was used to examine the bacteria found on the leaves of sixteen different types of plants, both wild and cultivated, from all around Kuwait. The 16S rDNA and total genomic DNA of the phyllosphere consortia included bacterial communities dominated by hydrocarbonoclastic (or carbon-utilizing) bacterial genera on their surfaces. The plant leaves were used to effectively remove volatile hydrocarbons from sealed microcosms in the

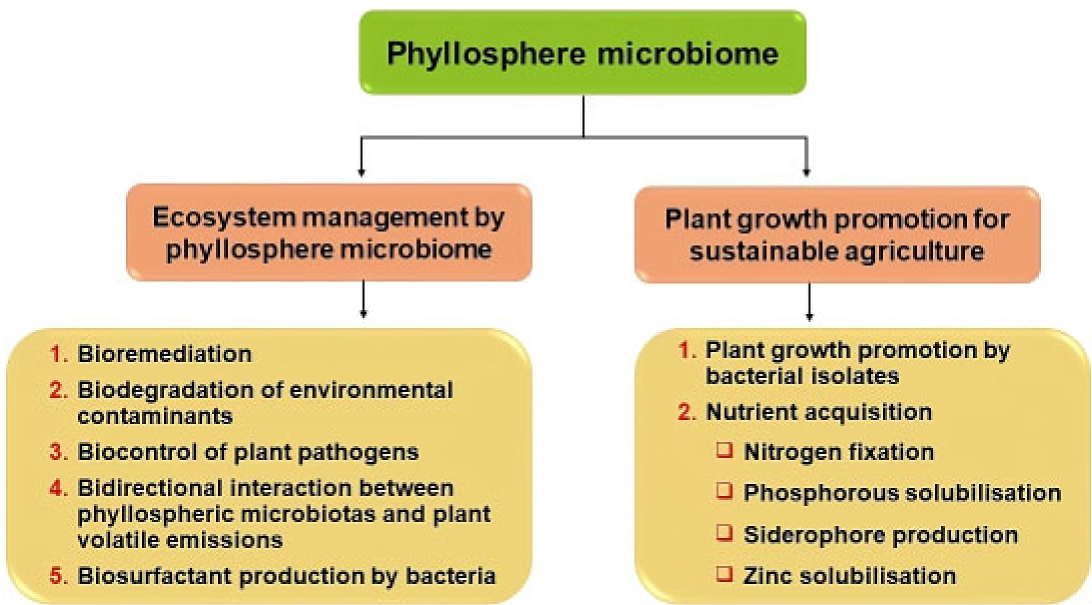

Figure 1. Ecosystem management and plant growth promotion by phyllobiomes

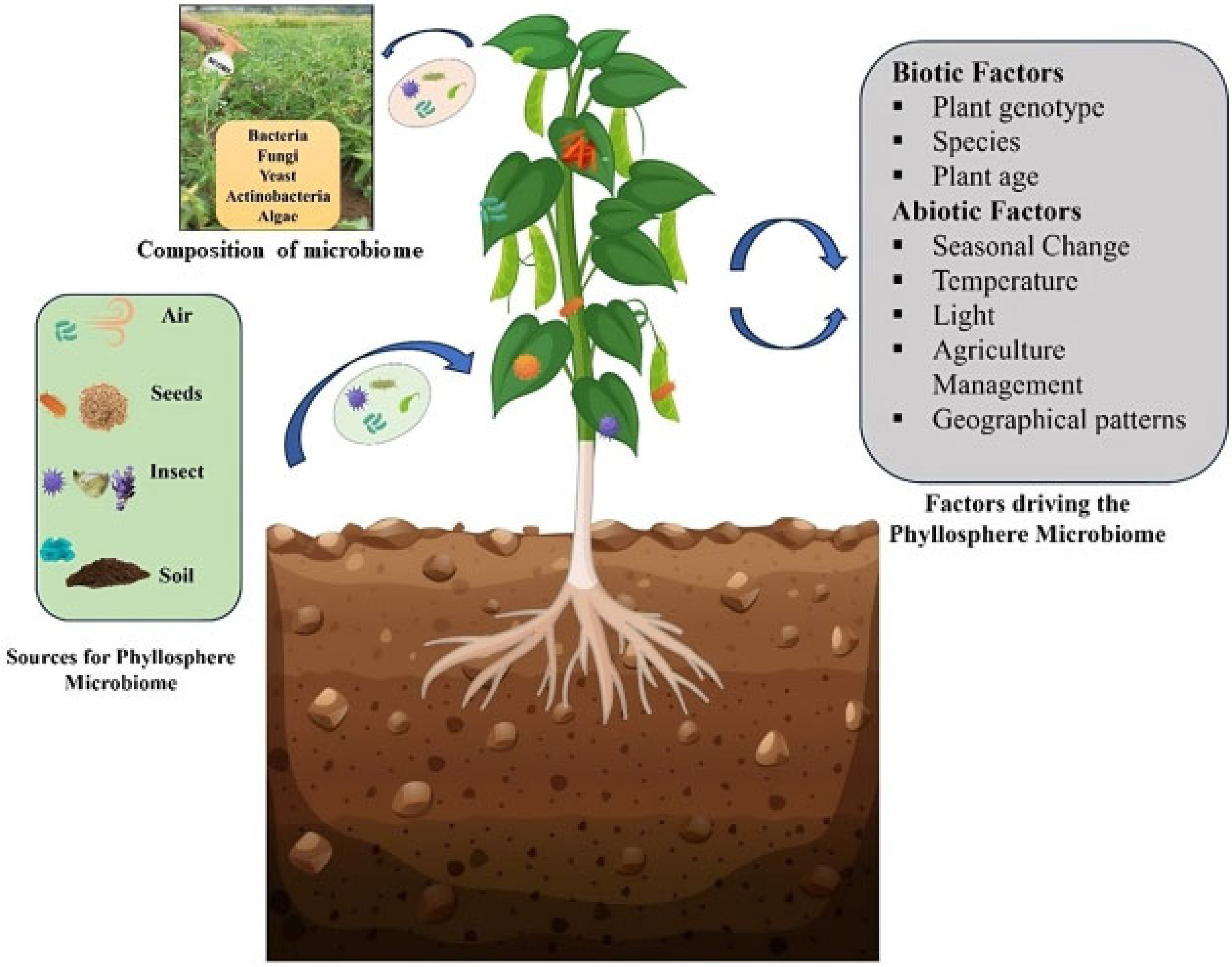

Figure 2. Driving factors for phyllomicrobiomes

lab. The genera *Arthrobacter, Flavobacterium, Halomonas, Marinobacter, Neisseria, Ochrobactrum, Ralstonia*, were the phyllospheric microflora present in most of the assessed plants. *Planomicrobium, Streptotrophomonas, Kocuria, Rhodococcus, Exiguobacterium*, and *Propionibacterium* were isolated from some leaf surfaces.

Biodegradation of environmental contaminants by phyllomicrobiomes

The most prevalent polyaromatic hydrocarbons (PAHs) in the ambient air are naphthalene and phenanthrene, which are produced by industrial operations, oil refining, and vehicle emissions. PAHs can be broken down by the microorganisms settling in the phyllosphere of these contaminated locations. In five highly polluted sites in Srilanka, two bacterial strains namely *Alcaligenes feacalis* and *Alcaligenes* sp.1ISO were isolated from the phyllosphere of ornamental plant species namely *Ixora chinensis*, *Ervatamia divaricata*, *Hibiscus rosa-sinensis*, and *Amaranthus cruentus* which showed a higher degradation ability to naphthalene and phenanthrene. These two strains were resistant to ampicillin because they both have plasmids. When these plasmids were transformed into *E. coli* JM109, it was found to effectively break down naphthalene and phenanthrene. Plasmids of those bacterial strains contain the genes nahR, nahU, and phnG, which are involved in the degradation of naphthalene and phenanthrene, respectively (Undugoda et al. 2016). Md Gulzar and Mazumder (2023) have discussed in their review of literature about various phyllobacterial species and their key role in host plants. It was indicated that *Citrobacter freundii, Microbacterium, Rhodococcus* inhabiting *Pisum* *sativum* and *Phaseolus vulgaris* are involved in reducing the extra burden on plants by degrading crude oil, n-octadecane and phenanthrene in the phyllosphere.

Bidirectional interaction between phyllospheric microbiota and plant volatile emissions

Plants are the major VOCs emitter in biosphere (>1000 Tg/yr) which release Volatile Organic compounds such as terpenes, monoterpenes, flavones, methanol, methane, and halogenated methane (C_1 compounds) (Laothawornkitkul et al. 2009). Methylotrophic microorganisms are ubiquitous, found in roots and leave of plants and also air. Methylotrophic microorganisms utilize the plant organic compounds containing a single carbon atom or lacking C–C bonds such as methanol (CH_3OH), formaldehyde (CH_2O), and chloromethane (CH_3Cl). Methanotrophic bacteria utilize methane as source of carbon and energy which is found in the phyllosphere of plants.

The Volatile Organic Compounds (VOCs) are produced by some phyllosphere microorganisms aid in pathogen defense apart from other functions. The phyllobacteria are involved in free diffusion of VOCs to the atmosphere and capturing the VOCs by the surface microbes, act as filters. Through specialized metabolic activities microbes metabolize the VOCs and adaptive response of microbes in the specialized environment such as in Volatile Organic Gases (VOGs). The VOCs emitted by some non-pathogenic microorganisms can either act directly to prevent plant pathogens or signal antimicrobial responses. Among various VOCs, terpenoids have been shown to exhibit a significant defensive role against pathogen infection. For example, *Enterobacter aerogenes*, an endophytic bacterium in maize (*Zea mays*), produce 2,3-butanediol, which acts as a phytohormone influencing tritrophic interactions and increases resistance against phytopathogens (Farre-Armengol et al. 2016).

Biosurfactant production by phyllosphere bacteria

Biomolecules with both hydrophobic and hydrophilic regions that are surface-active and amphiphilic are referred to as microbial surfactants, or biosurfactants. These materials are expelled extracellularly by microbes. Biosurfactants are produced by a variety of microorganisms, such as *Pseudomonas aeruginosa*, *Bacillus* sp., *Acinetobacter* sp., and *Candida antartica*. The surface bacteria can manufacture biosurfactant compounds, like syringafactin produced by *Pseudomonas syringae* (Krimm et al. 2005). This could increase the amount of sugar and water that are available, which could enhance the conditions for the growth of epiphytic bacteria (Lindow and Brandl 2003, van der Wal and Leveau 2011). Hygroscopic biosurfactants that are produced on waxy leaf surfaces seem to benefit bacteria because they make it easier for them to get nutrients and attract moisture to the area. The pre-colonized leaf surface has low diffusion of nutrients. Bacteria inside an aqueous sink on the leaf surface receive higher levels of nutrients and can produce biosurfactants that quickly adsorb to the cell surface and cuticular waxes, aiding in cuticular permeability. Once the leaf surface has dried, the biosurfactants remain adsorbed to the waxes adjacent to the bacteria and enhance the permeability of the cuticle to a small extent. Under high humidities, the biosurfactants attract atmospheric water to the cuticle adjacent to the bacteria, creating an aqueous sink that enhances the movement of nutrients across the cuticle (Burch et al. 2014).

Plant growth promotion by phyllosphere bacterial isolates

Methylotrophic bacteria have been identified in the phyllosphere of a variety of agricultural plants, including potatoes, radish, sugarcane, and pigeon pea. Using *Methylobacterium* sp. (NC4), cell-free culture filtrates improved wheat (*Triticum aestivum*) seed germination, with the highest values recorded at 98.3%. *Methylobacterium* sp. (NC28) produced the longest and healthiest seedlings. These helpful methylotrophs that produce cytokinin can be used to co-inoculate pink-pigmented facultative methylotrophs with other suitable bacterial strains to create bio-inoculants that will enhance plant growth and productivity in an eco-friendly way (Meena et al. 2012). In order to have a better understanding of the phyllosphere's lifestyle and the genetic foundations of plant growth promotion, A plant-probiotic methylotroph in the phyllosphere, *Methylobacterium oryzae* CBMB20^T, was isolated from rice stems and its whole genome was sequenced by Kwak et al. (2014). A tray and pot experiment was conducted to examine the reaction of Brinjal Bacterial Isolate (BBI) inoculation on three cultivars of Brinjal: Arka keshav, Arka shirish, and Arka kusumakar. The results of the tray trials demonstrated that, plants inoculated with BBI exhibited a significant increase in germination count, root length, shoot length, plant fresh weight, and dry weight than the un-inoculated control. According to a pot trial, bacterial inoculation with BBI considerably boosted the treated plants, increased shoot dry weight in comparison to the untreated controls. When inoculated with BBI, the brinjal cultivar Arka keshav, responded more favorably (Charles et al. 2021).

Abadi et al. (2020) found that members of genera *Bacillus, Pseudomonas, Microbacterium, Stenotrophomonas, Enterobacter, Pseudarthrobacter,* and *Kocuria* were the most dominant PGPB in maize phyllosphere. Foliar spray of *M. arborescens*, *B. subtilis* + *S. maltophilia*, *S. maltophilia*, *B. megaterium*, and *E. hormaechei* significantly increased the shoot dry weight by 10.40, 9.53, 8.86, 8.73, and 6.00% compared with the control, respectively. *M. arborescens* and *S. maltophilia* isolates with the ability to produce indole-3-acetic acid (IAA) had positive effects on dry weight of the shoot. *E.hormaechei* showed a marked nitrogenase activity, phosphate solubilization, and IAA production and was the most effective treatment in improving the uptake of most nutrients. The nitrogenase activity and IAA production were generally considered to be the most important PGP traits of the bacteria when applied via foliar spray. The findings indicate that the foliar application of the leaf-colonizing PGPB enhanced the growth and nutritional status of maize. Research findings by Arun et al. (2020) suggested that rice phyllosphere bacteria, *Bacillus megaterium* PB50 promotes plant growth and helps in drought stress mitigation in paddy.

Phylloplane bacteria were isolated from the three wheat varieties thrice during the plant growth. The bacterial load increased with the growing season and Sehar wheat variety carried maximum bacterial load (1.1×10^9 $CFUg^{-1}$). Succession of bacterial community was also observed during the plant growth. Isolates belonging to Sehar wheat variety phylloplane produced auxin in highest amounts (52.95 µg ml^{-1}) during second sampling when plant was showing rapid growth. Many isolates from all three varieties fixed nitrogen, solubilized phosphates and some isolates also produced hydrogen cyanide. The results clearly indicated that the beneficial bacteria associated with phylloplane of better yielding variety were showing better PGP abilities when compared to their counterparts on low yielding varieties. Isolates exhibiting best PGP profiles were identified as *Bacillus*, *Microbacterium*, *Acinetobacter*, *Proteus*, *Psychrobacter*, *Pseudomonas*, *Streptomyces* and *Kineococcus* sp. through 16S rRNA gene sequencing (Batool et al. 2016). In *Gossypium herbaceum* the bacterium *Acinetobacter* sp. application of ACC deaminase producing drought-tolerant *Acinetobacter* sp., improved growth and productivity in *Gossypium herbaceum* plants under drought stress (Sharath et al. 2021). Foliar spraying of *Bacillus megaterium* PB50 induced drought tolerance in rice plants by upregulating stress-responsive gene (bZIP23, HSP70, LEA, RAB16B and SNAC1) expression (Devarajan et al. 2021).

Very clear information on the bioprospects and molecular mechanisms of PPFM and plants were explored by Mondal et al. (2024). The mechanism of inhibition to plant disease causing pathogens by PPFM has been attributed to anti-microbial compounds, HCN, siderophore production. In industrial point of view, they are used for producing pigments, pharmaceuticals and in detergents. Sustainable agricultural practices consisting the use of PPFM in bioremediation, biodegradation, bio-adsorption, bio-mineralization and bio-transformation processes. To add, PPFM finds use in drought amelioration, halo tolerance, radiation resistance, ACC deaminase activity, Ammonia and IAA production and nitrogen fixation in specific conditions.

Solanki et al. (2024) investigated on the potential effect and interaction of PPFM in Chilli at Anand Agricultural Unversity, Anand, Gujarat. Solanceous crops such as Chilli, Potato, Brinjal, Tobacco, Tomato were selected for isolation of *Methylobacterium populi* and *M. radiotolerans* that were exhibiting significant improvement in plant biometric traits. Previous research findings of Ismail and Mohammed

(2023) in strawberry identified that *M. radiotolerans* isolated from cotton, increased the chlorophyll content, improved quality and yield of berries. Application of TNAU Azophosmet (*Azospirillum*, *Phosphobacteria* and *Methlyobacterium*) liquid biofertilizer consortium was found to increase the cob length and girth, yield of Pearl millet in various on farm trial and front line demonstrations conducted at the adopted villages of Krishi Vigyan Kendra, Cuddalore, Tamil Nadu (Gayathry et al. 2023). Gayan et al. (2023) have investigated and isolated leaf surface colonizing PPFM from low land paddy and vegetables, that were found to exhibit *in-vitro* nitrogenase activity, IAA, GA, HCN, Siderophore production.

Methylobacterium aminovorans Tm13, called as TNAU-PPFM is a biofertilizer formulated and recommended for drought mitigation by Tamil Nadu Agricultural University, Coimbatore. The cost-effective production strategy of TNAU-PPFM in Ammonium Mineral Salts (AMS) medium and the use of PPFM as a potential bio-inoculant for mass production with revenue generation capital venture by Farmers Producer Organization in Cuddalore district, Tamil Nadu have been suggested by Gayathry and Gnanachitra (2021).

Methylobacterium sp. PPFM-Ah in *Arachis hypogaea* improved plant health and also provided plant resistance against rot disease caused by *Aspergillus niger* and *Sclerotium rolfsi*. *Methylobacterium extorquens* PPFM-So78 *Sachharum officinarum* increased plant health and productivity (Madhaiyan et al. 2005, 2006). Maize (*Zea mays* L.) growth and yield response to foliar spraying of PPFM, NPK (19: 19: 19), and micronutrient combination under both surplus and water scarce situations was studied by Senthilkumar et al. (2022). Industrial production of Phosphorous solubilising bacteria especially *Bacillus megatherium* in large stirred tank fermentors, operational costs involved in commercialization and entrepreneurship, benefit cost ratio have been elaborated by Maheshwari et al. (2022).

Phyllosphere microorganisms and their role in nutrient acquisition

Nitrogen fixation activity of phyllosphere microbes have been witnessed by *Methylobacterium* species (strain L2-4) found in leaves fix nitrogen, increase biomass, and stimulate seed formation in *Jatropha curcas* by Mathaiyan et al. (2015), free living diazotrophs in Bamboo by Padgurschi et al. (2018) and Holm oak (*Quercus ilex*) by Rico et al. (2014), *Gluconacetobacter diazotrophicus* in Limber pine (*Pinus flexilis*) and Engelmann spruce (*Picea engelmannii*) were reported by Carrell and Frank (2014), Siderophore producing bacterial isolates like in wheat by Batool et al. (2016). Bacterial isolates of phyllosphere are involved in phosphorous solubilisation for crops like cotton, moong, mustard, pearl millet and wheat were studied by Tamnanloo et al. (2018). Zinc solubilisation in cotton, moong, mustard, pearl millet and wheat were reported by Kumari et al. (2018). *Pseudozyma aphidis* JYC356 in *Drosera spatulata* by Fu et al. (2016), *Bacillus* were reported in *Thale cress* by Bodenhausen et al. (2014) and Tomato by Enya et al. (2007).

Plant growth-promoting yeasts (PGPY) have been mainly isolated from the rhizosphere and phyllosphere of major crop plants such as wheat, maize, and rice. Twenty-three genera of yeasts have been reported to have the potential for plant growth promotion (PGP), most of which belong to the phylum Ascomycetes. Dominant PGPY genera include *Candida*, *Rhodotorula*, *Cryptococcus*, and *Saccharomyces*. PGPY are known to exhibit phyto-beneficial attributes viz., phytohormone production, phosphate solubilization, siderophore production, improved soil fertility, aid plants to tolerate abiotic stress and also compete effectively against plant pathogens (Nimsi et al. 2023).

Phyllosphere microorganisms in biocontrol of plant pathogens

Beneficial phyllosphere microorganisms and their capacity for biocontrol against particular pathogens were elaborately reviewed by Bashir et al. (2022). Alymanesh et al. (2016) indicated that *Crocus sativus, Ficus carica, Punica grantum* harbours *Pseudomonas* sp. that exhibits quorum quenching mechanisms against *Pectobacterium carotovorum* subsp. *carotovorum* by producing biosensor and 3-oxo-C6-Homo Serine Lactones. The phyllospheric microorganisms like *Achromobacter, Alcaligenes* and *Stenotrophomonas* were proved as biocontrol agents against a hemibiotrophic bacterial pathogen namely

Pseudomonas syringae pv. *tabaci* that causes wild fire disease in tobacco. *Bacillus mycoides* isolates controls the effect of *Cercospora beticola* in Sugar beet. *Pseudomonas graminis* is a phyllosphere microorganism that acts as a biocontrol agent against *Erwinia amylovora* in apples. *Pyricularia oryzae,* a pathogen in rice, is controlled by phyllosphere biocontrol inhabitants such as *Saccharothrix* and *Streptomyces.* Karan et al. (2022) identified and biochemically characterized *Bacillus subtilis* and *Pseudomonas fluorescens* in the phylloplane of rice that were inhibiting the growth of *Bipolaris oryzae* that causes brown leaf spot disease in paddy.

CONCLUSION

A sustainable substitute for conventional agricultural methods dependent on chemical inputs is the stimulation of plant development by the manipulation of the phyllosphere microbiome, such as using Pink Pigmented Facultative Methylotrophs (PPFM). The potential to use these interactions to address important issues facing modern agriculture is highlighted by the symbiotic relationships that exist between plants and the varied microbial populations that live in their aerial sections. In addition to increasing crop yields and lessening the environmental impact of industrial fertilizers and pesticides, beneficial microorganisms of the phyllosphere aid in nutrient uptake, hormone regulation, and pathogen resistance. There will probably be an increase in the creation and exploitation of microbial biostimulants made from phyllosphere microbiome components. These microbial biostimulants can be used to improve crop yield, nutrient uptake, and plant growth since they include advantageous microbes and their metabolites. According to the majority of cited work on phyllosphere microbiomes, there had been very few investigations on yeast and bacterial interactions in phyllosphere, and the review opens a broader and newer field of research area in this line.

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