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## Abstract

Methylo trophs are a diverse group of bacterial community utilizing a number of C1 carbon compounds as a source of carbon and energy. This peculiar group of microorganisms has capability to enhance plant growth by solubilizing phosphates, by producing siderophores, by inhibiting ethylene accumulation in plants in adverse conditions, by fixing atmospheric nitrogen, by producing phytohormones such as auxins and cytokinins, and by degrading various harmful and toxic compounds. The plant roots are colonized by different types of methylo trophic bacteria, and solubilized essential elements are provided to the plants making them healthier and strong. There are a number of beneficial biological interactions of methylo trophs with the plants. Interaction of methanotrophs with plants leads to the reduction in greenhouse effects in the environment. The interaction of methylo trophic bacteria with plants as endophytes, epiphytes, plant colonizers, phytohormone producers, and other types of beneficial association makes them very peculiar group of microbes interacting natural flora. Apart from higher plants, methylo trophic interaction was observed with bryophytes also as epiphytic as well as endophytic bacteria.

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## Keywords

Methylo trophs • PGPRs • Endophyte • Bacterial community • Phytohormone

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## 30.1 Introduction

Methylotrophic bacteria are ubiquitous, and a strong association and interaction with plants, within plants, and around the plant system is very common. They are abundantly present over plant leaf surfaces as pink-pigmented facultative methylotrophs. They participate in various plant-associated activities also. They can solubilize phosphate also and provide to the plants, promoting their growth. Plants in stress environment or extreme condition are influenced by this promising group of microbes. There are various novel potential methylotrophic bacteria reported to be in strong association with plants. They are also recognized as plant growth-promoting rhizobacteria, and several findings showed their colonization with plant roots. These specific reduced carbon-utilizing communities are present as both plant endophytes and epiphytes. Taking these considerations, methylotrophs associated with plants are here discussed with examples and recent developments.

## 30.2 Novel Methylotrophic Bacteria Associated with Plants

Like several novel bacterial strains, methylotrophic bacteria are also isolated from various ecosystems and reported novel after subsequent molecular characterization. Moreover, plant-associated epiphytic and endophytic methylotrophic strains were found to be novel after polyphasic approach. Most of the studies conclude *Methylobacterium* sp. as predominant plant-associated novel methylotrophic bacteria.

From *Populus deltooides* nigra (poplar tree), a novel aerobic PPFM (pink-pigmented facultative methylotroph) was isolated and identified as *Methylobacterium* sp. strain BJ001T. The phylogenetic analysis revealed its relatedness with *Methylobacterium extorquens*, *Methylobacterium thiocynatum*, *Methylobacterium rhodesianum*, and *Methylobacterium zatmanii*. The carbon substrate utilization pattern of bacterium was differed from other phylogenetically closed methylotrophs, specifically methane carbon source (Aken et al. 2004).

Novel methylotrophic bacteria were isolated from leaf tissue of rice plant and were identified as *Methylobacterium oryzae* CBMB27T. Molecular chronometer 16S rRNA gene-based phylogenetic analysis revealed the taxonomic position of *Oryza sativa* L. CBMB27T in a clad of *Methylobacterium oryzae*, *Methylobacterium fujisawaense*, and *Methylobacterium mesophilicum* showed homology with 98.3%, 98.5%, and 97.3%, respectively. The experiment was validated by DNA-DNA hybridization together with polyphasic approaches to observe the relatedness of novel strain CBMB27T with its closest species (Madhaiyan et al. 2009b).

In an earlier finding, three novel restricted facultative methylotrophic bacterial strains 301 T, 30S, and SIP-4, utilizing C1 carbon compounds, were isolated from Lake Washington, Seattle, USA. Their phylogenetic position was determined by genotypic and phenotypic characterization using polyphasic approach. The above characterization method and results assigned SIP-3 strain as *Methylovorus gluco-sotrophus*, while strains 301 T and 30S were grouped in *Methylotenera mobilis*

JLW8T clad based on 16S rRNA gene sequence homology, but they were proposed as a novel strain *Methylotenera versatilis* sp. nov. based on their genomic and phenotypic characterization (Kalyuzhnaya et al. 2011).

Three different strains of methylo-trophic yeast were isolated from leaf phyllo-plane of mango tree (*Mangifera indica*) and wine grapes (*Vitis vinifera*). Two strains KM13 and KM15 from grape leaf and one strain KM03 T from mango leaf were isolated. On the basis of various polyphasic characterization and nucleotide sequence-based phylogeny, these three strains were placed in the *Ogataea wickerhamii* clade. On the basis of various polyphasic approaches along with ITS region sequence analysis, strain KM03T was proposed as a novel species named *Ogataea kanchanaburiensis* sp. nov., while two other strains KM13T and KM15 were assigned as *Ogataea wangdongensis* sp. nov. (Limtong et al. 2013).

From wheat soil contaminated with tribenuron methyl, a novel bacterial strain was obtained. By the polyphasic approaches like phenotypic characterization, carbon substrate utilization, lipid estimation, G + C content analysis, DNA-DNA hybridization, and nucleotide-based phylogeny revealed this strain as *Methylopila henanense* sp. nov. This novel strain was placed in the clad of most closely related genus *Methylopila* after 16S rRNA gene sequence analysis (Wang et al. 2015). In an earlier finding, a novel bioinoculant for sustainable agriculture in the form of non-pathogenic phyllosphere methylo-trophic bacteria was applied to agricultural fields to increase germination ability, storage ability, or seed vigor (Rajan et al. 2012).

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### 30.3 Methylo-trophs as PGPR (Plant Growth-Promoting Rhizobacteria)

Methylo-trophs are well-known for their potential to minimize the biotic and abiotic stress factors affecting plants by their plant growth-promoting ability. Moreover, this subpopulation is indulged in the mechanism of plant growth promotion directly or indirectly.

Methylo-trophic bacteria are also referred to as plant growth enhancer, and several species are isolated and reported earlier from rhizosphere region of plants (Meena et al. 2012; Anitha 2010; Madhaiyan et al. 2009a, b). In a study, methylo-trophic bacteria having nitrogen-fixing ability were isolated from tropical legume plants *Sesbania aculeata* and *Crotalaria juncea*. Biochemical and molecular characterization identified the strain as *Methylobacterium nodulans* ORS2060. Under greenhouse condition, a significant increased nodulation in *C. juncea* and *M. atropurpureum* was observed along with higher nitrogenase activity (Madhaiyan et al. 2009a, b).

Looking at the potential of methylo-trophic strains, a study was framed earlier to assess their plant growth-promoting ability together with the synergistic effect of methylo-trophs, *Azospirillum*, and phosphobacteria. Investigation was done in a hybrid tomato plant CoTH1 under greenhouse condition. In pot experiment seeds were coated with the consortia of *Azospirillum* and phosphobacteria, while foliar spray of methylo-trophs was also applied, and a significant growth and yield was recorded. Apart from plant growth-promoting rhizobacteria (PGPR), phyllosphere

bacterial inhabitants have also an ability to enhance and promote plant growth (Basile et al. 1969). Methanol is assimilated to CO<sub>2</sub> by methylotrophs similar to plants, and therefore toxicity produced because of formaldehyde accumulation is avoided and reduced in plants (McGiffen and Mantney 1996).

Methylotrophs associated with crop plants are reported as nitrogen fixers (Lee et al. 2006; Madhaiyan et al. 2004), as biofertilizers (Keerthi et al. 2015; Rekadwad 2014; Chauhan et al. 2010), and as IAA-producing bacteria (Anitha 2010) and used as inoculants for making agriculture sustainable (Kumar et al. 2016). In an earlier investigation, bacterial species of genus *Methylobacterium* were isolated from leaf phyllosphere of different crop plants and identified with the help of functional gene sequences of *mxoF* gene. The HPLC analysis of culture filtrate confirms the cytokinin production from numerous *Methylobacterium* strains that enhance the seed germination and seed vigor of wheat plant. Such kind of plant growth regulator (cytokinin) producing potent methylotrophic bacteria can be exploited in the development of bioinoculants (Meena et al. 2012).

Plant root growth is regulated by a very specific compound ethylene, a pathway component of auxin biosynthesis (Hardoim et al. 2008; Madhaiyan et al. 2007). High ethylene concentration works as stress condition in plants that inhibit the root growth which leads to plant aging. ACC (aminocyclopropane-1-carboxylic acid) is the precursor of ethylene and converted to ethylene by the action of enzymes ACC synthase and ACC oxidase during auxin biosynthesis pathway. This higher concentration of ethylene is restricted by the bacterium converting ACC to ammonia and alpha ketobutyrate with the help of enzyme ACC- deaminase rather than ethylene. The *Methylobacterium* species such as *Methylobacterium oryzae* (Madhaiyan et al. 2007), *M. radiotolerans*, and *M. nodulans* (Fedorov et al. 2013) interact with different plant roots in stress environment, diminishing the stress effect and making plant healthier (Dourado et al. 2015; Glick 1995).

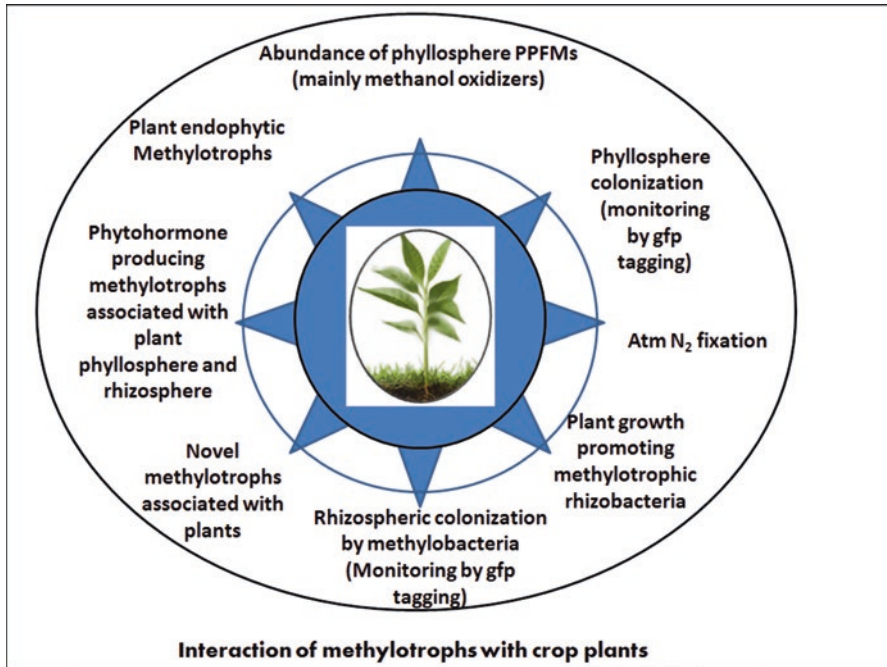
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### 30.4 Methylotrophic Bacteria as Plant Colonizers

Methanol-utilizing pink-pigmented facultative methylotrophs, commonly found over the surface of plant leaves, are characterized by both biochemical and molecular approaches. The colonization of this PPFM population was observed in red clover and winter wheat leaves in a study. The more consistent colonization was observed in the isolates from red clover leaves. These microbial communities have the potential to colonize the plant rhizosphere also after inoculation of seeds (Omer et al. 2004).

The colonization of *Methylobacterium extorquens* was observed by *gfp* (green fluorescent protein) expression in an investigation (Figueira et al. 2000) in which transformation was reported with a *gfp*-containing plasmid under the control of methane monooxygenase and *lacZ* promoter. With the help of epifluorescence microscope, the colonization ability of *Methylobacterium* sp. was monitored in the study.

After seed bacterization the colonization of *Methylobacteria* in phyllosphere and rhizosphere was observed along with phyllosphere colonization after foliar spray was also studied. The experiment was validated and confirmed by site localization



**Fig. 30.1** Various interactions between plants and methylotrophic bacteria

of *gfp*-tagged mutants using confocal microscopy (Fig. 30.1). The abundance of *Methylobacterium* sp. was found in phyllosphere of wheat plant in an earlier investigation (Verma et al. 2014).

In another study on *Perilla* plant, the distribution and colonization of facultative *Methylobacterium* spp. was determined. *Perilla*, a herb, is widely used as food in Japan, and the interaction of this herb with methylotrophic bacteria was studied extensively. The distribution study of PPFM in different vegetable leaves results in the maximum abundance of methylotrophs over *Perilla* plant leaves and about 15% of the total bacterial inhabitants there. The isolates from the seeds of *Perilla* plant were identified as *M. fujisawaense* DSM5686T and *M. radiotolerans* JCM2831T, indicating a special type of interaction between PPFM and *Perilla* plant (Mizuno 2013).

The abundant methylotrophic bacteria over the plant surface actively participate in carbon dioxide fixation and affect the plant growth. The culture-independent assessment of three different plant phyllosphere bacteria using metaproteogenomic approach revealed predominant alpha proteobacterial genus *Methylobacterium* along with *Sphingomonas*. Soybean, clover, and *Arabidopsis* phyllosphere-associated *Methylobacteria* have the ability to utilize methanol as sole carbon and energy. The results show the identification of unique methylotrophic traits and therefore give a good example of plant-microbe interaction (Delmotte et al. 2009).

In a model legume plant, *Medicago truncatula*, colonization of methylotrophic bacteria especially *Methylobacterium* sp. was observed by an inoculation experiment.

The ability to utilize methanol as a source of carbon and energy provides a selective advantage at the time of colonization of model legume plant. The competitive colonization ability between mutant and wild type *Methylobacterium extorquens* AM1 was determined. The fluorescent protein-labeled *Methylobacterium extorquens* AM1 were observed under fluorescence microscopy which revealed the major bacterial communities on leaf surface while abundance on the lower leaf side (Sy et al. 2005).

**Interaction of Methylotrophs with Water Plants** Possibly, metabolite exchange between water plants and methylotrophs displays a beneficial interaction. Macrophyte-associated methanotrophs were found in the water column in a study where methanotrophs oxidize methane by utilizing oxygen released by plants, while CO<sub>2</sub> and ammonia are provided to plants by oxidation. Methane oxidation carried out by methanotrophs therefore reduces the greenhouse effect in the environment by this mutual relationship (Iguchi et al. 2015). Ultimately methylotrophic bacteria maintain the biogeochemical cycle of carbon in the ecosystem.

The community structure of methanotrophs associated with both dryland and flooded rice ecosystem was illustrated in earlier investigation. Molecular characterization-based community composition showed the abundance of Type I and Type II methanotrophic community in flooded rice field soils (Dubey and Singh 2001).

The PPFM (pink-pigmented facultative methylotroph) abundance apart from crop association was also observed with coastal region plants. Root region soil of different plant species of Southern California coastal region showed the PPFM abundance, that is, a best example of water plant-PPFM interaction. The PPFM abundance was in the range of 10<sup>2</sup>–10<sup>5</sup> CFU/g dry soil of plant roots with variations across different plant species. In this natural ecosystem, this type of interaction suggests PPFM to be a better target for future work related to plant-microbe feedback. In the rhizosphere region of coastal sage scrub plants, PPFM abundance depends on both immediate and surrounding plant species (Irvine et al. 2012). Mangrove forest is another natural ecosystem of importance to mankind, and a diversified soil methylotrophic population was recorded from this fertile and dynamic ecosystem earlier. These potent methylotrophic strains have the ability to resist pathogenic fungus *Macrophomina phaseolina* (Kumar et al. 2015).

Wetlands are rich source of microbial assemblages, and this ecosystem is engaged in ecological control process. A number of methylotrophs are associated with wetland plants and are actively participating in nitrogen fixation process (Prasad et al. 2002; Barraquio and watanabe 1981). Fast accumulation of nitrogen in the roots of wetland plants indicates the methanotrophy during the development of peatland that ultimately induces the nitrogen fixation process. Additional CO<sub>2</sub> derived from methane is also fixed by methanotrophy in this ecosystem (Larmola et al. 2014). A novel methanotrophic bacterium *Methylocystis rosea* sp. from an arctic wetland soil of Norway was reported in a study having nitrogenase reductase structural gene (nifH) (Wartiainen et al. 2006).

### 30.5 Methylo trophs as Plant Endophytic Bacteria

This unique group of bacteria has properties to inhabit the plant internal compartments where they utilize methanol and other reduced carbon substrates to grow. They are actively participating in the metabolism of different plant metabolites. They are not pathogenic and are beneficial for plants in various aspects (Podolich et al. 2008; Pirttila et al. 2005; Madmony et al. 2005). Several endophytic bacterial communities are found within plant reproductive organs also (Madmony et al. 2005). The presence of endophytic methylo trophic bacteria induces the root formation along with enhanced biomass of soybean seedlings in a study (Holland and Polacco 1992). The endophytic bacteria reported in scots pine shoot tips were studied for their metabolic activity by in situ hybridization technique. These methylo trophic and other bacterial communities were found more abundant in summer season to the shoot tip and undetectable during winter season. This finding shows the temporal variation of the endophytic community, and highest endophytic numbers were also detected during spring season. The identified endophytic population in the shoot tip comprises *Methylobacterium* spp., *Pseudomonas fluorescens*, *Mycobacterium* sp., and *R. minuta*. Among all endophytic bacteria, *Methylobacterium* spp. was found most common and observed throughout the year (Pirttila et al. 2005) (Table 30.1).

Some another endophytic methylo trophs were observed and identified from poplar tree as *Methylobacterium populi* (Tanaka et al. 2008), and the location of the *Methylobacteria* inside the plant was examined through fluorescent in situ

**Table 30.1** A list of endophytic and epiphytic methylo trophic bacteria associated with various plant or plant parts

S.No.		Plant/plant parts	References
<b>Endophytic methylo trophs</b>			
1.	<i>Methylobacterium</i> sp.	Seed seedlings	Ferreira et al. (2008)
2.	<i>Methylovorus mays</i>	Plant shoot	Ivanova et al. (2000, 2008)
	<i>Methylobacterium mesophilicum</i>		Ulrich et al. (2008)
3.	<i>Methylobacterium extorquens</i> str. F and <i>Pseudomonas synxantha</i> str. G	Bud endophyte of scots pine	Laukkanen et al. (2000)
			Pirttila et al. (2000, 2003)
4.	<i>Methylobacterium</i> sp. and <i>Pseudomonas fluorescens</i>	Shoot tip	Pirttila et al. (2002, 2005)
5.	<i>Methylobacterium radiotolerans</i> , <i>M. oryzae</i> , <i>M. fujisawaense</i>	Mangrove plants	Dourado et al. (2012)
6.	Methanotrophs	Stem leaves of <i>Sphagnum</i> mosses	Raghoebarsing et al. (2005)
7.	<i>Methylobacterium</i> sp.	Potato tissues	Podolich et al. (2008)
<b>Epiphytic methylo trophs</b>			
8.	<i>Methylobacterium extorquens</i> (trans-zeatin producing)	<i>Arabidopsis</i> , maize, barley, and soybean surface	Koenig et al. (2002)
9.	<i>Methylobacterium</i> sp.	Crop plants phyllosphere	Meena et al. (2012)
10.	<i>Methylobacterium</i> sp.	<i>Funaria</i> protonema	Hornschuh et al. (2002)

hybridization technique. Mangrove plants like *Rizophora*, *Laguncularia*, and *Avicennia* spp. were also reported to be associated with the methylotrophic communities such as *Methylobacterium radiotolerans*, *M. oryzae*, and *M. fujisawaense*. These strains were also reported with their heavy metal tolerance ability (Dourado et al. 2012).

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## 30.6 Conclusion

Methylotroph-plant interaction is a best example of plant-microbe interaction that reflects the impact of this beneficial group of bacteria to environmental flora. The positive influence and interaction of methylotrophs with different parts of the plant make them healthier and strong enough in adverse conditions. Greenhouse effect also is inhibiting the growth of wider plant species in the environment, and methylotrophic communities (methanotrophs) are minimizing this plant growth-inhibiting effect. The abundant pink-pigmented facultative methylotrophic bacteria over plant leaf surface are also involved in plant growth promotion apart from rhizospheric methylotrophs. Plant-colonizing methylotrophic communities are also responsible for creating induced systemic resistance in plants. The present compilation enlightens the facts that endophytic or epiphytic methylotrophs interacting with various plant species and plant parts enhance our antiquity to know the physiological mechanism, activity, and abundance of methylotrophic communities.

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