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Pink Pigmented Facultative Methylotrophs (PPFMs): Potential Bioinoculants for Sustainable Crop Production

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Abstract

Bacteria belonging to the genus *Methylobacterium*, popularly known as pink pigmented facultative methylotrophic (PPFM) bacteria, are well known for their distinct ability to use single-carbon compounds like methanol, formate and formaldehyde, and also a variety of multi-carbon substrates lacking carbon-carbon bonds. These bacterial groups are ubiquitously distributed, especially in phyllosphere and rhizosphere, and their occurrence have been reported in more than 100 species of plants so far. PPFMs have profound influence on soil fertility, crop growth and yield. The ability for phosphate acquisition, nitrogen fixation, iron chelation and phytohormone production indicate the possibility of developing them as promising biofertilizer candidates. In addition, many of them possess biocontrol activity against several phytopathogens. PPFMs induce several physiological changes in plants, making the plants more resistant to biotic and abiotic stress. They can therefore be promising alternatives to conventional chemical inputs in sustainable agricultural systems.

Keywords: *Methylobacterium,* Methylotrophs, Plant Growth Promotion, PPFMs, Biocontrol

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INTRODUCTION

Phyllosphere harbours large, complex and dynamic communities of microorganisms, where bacteria constitute the dominant microbial inhabitants. It forms a significant microbial habitat that supports organisms of diverse nutritional and physiological requirements. The leaf surface area of terrestrial plants possibly be occupied by microbes is reported to be around 6.4×10^8 km^2, that would harbour bacterial populations of about 10^{26} cells. Plants are potential reservoir of structurally and functionally diverse natural compounds ranging from quite simple esters to more complex molecules like carbohydrates, polyketides, flavanoids, lignans, terpenoids, alkaloids, and tannins.

Of the diverse natural products, methanol, a simple organic molecule, formed as a by-product of pectin demethylation during cell wall metabolism is released from plants via epidermal stomatal pores. Pectin, a major plant cell wall component, is structurally a heteropolysaccharide enriched with α-D-galacturonate residues, and a number of sugars such as α-L-arabinose, α-L-rhamnose and β-D-galactose in smaller amounts. Galacturonate methyl esters that are present in the cell wall helps in the transport of compounds through it during cell wall expansion. Demethylation of these methyl esters by methylesterase produces methanol as a by-product.[1] Emission of methanol through stomata by the transpiration stream leads to the enrichment of plant surfaces with methanol.[2,3]

Several microorganisms have evolved the interesting characteristic to utilize mono carbon (C_1) compounds like methanol and methane or complex carbon compounds lacking carbon-carbon bonds (dimethyl ether and dimethylamine) as the carbon source. These bacteria are commonly referred to as methylotrophs and the ability of an organism to utilize single carbon compounds as the exclusive energy source for its growth is known as methylotrophy.[4] Among the methylotrophic organisms, facultative methylotrophic (FM) bacteria of the genus *Methylobacterium* and *Methylorubrum* have been widely studied and are generally known by the term pink pigmented facultative methylotrophic (PPFM) bacteria. These facultative methylotrophic bacteria with unique physiological characteristics are distributed ubiquitously in/on plants.

PPFMs have been studied widely for their plant growth promoting ability by a plethora of mechanisms. Important modes of action include secretion of plant growth stimulating compounds like indole-3-acetic acid (IAA), cytokinin, Gibberellic acid (GA), 1-aminocyclopropane-1-carboxylate deaminase (ACC) and increasing the availability of essential nutrients. These mechanisms alone or in combination positively influences the growth and development of the host plant. Moreover, biocontrol ability of PPFMs is considered another noticeable beneficial trait which lessen the detrimental effect of various phytopathogens. Thus, plant beneficial PPFMs can play a significant role in crop cultivation and many researches suggest the possibility of their application in agriculture as an excellent bioresource to reduce the detrimental impacts of chemical inputs. Keeping in view of all the beneficial attributes of PPFMs, this review aims to provide a concise summary of the findings from various relevant studies describing the potential of pink pigmented facultative methylotrophs as promising alternative to conventional hazardous chemical inputs for eco-friendly and sustainable crop production.

Characteristics of PPFMs

PPFMs are obligate aerobic Gram-negative rods, which can grow on single-carbon substrates especially methanol and methylamine and also on an array of multicarbon containing compounds.[3,4] The average cell size of the bacterium is approximately 1.0 µm long by 0.5 µm wide. The major bacterial storage compound, poly-β-hydroxy butyrate (PHB) granules were identified in cells of *Methylobacterium* spp. using PHB granule staining.[5] Most studies have shown that *Methylobacterium* are Gram negative; however, some reports observed them to be Gram variable.[6] Many studies documented the ubiquitous presence of PPFM in soil, freshwater, lake sediments, leaf surface, nodules and dust. Bassalik[7] described the first *Methylobacterium* strain isolated from earth worm casts and called it as *Bacillus extorquens.* Later, Kuono and Ozaki[8] isolated 59 PPFM strains from many soil and water samples. Patt *et al*.[9] isolated and reported the first PPFM strain with methane utilization

ability. The ubiquitous nature of PPFM was first described by Green and Bousefeild.[10] Considering the methanol utilization ability, PPFMs are usually isolated on Ammonium Mineral Salt (AMS) agar medium amended with methanol as the exclusive carbon source. They utilize methanol by oxidizing it to formaldehyde by means of pyrroloquinoline quinone (PQQ)-dependent methanol dehydrogenases (MDHs).[11] There are two paralogous MDH enzymes present in PPFMs, *viz.* a Ca^{2+}-dependent MxaFI and lanthanide (Ln^{3+})-dependent XoxF.[12] Lanthanide (Ln^{3+})-dependent XoxF is highly conserved in *Methylobacterium* species than Ca^{2+}-dependent MxaFI.[13]

PPFM as plant associated bacteria

Presence of *Methylobacterium* has been described on a wide array of sources like root of rice,[14] leaves of rice,[15,16] stem of rice,[17] root nodule of crotalaria,[18] South African legumes,[19] stem nodule of *Sesbania rostrata*,[20] soil,[21-27] soyabean,[28] vegetables,[29] *Cucurbita pepo*,[30] seeds of rice,[31] brassica,[32] *Combretum erythrophyllum*,[33] potato,[34] banana,[35] palm oil tree,[36] palm oil,[37] siam squash and corn,[38] and soyabean[39] by various workers. All these evidences helped gaining insights into the distribution of PPFMs in nature especially on plants. Plant-*Methylobacteria* beneficial communication could be considered as a best model for symbiotic association between plants and microbes. Host plants release metabolic by-products including carbon source majorly in the form of methanol which are utilized by associated Methylobacteria. In turn, bacteria offer phytohormones needed for the growth and metabolism of the host. Such mutually beneficial relations generally indicate the chance of coevolution of symbiotic bacterial partner.[40] Generally, *Methylobacterium* spp. are present throughout the plant, especially the leaf surfaces, stem, flowers and roots. Austin *et al*.[41] first described the diversity of *Methylobacterium* in the phyllosphere region of *Lollium perenne*. Later, they have been reported as the most dominant phyllosphere population from more than seventy plant species tested and are mostly found as common prokaryotic epiphytes.[42-45] However, they can colonize plants as endosymbionts[46] and a few members can reside in intracellular spaces of meristematic cells.[47] Endophytic and intercellular colonization of bacteria supports active interaction of bacterial symbionts with host plant. Colonization of *Methylobacterium* spp. in intercellular spaces of tomato were observed by Poonguzhali *et al*.[48] Undoubtedly, all these previous reports establish the ubiquitous presence of PPFM bacteria in the nature. Almost all the information pertaining to colonization of *Methylobacterium* in plants imply their active cross talk with host plants. Besides, a few researchers have made attempts to understand and elucidate the biology of *Methylobacterium* spp. found in untapped habitats such as biological soil crusts,[49] Lichen like *Lepraria* sp.,[50] spores of the mycorrhizal fungus *Glomus iranicum* var. *tenuihypharum*,[51] tungsten mine tailings[52] and Philippine fermented food.[53]

The genetic diversity of these pink microbial community has been studied by different techniques such as Restriction fragment length polymorphism, Restriction analysis of polymorphic DNA and Amplified ribosomal DNA restriction analysis. These finger printing techniques could discriminate distinct microbial communities amongst PPFMs. For the first time, PPFMs inhabiting maize, cotton, and sunflower phyllosphere were detailed based on utilization profile of carbon source and RAPD data by Balachander *et al.*[54] It revealed the presence of six diversified groups of PPFM, wherein four different groups were found harbouring the phyllosphere of sunflower and maize and only two groups on cotton phyllosphere.

Genetic diversity of PPFM assessed using molecular tools and differential carbon source utilization profile identified *Methylobacterium populi*, *M. thiocyanatum*, *M. suomiense*, *M. aminovorans*, and *M. fujisawaense* as the predominant colonizers in the phyllosphere of crop plants like cotton, sunflower, maize, soybean and mentha.[55] Further, the genetic diversity of the heavy metal tolerant *Methylobacterium* spp. community in a mangrove forest has been unveiled with the help of *in vitro* assays.[56] Kaur *et al*.[57] assessed the diversity and heterogeneity of PPFM bacteria from the leaves of five kharif crops *viz.,* rice, maize, millet, mung bean and urad bean through plant growth promotion screening and ARDRA profiling and noticed the prevalence of four distinct groups of PPFMs in these plants. Based on 16S rRNA phylogenetic gene sequencing,

a high abundance of sequences closely related to *Methylobacterium radiotolerans* was reported on sugarcane plants.[58]

Assessment of the influence on the diversity and community changes of PPFM in transgenic Bt-cotton compared with the conventional cotton plants by means of a polyphasic approach that included differential carbon source utilization profiling and DNA based techniques showed that diversity richness of PPFMs in the phyllosphere, rhizoplane and internal tissues has not differed among *Bt* and non-*Bt*-cotton plants.[59] Although much remains to be explored, the documented data pertaining to the genetic diversity of *Methylobacterium* might give a crucial insight to select potential plant associated bacteria with plant growth-promoting characteristics for utilization in sustainable agriculture.

Carotenoid Pigment Production: A major characteristic of PPFM

Carotenoids are a group of yellow, orange, or red-colored lipophilic isoprenoid molecules present in all kingdoms of life. These natural pigments play diverse functional roles such as capturing and processing of light, photoprotection, specific coloration across genera and species, and pollinator attraction in both photosynthetic and non-photosynthetic biological systems.[60,61] Approximately, 1100 different carotenoids compounds have been identified so far from varied sources with diverse colours and they provide attractive colours to its source of origin.[62] Bacteria belong to the genus *Methylobacterium* possess a characteristic pinkish colour due to the presence of non-diffusible and non-fluorescent carotenoids, mainly xanthophylls[63,64] and hence named as pink-pigmented facultative methylotrophs.

Generally, accessory light-harvesting carotenoid complexes are found with chlorophyll molecules in green plants. In photosynthetic organisms, these light capturing complexes protects the chlorophyll molecules from photooxidation by absorbing and transferring light energy to chlorophyll molecules. More importantly, its anti-oxidant or oxygen free radical quenching activity protect the cell in both phototrophic and non-phototrophic organisms, usually under biotic and abiotic stress conditions. The production of carotenoid pigments makes the producer bacteria tolerant to extreme light condition and radiation.[65] Abiotic stresses cause accumulation of reactive oxygen species, that leads to oxidative injury to the organisms. To overcome the lethal effects of ROS, many organisms possess an evolved strategy *viz*., accumulation of carotenoid pigment by up-regulating carotenoid biosynthetic pathway.[61] Carotenoid pigments produced by PPFMs as secondary metabolites serve as a reliable and useful chemotaxonomic identification marker of the genus.[66] Biosynthesis of carotenoids makes them resistant to extreme light conditions, high or low temperatures and freezing conditions and also to UV and ionizing radiations.[67]

The colonies formed by *Microbacterium arborescens*-AGSB, a Gram-positive bacterium, collected from coastal sand dune vegetation, *Ipomea pes-caprae* were predominantly orange pigmented.[68] This study revealed the light induced biosynthesis of carotenoids pigment in *Microbacterium arborescens*-AGSB helps them to survive under stress conditions. Detailed chromatographic and spectrophotometric analysis of carotenoids in *Methylobacterium* genus has shown that majority belong to oscilloxanthin,[64] C_{40} carotenoid astaxanthin[69] and lycopene type carotenoids.[68] The ability to produce carotenoid pigments by PPFM can be made use of in different industries.[70-73] Several attempts have been made to recover the maximum amount of carotenoid pigments from PPFM,[74,75] and during recent year, the optimum conditions for the extraction when bacteria were grown in Ammonium mineral salt medium was reported to be at 25˚C, pH of 7.5, having 0.5% of methanol as carbon source.[76]

Plant Growth Promotion Mediated by PPFMs

PPFMs promote crop growth through multitude of mechanisms like indole-3-acetic acid production,[77,78] cytokinin production,[79] vitamin B_{12} production,[80] siderophore production,[81] ACC deaminase production,[82] nitrogen fixation and nodule formation[83] and phosphorus solubilization.[84] Furthermore, significant biocontrol activity of *Methylobacterium* spp. against phytopathogens protects the plants from destructive pathogens and thereby improves the health of plants. All these characteristics emphasize the potential of the PPFMs in crop production. Strikingly, much progress has been made over the past few years

in understanding the beneficial traits of PPFM. A concise information on plant growth promoting traits of *Methylobacterium* is given below (Table 1; Figure 1).

Phytohormone Production

Soil and plant-associated bacterial groups can synthesize and excrete one or more phytohormone. Among the various plant growth hormones, Auxins are found to be the most essential phytohormone for normal plant growth and development and till date, there have been no reports on plants lacking auxin synthesizing ability. It has been well documented that microbially excreted auxins exert positive influence on plant growth. Though, plants synthesize various auxins, Indole-3-acetic acid (IAA) is the most profound auxin as it is directly involved in several crucial developmental processes. Hence, IAA producing bacteria can potentially involve in increasing the plant's auxin pool.[85]

A large number of reports have described indole-3-acetic acid (IAA) production by methylotrophs. IAA is synthesized using different pathways by the producer organisms. Based on the intermediaries formed, these pathways are classified into indole-3-acetamide (IAM), tryptamine and indole-3-acetonitrile and indole-3-pyruvic acid (IPyA) pathway.[86] Of these, most important IAA biosynthetic pathways operating in PPFM are the IAM and the IPyA pathways. IAA produced by methylotrophic bacteria via, IAM and IPyA pathways has significant effects on growth of plants.[87] Ivanova *et al*.[87] first reported the production of significant amount of indole acetic acid in culture supernatants of four different methylotrophic bacteria. IAA produced by *Methylobacterium* has been found to influence seed proliferation and seedling growth of various plants. [77, 88-90] Based on colorimetric assay the presence of indole compounds was observed in PPFM culture supernatants also.[77] IAA synthesized by PPFM has influence on the root growth and development of various host plants also.[91] Thangamani and Sundaram[92] reported that among 16 *Methylobacterium* isolates tested three isolates

Table 1. Plant growth promoting attributes of PPFM in various crops

Crop plant	Associated methylotrophs	Source	Activity	Ref.
Rice	*Methylobacterium extorquens, Methylobacterium fujisawaense*	Phyllosphere	IAA production	91
Rice	*Methylobacterium* sp. CBMB-20	Rhizosphere	N_2 fixation	15
Soybean	Pink-pigmented facultative methylotroph	Phyllosphere	IAA production	93
Tomato	*Methylobacterium suomiense*	Rhizosphere	Root colonization	48
Red pepper	*Methylobacterium suomiense*	Rhizosphere	Root colonization	192
Groundnut	Pink-pigmented facultative methylotroph	Phyllosphere	IAA production	78
Sugarcane	*Methylobacterium* sp.	Stem, root, Rhizosphere	IAA production, PGP activities	193
Red pepper	*Methylobacterium* oryzae	Rhizosphere	Biofertilizer	194
Mung bean	*Methylobacterium organophilum*	Mud	Biofertilizer	133
Red pepper	*Methylobacterium* sp.	Phyllosphere	IAA and cytokinin production	195
Combretum erythrophyllum	*Methylobacterium radiotolerans* MAMP 4754	Seed	Synthesis of heavy metal resistant proteins, plant growth-promoting compounds	196
Banana TNMB03	*Methylobacterium salsuginis*	Leaf	Cytokinin production, ACC deaminase activity, Biochemical changes in plant	35
Poplar	*Methylobacterium* sp. CP3	Seed of *Crotalaria pumila*	IAA production, Phytate mineralization, Zn tolerance	197

indicated the accumulation of indole compounds in PPFM culture supernatants. These three isolates produced IAA amounting from 6 to 13.3 µg mL^{-1} in the presence of L-tryptophan. Radha[93] and Jones[94] have independently documented the production of IAA by different PPFM strains ranging from 9.04 to 28.15 µg mL^{-1} and 0.14 to 25.15 µg mL^{-1} of culture filtrate, respectively. Anitha[78] isolated PPFMs from the phyllosphere of different crops by leaf impression method and screened eight isolates for their influence on seed germination and production of IAA. Using HPLC, amount of IAA produced by different isolates was estimated and a maximum of 2.32 µg mL^{-1} of IAA was produced even in the absence of tryptophan by the isolate obtained from ground nut leaf (PPFM-GN). An increase in plant IAA concentration with the inoculation of *Methylobacterium* isolate and subsequent plant growth promotion was reported by Lee *et al*.[15]

Besides Indole acetic acid, Cytokinins also influence physiological functions of plants. Root functions of plants can be altered by change in level of cytokinin concentration in plants. Potential involvement of plant-growth promoting rhizobacteria (PGPR) like *Azospirillum, Azotobacter, Bacillus*, *Pseudomonas* spp. and *Rhizobium* in cytokinin production in pure cultures has already been described.[95-102] Methylotrophic strains present on phyllosphere have also been found to produce cytokinin, with many of them able to excrete it into the growing medium.[103-105] Study by Madhaiyan *et al*.[106] demonstrated that PPFM inoculation on true seeds of sugarcane increases the percentage and rate of germination. A higher PPFM population has been observed

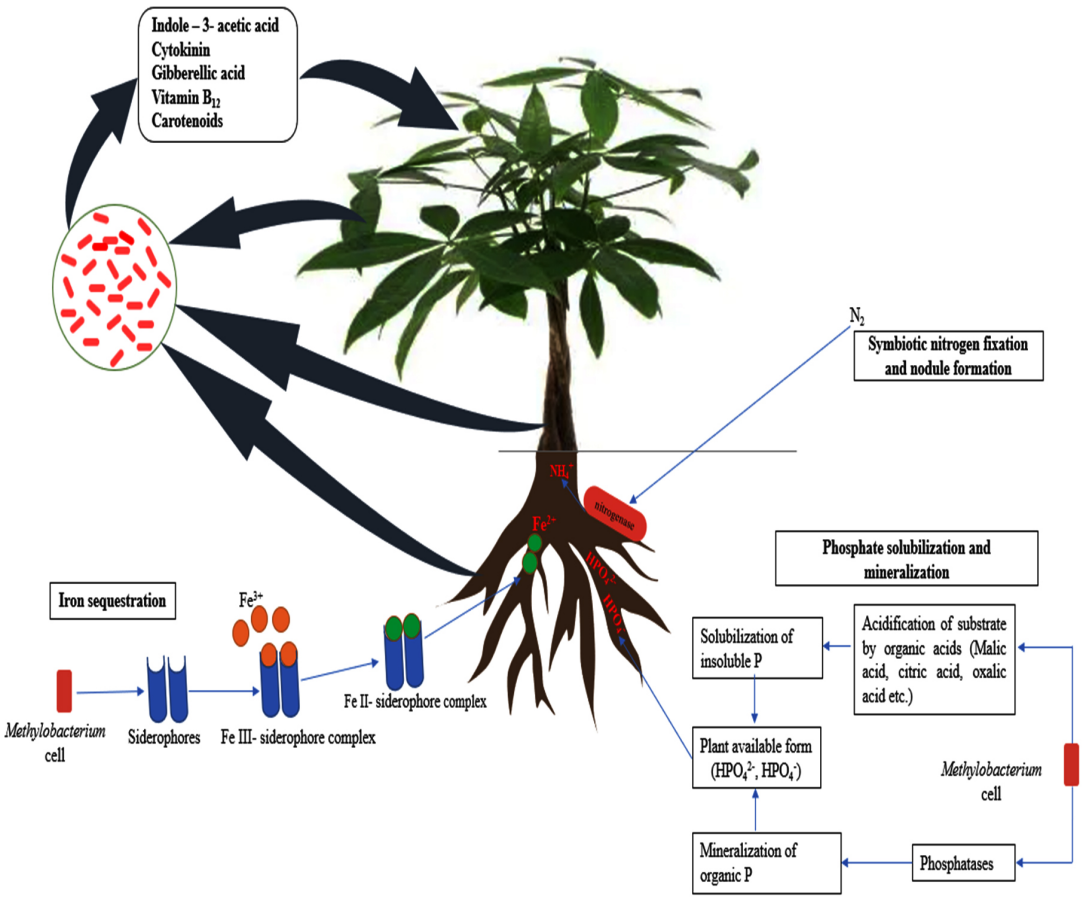

Figure 1. Schematic representation plant growth promoting mechanisms of PPFMs

when a combination of seed imbibition, soil application and phyllosphere spray were given. An immunological assay reported a significant increase of cytokinin both in mature and young leaves of sugar cane plants. Foliar spray of methanol or PPFMs results in increased PPFM populations which in turn caused a higher concentration of bacterially produced cytokinin and increased cytokinin contributed to improvement in yield of cotton and sugarcane.[107] Quantification of cytokinin produced by phyllosphere inhabiting *Methylobacteria* isolated from sugarcane, pigeon pea, mustard, potato and radish ranged between 1.09 to 9.89 µg mL^{-1} in the culture filtrate and treating wheat seeds with these cell-free culture filtrates registered a significant improvement in seed germination.[79] With a similar approach, El-Gawad *et al*.[108] described cytokinin production of PPFM bacteria obtained from cotton, datura, snap bean, castor oil and peanut plants with a maximum of 2.07 µg ml^{-1} of culture filtrate. An exhaustive cytokinin profiling of *Methylobacterium* strains was conducted by Palberg *et al*.[109] recently. Analytical results obtained from High performance-liquid chromatography-tandem mass spectrometry (HPLC–MS/MS) could uncover the immense potential of *Methylobacterium* strains to produce most active cytokinin form, trans-Zeatin (tZ), ranged from 0.46 to 82.16 pmol mL^{-1} and which marked higher than tZ produced by any other plant growth promoting bacteria reported so far. Despite a number of exclusive studies on the cytokinin production potential of PPFMs, still there is lack of knowledge on exact role of *Methylobacterium* produced cytokinins in plants. Therefore, further elucidation is required to understand its precise mechanism in plants.

Gibberellic acid (GA3), a plant growth hormone, is a key growth regulator involved in cell division and tissue differentiation, net assimilation rate, dry matter accumulation, leaf expansion and elongation, regulation of transpiration rate, flowering and photosynthesis.[110,111] Apart from these functions, GA plays a pivotal role in regulating plant development and growth under various abiotic stress conditions.[112] Plant growth promoting effect of gibberellins produced by many plant-growth promoting bacteria (PGPB) were reported by several workers.[113-116] For the first time, Rajan *et al*.[117] reported gibberellic acid production in *Methylobacterium* obtained from vegetable crops and was found to be ranging from 10.9 µg mL^{-1} to 106.97 µg mL^{-1} of the culture filtrate. Studies by Radha[93] and Jones[94] also revealed the production of gibberellic acid by methylotrophs which ranged from 24.11 to 70.30 µg mL^{-1} and 53.2 to 273.2 µg mL^{-1}, respectively. Further, Sheela *et al*.[118] have successfully demonstrated the GA production potential of different *Methylobacterium* strains and estimated a maximum amount of 59.13 µg mL^{-1} of GA. PPFM strains isolated from chilli leaves, rhizosphere soil and roots samples produced GA from 4.77 µg mL^{-1} to 128.28 µg mL^{-1} of culture filtrate among different isolates as reported by Savitha *et al*.[119]

Detailed investigations on phytophormone synthesize and release by plant associated *Methylobacterium* community, generally encountered on leaf surfaces, may provide insight into their beneficial activities. It is also possible to improve the PPFM strains by developing hormone over-producers which may have direct influence on plant growth and development.

Siderophore Production

Siderophore mediated sequestration and transport of Fe^{3+} is an efficient strategy evolved in bacteria to meet iron requirements.[120] Bacteria produces low-molecular-weight Fe chelating compounds, siderophores, that helps to sequester and transport the element into bacterial cells. Siderophore production by rhizospheric microorganisms is beneficial to plants as phytopathogens are out-competed by the producer strain under limited iron supply.[121] This competitive advantage determines how bacteria can survive and provide benefit to the host plants.

Siderophores, either hydroxamate-type or catecholate-types are produced by plant growth promoting bacteria. Under iron limiting conditions, *Methylobacterium* spp. also produce siderophore which transport the Fe-siderophore complex by the use of specific proteins. Siderophores produced by them are anti-pathological factors which can also be considered as indicator of biocontrol efficiency.[122] *In vitro* production of siderophores by the pathogen *Xylella fastidiosa* and PPFM *Methylobacterium extorquens* tested by Silva-stenico *et al*.[123] found that the culture

supernatants of *X. fastidiosa* did not contain both hydroxamate and catechol siderophores, whereas hydroxamate siderophores have been detected in the culture supernatants of *M. extorquens*. In citrus plants, *Methylobacterium* spp. inhabiting same ecological niche of *Xylella fastidiosa* subsp. *pauca* (Xfp) was found to be incapable of producing catechol-type siderophores but were also producing hydroxamate-type siderophores. Interestingly, *in vitro* growth of the pathogen was found to be increased in the presence of endophytic *M. mesophilicum* produced siderophores which occupy the same niche.[124] Simionato *et al*.[122] reported the production of siderophores by *Methylobacterium mesophilicum* (ARS 1/5 and ARS 1/6 strains). *Celosia* species is an iron rich plant with pink pigmented leaves and flowers. Gholizadeh and Kohnehrouz[125] postulated the occurrence of both highly efficient iron-uptake bacteria and PPFM bacteria on the leaves of *Celosia* species. The prediction was experimented by probing with a cDNA fragment coding for *Methylobacterial*-type Fe siderophore receptor within *Celosia* leaf cDNA microflora. The results indicated the inhabitation of efficient iron scavenging bacteria, most probably PPFM, on the surface of plants with high iron content.

Positive results were obtained when *Methylobacterium phyllosphaerae* MB-5 and CBMB-27 were screened for synthesis of amino acid conjugated hydroxamate type of siderophore under laboratory conditions, whereas, both the strains not contained catecholate type of siderophores during iron limitation.[126] According to Senthilkumar *et al*.,[35] all the 28 endophytic *Methylobacterium* isolates obtained from south Indian banana cultivars were shown to have iron siderophore complexes production in CAS agar medium, indicated by an yellow halo zone formation around the bacterial colonies. The experimental results demonstrated that these endophytic *Methylobacterium* species ensure plant growth promoting nutrients/compounds to the host plants. *Methylobacterium* genomes contain different types of siderophores and TonB-dependent receptors (TBDRs) with diverse roles. Siderophore mutant *Methylobacterium* strain was unable to utilize methanol as carbon source, but they could solubilize insoluble anthanides oxide, suggesting their crucial role in methylotrophy. Besides, siderophores have important role in lanthanide uptake, oxidative and nitrosative stress tolerance, biofilm formation, and heavy metal sequestration.[127]

Reports suggest members of *Methylobacterium* as a potent source of siderophores which are successfully involved in iron scavenging and transport. Furthermore, siderophore production helps in root pathogen suppression by competitive exclusion, and promotes growth and development of the host plants.

Nitrogen fixation

Nitrogen, a vital mineral nutrient, is indispensable for development and growth of plants.[128] It forms the building blocks of many structurally and physiologically relevant molecules like proteins, nucleic acids, chlorophyll and coenzymes. Moreover, it constitutes an important component of ATP, energy currency of the cell.[129] There are numerous microorganisms, referred as diazotrophs, especially eubacteria, which can add substantial amount of nitrogen into soil by N_2 fixation. Diazotrophic microorganisms provide fixed nitrogen in exchange of carbon source from plants.[130] The beneficial effects of diazotrophic organisms have been well documented.

There has been remarkable research progress in the area of *Methylobacterium* mediated nitrogen fixation and the involvement of *Methylobacterium* mediated nitrogen acquisition by host plants. In the past few years, *Rhizobia* were classified under three different phylogenetic branches within the alpha-2 subclass of *Proteobacteria*. Of the three branches described, first branch contains the genera *Rhizobium*, *Sinorhizobium*, *Mesorhizobium*, and *Allorhizobium* with *Agrobacterium*, second branch with *Bradyrhizobium* with photosynthetic free-living *Rhodopseudomonas*, and third contains the genus *Azorhizobium* as well as the chemoautotroph *Xanthobacter*. Later, Sy *et al*.[83] described *Methylobacterium* as a fourth rhizobial branch within alpha-subclass of *Proteobacteria* and introduced a new species of *Rhizobium*, *Methylobacterium nodulans*, isolated from *Crotalaria* legumes using *nodA* amplification assays. Though the wide spread occurrence of *Methylobacterium* in various crops has already

been well known, their symbiotic relationship with host plants was unknown until recently. In this concern, *Methylobacterium nodulans* capable of inducing nodulation in plants was the first nodule forming *Methylobacterium* species identified. This study could reveal the relatedness of *nodA* gene present in *M. nodulans* with *nodA* gene of *Bradyrhizobium* and was believed to be acquired by horizontal gene transfer mechanisms. It was for the first time, Raja *et al*.[131] reported that a phyllosphere colonizing, non-nodulating Methylotroph, *Methylobacterium* spp. MV10. possess functional *nifH* gene which was quite different from *M. nodulans*. A partial sequencing of genome of *Methylobacterium extroquens* helped identifying a few genes with close similarity to symbiosis-associated genes of *Rhizobia* and *Agrobacterium*.[132]

Lee *et al*.[15] experimented the potentiality of diazotrophic rice methylotrophs like *Methylobacterium* sp. CBMB20, *Enterobacter* sp. CBMB30, *Burkholderia* sp. CBMB40 in improving the rice seedling growth. These isolates exerted a discernible influence on germination of seed and seedling vigour index, and biomass production of rice seedlings. *Methylobacterium organophilum*, isolated from hot spring mud, a thermophilic nitrogen-fixing species, fixed di-nitrogen efficiently even at elevated temperature.[133] The characteristic feature of *Methylobacterium* to fix atmospheric nitrogen and colonize leaf tissues have been shown to improve tolerance of Jatropha (biodiesel crop) under low soil nutrient conditions. Exploitation of nitrogen fixing *Methylobacterium* was reported to have improved the productivity and green index of Jatropha biofuel.[134] Recently, a preliminary assessment of three endophytic *Methylobacterium* sp. obtained from Palm oil revealed their ability to proliferate in nitrogen-free media, suggesting the nitrogen fixing ability of *Methylobacterium*.[37]

Despite considerable research on methylotroph mediated nitrogen fixation, there are still gaps in our understanding of its precise mechanism. When *Methylobacterium* mediated nitrogen fixing mechanisms are well understood, future researchers may be able to develop successful and promising strains to improve plant growth and development.

Phosphorus solubilization

Phosphorous is a limiting nutrient which is very essential for biological growth and development as it is involved with life sustaining metabolic processes of plants such as photosynthesis, signal transduction, energy transfer, macromolecular biosynthesis and respiratory process. Phosphate solubilization process is considered as equally important as nitrogen fixation process.[135] Though P is quite abundant in soil, it remains mostly unavailable to plants. Generally, P in the soil exists in two different forms, either in inorganic (bound, fixed, or labile) or organic (bound) forms. However, plants can take up P only in soluble forms such as mono- and dibasic phosphate forms.[136] Therefore, it is evident that the phosphate solubilization is an extremely important and necessary process. Supply of plant essential nutrient through any biological means, especially microorganisms, is a better and promising choice in sustainable agriculture. Microorganisms play a central role in solubilizing the unavailable inorganic, but insoluble P fraction of soil and make them available for uptake by the plants easily.

Microorganisms offer various means to mineralize phosphates like rock phosphate, tricalcium phosphate, aluminium phosphate and organic phosphorus which have complex-structural characteristics, present in soil to improve the availability of accessible forms of P, like orthophosphate to plants.[137,138] The mechanisms underlying microbe mediated P solubilization has been well documented. Of various mechanisms, secretion of organic acids of low molecular weight is the primary mechanism of P solubilization by microorganisms. Amongst them, acids like carboxylic acid, formic acid, succinic acid, lactic acid, glycolytic acid, fumaric and propionic acid[139] brings down the rhizosphere pH which in turn cause the release of bound phosphate forms.[140] Another well studied phosphate solubilizing mechanism is the release of extracellular enzymes such as phytases, nonspecific acid phosphatases and C-P lyases phosphatases by phosphorous solubilizing bacteria that mineralize insoluble organic phosphate.[141,142] Obviously, secretion of extracellular enzymes would help them to gain competitive advantage over deleterious pathogens.

Hitherto, elaborate studies are lacking on phosphate solubilization by PPFM. A detailed study to understand *Methylobacterium*-mediated phosphorous solubilization under *in vitro* conditions was done by Jayashree *et al*.[143] This study recorded P-solubilization index of thirteen PPFM isolates grown for 7 days on NBRIP-BPB plates which ranged from 1.1 to 2.7. A thorough examination of these isolates under *in vitro* conditions could identify *Methylobacterium* as potential phosphate solubilizer with diverse mechanisms to solubilize organic phosphate. Later, Kumari[144] reported P solubilization index ranging from 1.28 to 1.85 of four different facultative methylotrophic strains that solubilized tricalcium phosphate in Pikovskaya's agar medium. Agafonova *et al*.[84] reported phosphate solubilization activity as a newly revealed characteristic feature of methylotrophs and explicated their phosphate-solubilizing activity in association with different plants. A first report on the presence of all the genes responsible for the synthesize of three phosphatase enzymes in *Methylobacterium oryzae* was published by Kwak *et al*.[145] Recently, Rahim *et al*.[36] demonstrated the phosphate solubilizing potential of nine newly isolated *Methylobacterium* sp. In Pikovskaya broth, the *Methylobacterium* isolate EPPD1 solubilized 4.12 mg/mL of inorganic phosphate whereas isolate ENPD2 solubilized an amount of 3.97 mg/ml of inorganic phosphate in Pikovskaya and 3.3 mg/ml in NBRIP broth.

Significant advances have been made in the area concerning to *Methylobacterium* mediated phosphate solubilization. Nevertheless, search for new potential phosphate solubilizing *Methylobacteria* should be augmented to develop promising candidates of PPFM for commercial inoculum development.

Modulation of Ethylene Levels in Plants

The gaseous hydrocarbon ethylene is a unique phytohormone with a number of biological roles related to seedling growth, ripening of fruits, germination of seed, abscission of leaves and petals, organ senescence and biotic and abiotic stress induced responses. Ethylene improves the plant growth and also hinder the developmental processes which depends up on the cell type and plant species. Generally, decrease in levels of ethylene in plants enhances root extension, but increased ethylene levels in plants, especially in fast growing roots, can hinder important developmental processes, mainly root elongation.[146] Thus, beneficial role of this vaporous hormone is reported at very low concentrations. Elongation of shoot and root is normally inhibited by action of ethylene. High levels of ethylene is harmful which causes small lateral root proliferation.[147] Moreover, stress regulating activity of ethylene has also been elucidated well.[148] Various abiotic stress like salinity, drought, flooding of water, and presence of heavy metals dramatically increases endogenous level of 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in plants, which in turn cause higher concentration of ethylene.[149] Accumulation of larger volumes of ethylene leads to further stresses in plants like reduced ability to nutrient uptake, water absorption etc.[150]

Degradation of the precursor molecules, ACC, would forbid the synthesize and accumulation of ethylene and thereby prevent the detrimental effects of the high ethylene levels.[151] The enzyme ACC deaminase (EC 4.1.99.4), first characterized by Honma and Shimomura[152] has been shown to degrade ACC to alpha-ketobutyrate and ammonium. Therefore, it was assumed that plant growth promoting bacteria with high locally induced ACC deaminase activity could be a powerful strategy for ameliorating plant stress. In this regard, it has been proved that ACC deaminase-containing PGPB could effectively be used to overcome the deleterious consequences caused by abiotic stresses. *Achromobacter*,[153] *Bacillus*,[154,155] *Burkholderia*,[156,157] *Ensifer*,[158] *Mesorhizobium*,[159] *Pseudomonas*,[155, 160,161] *Streptomyces*,[162] and *Variovorax*,[163] are some examples of well documented ACC deaminase-producing bacterial genera.

Only a few research publications on ACC deaminase activity in *Methylobacterium* spp. exist. The inhabiting activity of rice 1-aminocyclopropane-1-carboxylate deaminase (ACCD) on phyllosphere *Methylobacteria* has been detected and assessment of its functional regulatory role in determining ethylene level in rice and tomato seedlings showed that the enzyme activity notably lowers the ethylene level (60–80%) in the plants. A key finding made in this study was the homology of *accD* gene sequence of the rice

phyllosphere *Methylobacterium* with *Rhizobium leguminosarum* (98% similarity).[164] Based on the results of a gnotobiotic root elongation assay conducted on canola seedlings, Madhaiyan *et al*.[82] reported the occurrence of ACC deaminase in *Methylobacterium* spp. ACC deaminase activity of *M. fujisawaense* caused substantial lowering of ethylene levels in canola seedlings. Madhaiyan *et al*.[17] also found the presence of *M. oryzae* sp. nov., an aerobic ACC deaminase producing PPFM bacterium in stem tissues of rice. The isolate was reported to be closely related to *M. fujisawaense*, *M. radiotolerans* and *M. mesophilicum*. *Methylobacterium oryzae* strains CBMB20 and CBMB110 showed significant variation in their ability to utilize ACC and they produced 94.5 and 24.7 nmol α-ketobutyrate mg^{-1} of protein h^{-1}, respectively. Seed treatment with theses strains increased the root length of pepper and tomato plants attributed to their ACC deaminase activity compared to control plants under gnotobiotic conditions.[165] Treatment of tomato and red pepper plants with *Methylobacterium* reduced the ethylene emission compared to control plants under greenhouse conditions also.[166] Recently, Senthilkumar *et al*.[35] demonstrated the positive influence of endophytic *Methylobacterium* possessing ACC deaminase activity isolated from tissue culture banana plantlets of South Indian banana cultivars. Regulation of *acdS* gene encoding aminocyclopropane carboxylate deaminase (AcdS) by an AcdR homologous protein in epiphytic phytosymbiotic methylotroph *Methylobacterium radiotolerans* JCM2831 was proposed by Ekimova *et al*.[167] The transcriptional regulatory protein encoded by an open reading frame activates the acdS gene expression when ACC or 2-aminoisobutyrate is present as an inducer. It can regulate the transcription initiation process even in the absence of inducer molecule, when present excessively. A better understanding of ACC deaminase enzyme activity in *Methylobacterium* is needed to extend their integration in sustainable crop production.

PPFM as potential plant-growth promoters

Plethora of methylotrophic bacterial species are known to live in close intimacy with plants, both terrestrial and aquatic, by living along on roots, leaf surfaces, buds and other plant parts. Numerous benevolent attributes of PPFM have been explored and reported by various researchers (Table 1; Figure 1). Inoculation of either *Methylobacterium* or methanol spray

Table 2. Biological control of plant diseases by PPFM

Methylotrophs	Pathogen(s)	Source	Ref.
Methylobacterium sp. PPFM-Os-07	*Rhizoctonia solani*	Rice phyllosphere	14
Methylobacterium sp.	*Aspergillus niger, Sclerotium rolfsii*	Groundnut phyllosphere	185
Methylobacterium sp. Co-47 *Methylobacterium* sp. MV-10 *Methylobacterium* sp. LE-1 *Methylobacterium* sp. AM-1	*Macrophomina phaseolina, Phytophthora infestans, Fusarium oxysporum, Fusarium udum, Pythium aphanidermatum, Sclerotium rolfsii*	Rice phyllosphere	187
Methylobacterium fujisawaense TNAU 14 *Methylobacterium* sp. Co-47 *Methylobacterium* sp. MV-10	*Meloidogyne incognita*	Tomato rhizosphere	191
Methylobacterium sp. LE-1 *Methylobacterium* sp. AM-1	*Rhizoctonia solani*	Rice phyllosphere	188
Methylobacterium rhodinum *Methylobacterium aminovorans*	*Rhizoctonia solani*	Soil	198
Methylobacterium sp. GPPFM13	*Macrophomina phaseolina*, *Sclerotium rolfsii*, *Pythium myriotylum, Colletotrichum gloeosporioides* *Fusarium oxysporum*	Ginger phyllosphere	177
Methylobacterium populi	*Colletotrichum capsici*	Chilli phyllosphere	190

has shown profound increase in dry matter production and plant height of cotton against uninoculated control.[168] Discernable variation in photosynthetic activity was noticed in rice cultivar Co-47 treated with *Methylobacterium* due to increased chlorophyll content, stomatal number and maleic acid content.[14] A remarkable improvement in germination was noted compared to uninoculated control when sugarcane true seeds were treated with PPFM strains. Strikingly, a combination different method of PPFM application such as seed treatment, soil drenching and phyllosphere spraying helped increasing the height of plants, specific leaf area, internodal numbers and cane yield significantly.[106] Yet another interesting evidence was provided by Lee *et al.*[15], wherein diazotrophic bacterial strains including *Methylobacterium* spp., not only improved seed germination but also biomass and seedling vigour index (SVI) of rice seedlings.

ACC deaminase producing *Methylobacterium fujisawaense* could reduce the synthesis of ACC and hence lowered the deleterious ethylene levels in seedlings of canola when grown under gnotobiotic conditions. Lowered ethylene level could induce canola seedlings root elongation.[82] A gnotobiotic root elongation assay was carried out to test the efficacy of two *Methylobacterium* strains namely *Methylobacterium* sp. strain CBMB20 and CBMB110. Seeds of red pepper and tomato imbibed with *Methylobacterium* strains showed substantial increment in root length compared to uninoculated control and *M. extorquens* miaA$^-$ knockout mutant treated plants. Furthermore, accumulation of indole-3-acetic acid, *trans*-zeatin riboside and dihydrozeatin riboside was noted in the extracts of red pepper plants. In the same way, accumulation of *trans*-zeatin riboside and dihydrozeatin riboside was recorded in tomato plants extracts.[85] Radhika *et al*.[169] recorded highest maize cob yield when plants were sprayed with methylotrophic bacteria. In another investigation, high chlorophyll content was measured from soyabean plants which received both seed inoculation and foliar spray of *Methylobacterium*.[170]

Methylobacterim spp. are known to enhance rice plant growth in a multitude of ways. When effect of eight *Methylobacterium* isolates on seed germination was monitored, PPFM-SOY (isolated from soybean leaf) and GN (isolated from groundnut leaf), were shown to improve the germination of heat-treated seeds of paddy, maize and soybean. When the heated seed of soybean was treated with PPFM-SOY, 14.28 per cent increase in germination was obtained compared to untreated heated seeds. Same level of increase

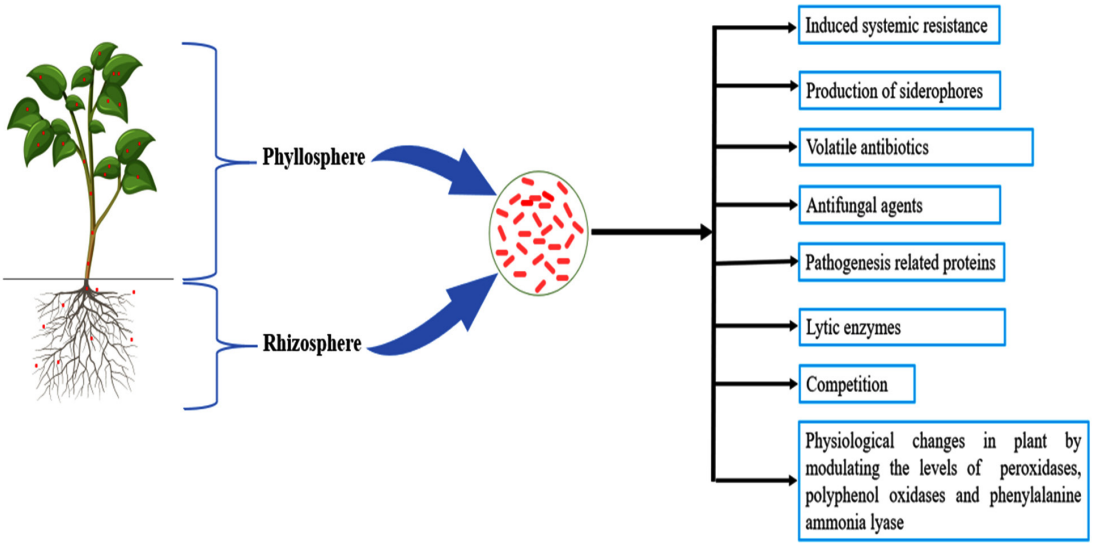

Figure 2. Biocontrol mechanisms of PPFMs against various phytopathogens

in germination was observed on treatment with PPFM-GN. When normal seeds were treated with PPFM-SOY and PPFM-GN, 23.21 and 7.14 per cent increase in germination was observed respectively. Treatment of heated maize seeds with PPFM-SOY and PPFM-GN resulted in an increase of 27.50% and 30.0% over control respectively. For paddy seeds also, 13.88% and 11.11% increase over control was recorded on treatment with PPFM-SOY and PPFM-GN respectively.[89] Among selected methylotrophic bacteria tested in a pot culture study, PPFM50 significantly increased the shoot biomass, height, stem girth, leaf area, chlorophyll content, and tuber yield of *Coleus forskohlii*. Markedly, 216.10 per cent increase in tuber yield was observed against reference strain (216.10%) and uninoculated control (136.07%).[171]

In a two-year field experiment, application of PPFM alone was found improving growth attributes like leaf number per plant, chlorophyll content, and yield attributes like pod number per plant of snap bean. Moreover, total sugars, ascorbic acid, amino acids, and protein content of pods were also increased significantly.[108] Effect of inoculation of *Methylobacterium* spp. possessing ACC deaminase (ACCD) and indole-3-acetic acid activity on tomato and red pepper seedling performed under gnotobiotic and greenhouse condition was found to be comparable to exogenous applications of synthetic IAA.[172] Increased production of IAA by the foliar application of *M. extorquens* MP1 isolated from Peach (*Prunus persica* L.) phyllosphere and *M. zatmanii* MS4 from Strawberry (*Fragaria ananassa* L.) employing leaf imprint method augmented the growth of tomato plants compared to uninoculated control.[173] *Methylobacterium extorquens* MM2 obtained from the phyllosphere of mustard leaf increased the production of IAA in plants which in turn enhanced the plant growth.[66] *Methylobacterium* sp. 2A isolated from *Solanum tuberosum* L. cv. Desirée plants significantly increased biomass of potato plants along with root hair density. Besides, its strong biocontrol activity against fungal phytopathogens has been evidenced in dual confrontation assays.[34] A recent report showed that inoculation of microbial consortium consisting of rhizobium, AMF, PPFM and *Bacillus altitudinis* - FD48 significantly improves the growth and yield of groundnut.[174]

Positive responses of a *Methylobacterium* application have also been experimented on wheat,[79] barnyard millet (*Echinochloa frumentacea* Var. COKV 2),[175] biodiesel plant *Crambe abyssinica*,[176] Ginger,[177] rice,[16,178] cotton[179,180] and cardamom.[181] All these high-throughput studies have been undertaken to gather knowledge about consequences of interactions between *Methylobacterium* and their host plants. The combination of multiple plant growth promoting characteristics keeps PPFMs as an attractive microbial tool in agriculture. They are categorized as biosafety level one organisms as there is no report of *Methylobacterium* mediated pathogenicity in plants till now. Taking into account of their beneficial attributes to the host plants various *Methylobacterium* based biofertilizers have been launched to the markets. For instance, Newleaf Symbiotics, a company designing next generation of Agri biologicals as biocomplements to existing chemicals, developed a commercial product composed only of *Methylobacterium* to accelerate the growth of cotton, tomato, peanut, rice, corn, soybean, and wheat.[182] Even though, many potential *Methylobacterium* strains have been described previously, relatively small number of products are currently available in the market.

Very recently, a seed coating technology using immobilized cells of plant growth promoting *Methylorubrum aminovorans* to improve seed quality of cotton was introduced by Pragathi *et al*.[183] This novel technology uses microbial cells of *Methylorubrum aminovorans* immobilized in a composite nanofibre matrix composed of Chitosan and Poly Vinyl Alcohol (PVA) as an effective localized delivery system. Yet another similar study conducted by Mukiri *et al*.[184] put forwarded a seed invigouration technique for groundnut plants that uses electrospun Polyvinyl alcohol (PVA) nanofibre containing immobilized microbial cells of *Methylorubrum aminovorans*. Application of encapsulated *Methylorubrum aminovorans* was successful in enhancing root colonization followed by improving seed germination, seedling vigor and growth of groundnut plants.

PPFM as Biological Control Agents of Plant Diseases

Biocontrol activity of PPFM on soil borne phytopathogens has been recorded in addition

to its positive effect on plant growth[14] (Table 2; Figure 2). PPFM have also been well elucidated for their induced systemic resistance (ISR) activity against various plant pathogens.[14,121,185]

Seed treatment or foliar spray of *Methylobacterium* on rice induced the pathogenesis related proteins which protected the plants against sheath blight pathogen *Rhizoctonia solani* under pot culture conditions.[14] PPFMs bring about several physiological changes in plants, making the plants more resistant to pathogens. *M. extorquens* CO-47 induced the accumulation of peroxidase, polyphenol oxidase, phenylalanine lyase and phenols in plants and subsequently suppressed the pathogen *Rhizoctonia solani*.[14] *Methylobacterium* spp. treated groundnut plants challenged with *Aspergillus niger* or *Sclerotium rolfsii* resulted in enhancement of seed germination and seedling vigour index. It also caused the increase in the activities of β-1,3- glucanase, phenylalanine ammonia lyase (PAL) and peroxidase (PO). Also, presence of five isozymes of polyphenol oxidase and PO were noticed in *Methylobacterium* treated plants when challenged with the pathogens.[185] Application of *Methylobacterium* strains on tomato induced the defence response against the plant pathogen *Ralstonia solanacearum*.[186] As already stated, *Methylobacterium* spp. synthesize anti-phytopathogen factors, such as siderophores.[136] The antagonistic effect on the fungal pathogens tested may also be attributed to the salicylic acid, a type of siderophore, produced by PPFM isolates as already proved in *Methylobacterium oryzae* CBMB20 challenge inoculated with *Pseudomonas syringae* pv. tomato in tomato plants compared to control or *M. oryzae* treated plants under growth chamber and green-house conditions.[121] According to Poorniammal *et al*.[187] volatile antibiotics produced by *Methylobacterium* ceases mycelial growth of *Sclerotium rolfsii*, *Fusarium udum, Fusarium oxysporum*, *Pythium aphanidermatum, Colletotrichum capsici,* and *Cercospora capsici,* and also inhibit the growth of *Xanthomonas campestris* with various biocontrol efficacies under *in vitro* conditions. *Methylobacteria* isolate CO-47 hindered the mycelial growth of *Rhizoctonia solani* and the inhibition zone measured under *in vitro* conditions was 1.4 cm.[188] Methylotrophs inhabiting mangrove sediment have been found to be powerful biocontrol agent against root rot pathogen *Macrophomina phaseolina*.[189] As reported by Santosh *et al*.[190] inoculation of PPFM isolates to chilli grown under field conditions remarkably reduces the anthracnose disease caused by *Colletotrichum capsici.*

Another interesting finding made was the biocontrol potential of *M. fujisawaense* against *Meloidogyne incognita* (Kofoid and White) chitwood race 3. *M. fujisawaense* filtrate was found to be highly effective in inhibiting egg hatching and reducing root penetration of *M. incognita* in tomato plants.[191] Literature published on biocontrol activity of *Methylobacterium* to date are consistent and conclusive. Induced systemic resistance activity in plants on methylotrophic bacterial treatment suggests the possibility that PPFM bacteria could be used as a means for biological control of plant diseases.

CONCLUSION

Pink Pigmented Facultative Methylotrophs (PPFMs) are generally regarded as ubiquitous colonizers of several, if not all plants. Their beneficial interactions with host plants and the symbiotic nature, and other valuable attributes are attracting greater attention. Methylotrophic bacteria with plant growth promotion ability are widely accepted as efficient and potential microbes for enhancing agricultural yield, and hence can be developed into a reliable component in sustainable agricultural systems. Multiple mechanisms of plant growth promotion, such as phytohormone production, nutrient acquisition and biocontrol activities emphasize the potential of the PPFMs in crop production. Since PPFMs can promote plant growth as well as prevent infection by phytopathogens, they can be used as better alternatives to chemical fertilizers and fungicides in sustainable agriculture. The importance of plant microbiome in plant and crop health is getting realized of late. The innovations focusing on core microbiome understanding of crop plants could help integrate PPFM as a component in synthetic microbiome development which would open up environmentally-friendly opportunities to take care of the current crop production challenges.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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All datasets generated or analyzed during this study are included in the manuscript.

ETHICS STATEMENT

Not applicable.

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