



Biodiversity of methylotrophic microbial communities and their potential role in mitigation of abiotic stresses in plants

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Abstract

Methylotrophic bacterial community is very important group of bacteria utilizing reduced carbon compounds and plays significant role in plant growth promotion (PGP), crop yield and soil fertility for sustainable agriculture. Abiotic and biotic stresses are very important factors affecting PGP in agriculture. A vast number of microbial communities play an important role in abiotic stress tolerance. The PGP methylotrophic microbes have been reported well enough to mitigate different types of biotic and abiotic stresses. The abiotic stress tolerance was well documented by several methylotrophic bacterial communities such as *Hyphomicrobium*, *Methylarcula*, *Methylobacillus*, *Methylobacterium*, *Methylocapsa*, *Methylocella*, *Methyloferula*, *Methylhalomonas*, *Methylomonas*, *Methylophilus*, *Methylopila*, *Methylosinus*, *Methylotenera*, *Methylovirgula* and *Methylovorus*. The abiotic stress tolerance ability of different methylotrophs and their colonization in different parts of plants under severe low temperature, high temperature, drought and salt stress conditions have been investigated in various studies. The methylotrophic communities help in proliferation of plant directly through solubilization of phosphorus, potassium and zinc, production of phytohormones viz., auxins and cytokinins; production of Fe-chelating compound, biological nitrogen fixation and ACC-deaminase activities or indirectly through productions of ammonia, siderophores and secondary metabolites. The auxin and cytokinin secreted by methylotrophs influence seed germination and plant root growth and help plants to endure water stress. On the plant surface, the abundant methylotrophs exude osmo-protectants such as sugars and alcohols which ultimately help to protect the plants from desiccation and excessive radiations. The utilisation of these potent methylotrophic strains may facilitate proper crop production, PGP by ameliorating abiotic stresses.

Keywords Abiotic stress · Biodiversity · Methylotrophs · Plant growth promotion · PPFMs (Pink Pigmented Facultative Methylotrophs)

Introduction

Plants are sensitive to the environmental changes and therefore their growth and development are greatly affected by

several biotic and abiotic factors. Several microbial communities prevalent in soil, facilitate plants to grow in adverse environmental conditions. This plant-microbe interaction is very beneficial and climate resilient through which plant growth is not affected under biotic and abiotic stress conditions. Therefore, the natural microbial communities inhabiting inside the soil ecosystem make the agriculture sector more sustainable (Kumar et al. 2017; Kumar et al. 2016; Rana et al. 2018). Out of these diverse microbial communities, methylotrophs are another separate large bacterial population. Methylotroph is a unique group of microorganisms, which consume methane and its derivatives, such as; methanol, methylamine, etc. Methylotrophic bacteria are well enough to survive in all types of environmental conditions including low temperature (Romanovskaia et al. 2005; Sapp et al. 2018; Schouten et al. 2000; Yadav 2015; Yadav et al. 2017d); high

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temperature (Amin et al. 2017; Bodrossy et al. 1997, 1999; Trotsenko et al. 2009; Verma et al. 2016b); hyper saline (Doronina et al. 2003b, 2013, 2000b; Poroshina et al. 2013; Shmareva et al. 2018); drought (Kerry et al. 2018; Sivakumar et al. 2017; Verma et al. 2014); acidic habitats (Dedysh et al. 2000; Röling et al. 2006; Verma et al. 2013; Vorob'ev et al. 2009) and alkaline habitats (Doronina et al. 2003a, 2005, 2003b; Shmareva et al. 2018; Trotsenko et al. 2007). Plants receive valuable nutrients from this sub-population in stress and therefore plants acquire abiotic stress tolerance.

The global necessity to increase agricultural production from a decreasing land resource base has placed considerable strain on the fragile agro-ecosystems. Soil and plant microbiomes are considered vital for maintaining the sustainability of agriculture production systems. There are many links between microbial diversity and ecosystem processes (Yadav et al. 2018a). The plant growth promoting (PGP) methylotrophic microbes help plant for growth, yield and adaptation under diverse unfavourable environmental conditions. The plant microbiomes (rhizospheric, epiphytic and endophytic) play a vital role in plant growth and adaptations. The subpopulation of pink pigmented facultative methylotrophic (PPFMs) bacteria is abundantly present as plant epiphytes and endophytes as well rhizospheric and has been reported worldwide (Verma et al. 2016b, 2015; Yadav 2009). The methylotrophic microbes present in rhizospheric zone of plants are influenced by root exudates (Meena et al. 2012). A number of novel methylotrophic bacteria have been sorted out allied with the plant rhizosphere as rhizospheric methylotrophs e.g. *Methylobacterium soli*, *Methylobacterium goesingense*, *Methylobacterium variabile*, *Methylobacterium suomiense*, *Methylopila helvetica*, *Methylobacterium thiocyanatum*, *Methylopila capsulata* and *Methylobacterium aminovorans* (Cao et al. 2011; Doronina et al. 1998, 2002; 2000c; Gallego et al. 2005c; Idris et al. 2006; Urakami et al. 1993; Wood et al. 1998); from the phyllosphere as epiphytic methylotrophs e.g. *Methylobacterium cerastii*, *Methylobacterium gossipiicola*, *Methylobacterium phyllosphaerae*, *Methylobacterium phyllostachyos*, *Methylobacterium platani*, *Methylobacterium pseudosasicola*, *Methylobacterium thuringiense* and *Methylobacterium trifolii* (Kang et al. 2007; Madhaiyan and Poonguzhali 2014; Madhaiyan et al. 2009, 2012; Wellner et al. 2013; Wellner et al. 2012) and from internal part of plant as endophytic methylotrophs *Methylobacterium nodulans* and *Methylobacterium populi* (Jourand et al. 2004; Van Aken et al. 2004). The methylotrophic microbial communities have been sorted out as most ubiquitous as plant microbiomes in form of phyllospheric, rhizospheric and endophytic. Along with plant microbiomes several novel methylotrophs have reported from diverse natural habitats

(Gallego et al. 2005a; Gallego et al. 2006; Kalyuzhnaya et al. 2006; Kato et al. 2008; Patt et al. 1976).

Methylotrophs, being associated with plants have the ability to enhance the plant growth and improve the soil health. Methylotrophs perform different functions for improvement of crop yield and quality. Various biological processes including Nitrogen-fixation (Jourand et al. 2004; Raja et al. 2006; Rekadwad 2014; Sy et al. 2001); P, K and Zn solubilization (Agafonova et al. 2013; Jayashree et al. 2011b; Verma et al. 2013, 2014, 2016b); production of Fe-chelating compounds (Lacava et al. 2008; Verma et al. 2014, 2016b; Verma et al. 2015); production of PGP hormones such gibberellic acids, auxin and cytokinin (Chanratana et al. 2017; Ivanova et al. 2001; Meena et al. 2012; Omer et al. 2004; Pattnaik et al. 2017; Trotsenko et al. 2001) and ACC deaminase activities (Abeles et al. 1992; Chinnadurai et al. 2009; Madhaiyan et al. 2007a, 2006a, 2007b) are performed by methylotrophs. The methylotrophic microbes act as biocontrol agents against diverse plant pathogenic microbes through in-direct PGP attributes of siderophores, ammonia, HCN and diverse groups of secondary metabolites including extracellular hydrolytic enzymes (Madhaiyan et al. 2004, 2006b).

The methylotrophic microbes associated with crops may promote plant growth in terms of increased biomass, chlorophyll content, germination rates, hydraulic activity, leaf area, nitrogen content, Fe and Zn content, protein content, roots and shoot length, yield and tolerance to abiotic stresses like acidic and alkaline, draught, flood, radiation, salinity and temperature. The PGP methylotrophs as single bioinoculants or with co-inoculated with others beneficial PGP microbes (*Arthrobacter*, *Bacillus*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Serratia*, *Azotobacter*, *Azospirillum*) as microbial consortium may be used as bioinoculants/biofertilizers of biocontrol agents for enhanced crops production and soil fertility for sustainable agriculture (Verma et al. 2016a; Yadav et al. 2017a, b, c). The present critical review describes the different types of association between plant microbiome and environments. Further, the phydiological, biochemical and molecular aspects are also explored. This review may help in the development of biotechnological applications of plant-microbe interaction and particularly, methylotrophs-plant interaction in plant growth development and crop improvement under natural and abiotic stress environment.

Enumeration and characterization of methylotrophic bacterial communities

Plant microbiomes, specially the rhizospheric microbes are influenced by substances or roots exudates surrounding the host plants. To know the population of methylotrophic bacterial communities associated with crops, different techniques may be used. Methylotrophic microbes may be isolated from

rhizosphere by serial dilution and standard spread/pour plate technique and ammonium mineral salt (0.70 g K_2HPO_4 ; 300 μ g H_3BO_3 ; 0.5 g NH_4Cl ; 0.54 g KH_2PO_4 ; 0.2 g $CaCl_2 \cdot 2H_2O$; 10 μ g $CuCl_2 \cdot 2H_2O$; 30 μ g $MnCl_2 \cdot 4H_2O$; 200 μ g $CoCl_2 \cdot 6H_2O$; 20 μ g $NiCl_2 \cdot 6H_2O$; 60 μ g $Na_2MoO_4 \cdot 2H_2O$ 1 g $MgSO_4 \cdot 7H_2O$; 4.0 mg $FeSO_4 \cdot 7H_2O$; $ZnSO_4 \cdot 7H_2O$ per litre composition) as a selective media (Corpe 1985). The epiphytic methylotrophic bacteria may be isolated by leaf imprinting technique (Holland et al. 2000). In the leaf imprinting method, the leaves should be pressed on the solidified plates of the ammonium mineral salt medium. After 30–45 min of imprinting the leaf should be removed from the plates and plates should be incubated at the 5–55 °C in the BOD incubator for 7–30 days for isolation of psychrophilic, mesophilic and thermophilic bacteria. For isolation of endophytic methylotrophic population, surface sterilization techniques are followed. Plant samples (root, stem or leaf) should be sterilized for 1–3 min with 70% C_2H_5OH followed by 3–5 min with 1–3% $NaOCl$ and finally residual $NaOCl$ is removed by repeated washing with sterile double distilled water (Suman et al. 2016). Various growth conditions were used for the development of abiotic stress tolerant methylotrophic bacteria. This includes growth of halophilic methylotrophs in AMS (Ammonium mineral salt) media supplemented with 5–20% $NaCl$ concentration; growth of drought tolerant methylotrophs in 7–10% PEG (Polyethylene Glycol); growth of alkaliphilic methylotrophs in pH from 8 to 11; growth of acidophilic methylotrophs in pH 3–5; growth of psychrophilic methylotrophs in low temperature (>5 °C) and growth of thermophilic methylotrophs in high temperature (>45 °C).

Identification of methylotrophic bacteria is confirmed by molecular method, Genomic DNA of bacteria is extracted and purified using well established method. The isolated genomic DNA is analysed by agarose gel-electrophoresis techniques using 0.8% agarose and quantified by spectrophotometry techniques. The purified genomic DNA may be amplified using the universal primers pA (5'-AGAGTTTGATCTG GCTCAG-3') and pH (5'-AAGGAGGTGATCCA GCCGCA-3') (Edwards et al. 1989). The amplicon of 16S rRNA gene may be analysed through electrophoresis techniques using 1.2% agarose gel and purified. The technique amplified rDNA restriction analysis (ARDRA) may be used for reduction of numbers of methylotrophic microbial population using three different restriction endonucleases *Msp* I, *Alu* I, and *Hae* III. After the ARDRA, the clustering analysis may be done using NTSYS-2.02e software package (Numerical taxonomy analysis program package, Exeter software, USA), and dendrogram should be constructed for selection of representative strains. PCR amplified 16S rRNA gene product may be purified and sequenced and the partial 16S rRNA gene sequences should be analysed with Codon Code Analyser and compared with sequences available in the NCBI

GenBank database (<https://www.ncbi.nlm.nih.gov>). The phylogenetic tree can be constructed to know the taxonomical affiliations of methylotrophic communities using MEGA 4.0.2 software (Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0) (Fig. 1). The PPFMs may be screened for the presence of methanol dehydrogenase (*mxhF* gene) using specific primers 1003f (5'-GCG GCA CCA ACT GGG GCT GGT-3') and 1561r (5'-GGG CAG CAT GAA GGG CTC CC-3') (McDonald et al. 1995). The amplified *mxhF* gene product may be sequenced and should be compared with GenBank database and the phylogenetic tree may be constructed using MEGA 4.0.2 software (Fig. 2).

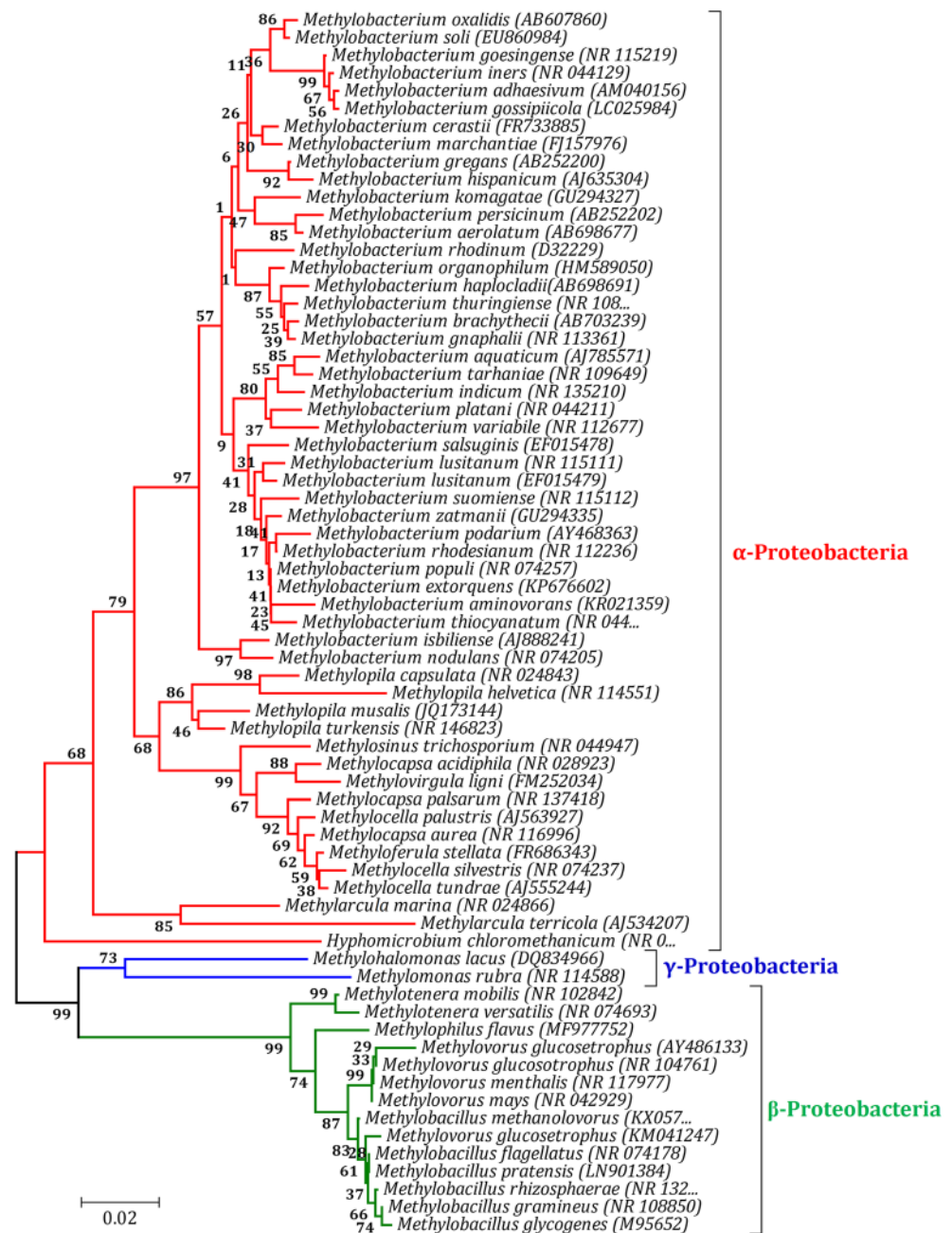
The methylotrophic bacteria from diverse habitats may have potential application in industry, agriculture and medicine. The methylotrophic bacteria may be screened for different hydrolytic enzymes production using standard protocols included 1-aminocyclopropane-1-carboxylate (ACC) deaminase activities (Jacobson et al. 1994); ammonia production (Cappucino and Sherman 1992), biological N_2 -fixation (Boddey et al. 1995); gibberellins production (Brown and Burlingham 1968), HCN production (Bakker and Schippers 1987), phosphorus solubilization (Pikovskaya 1948), K-solubilization (Hu et al. 2006), production of phytohormones indole-3-acetic acid (Bric et al. 1991), Fe-chelating compounds production (Schwyn and Neilands 1987); Zn-solubilization (Fasim et al. 2002); biocontrol against different fungal pathogens (Sijam and Dikin 2005).

Biodiversity of methylotrophic bacteria

Different classes of methylotrophic bacteria have been reported from diverse extreme habitats as plant microbiomes. The methylotrophic bacterial communities belong to diverse classes of proteobacteria namely α , β and γ -proteobacteria. The class α -proteobacteria has been reported as most dominant followed by β -proteobacteria (Fig. 3). In a review on seven different families of plant associated methylotrophs, namely Beijerinckiaceae, Hyphomicrobiaceae, Methylobacteriaceae, Methylococcaceae, Methylocystaceae, Methylophilaceae and Rhodobacteraceae have been sorted out (Fig. 3b). The methylotrophic bacterial communities belong to 15 different genera such as *Hyphomicrobium*, *Methylarcula*, *Methylobacillus*, *Methylobacterium*, *Methylcapsa*, *Methylocella*, *Methyloferula*, *Methylhalomonas*, *Methylomonas*, *Methylophilus*, *Methylopilula*, *Methylorinus*, *Methylotenera*, *Methylorivirgula* and *Methylorivorus* (Fig. 3c).

Bassalik (1913) described first *Methylobacterium* in the literature, which was isolated from earthworm. Kouno and Ozaki (1975) isolated and characterized 59 different methylotrophs from soil and water samples. Patt et al. (1976) described a new genus of methane-oxidizing bacteria

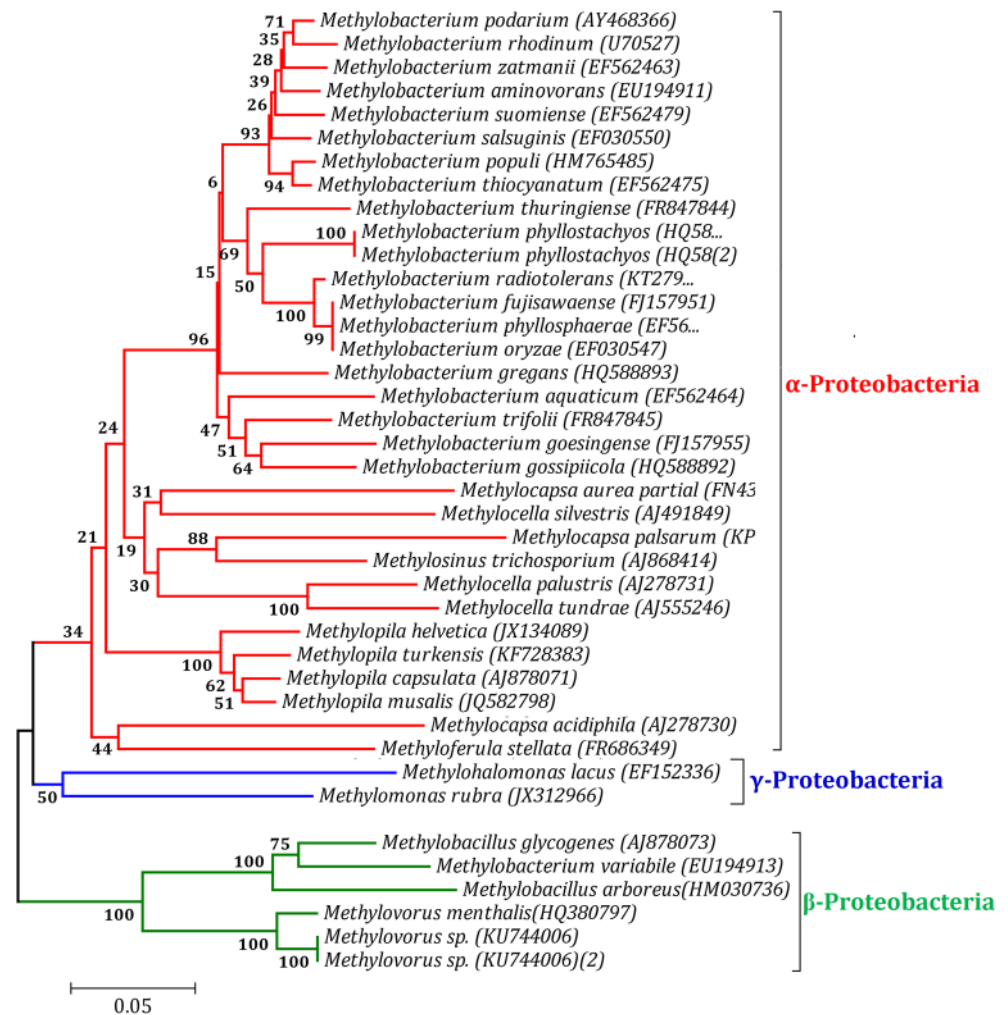
Fig. 1 Phylogenetic profiling of methylophilic bacterial communities using 16S rRNA genes obtained from NCBI GenBank database



and named it *Methylobacterium organophilum* XX (= ATCC 27886). *M. organophilum* is rod-shaped, methane-oxidizing bacteria. Wood et al. (1998) isolated and characterized a novel species of pink-pigmented methylotroph, *Methylobacterium thiocyanatum*. Balachandar et al. (2008) reported prevalence of several epiphytic strains of methylotrophs found in cotton, maize and sunflower phyllosphere. The phyllospheric microbes are reported as niche-specific such as, *Methylobacterium extorquens* C5, *Methylobacterium thiocyanatum* C1 from cotton; *Methylobacterium aminovorans* M4, *Methylobacterium extorquens* M3,

Methylobacterium fujisawaense M2 and *Methylobacterium thiocyanatum* M1 from maize; *Methylobacterium aminovorans* S4, *Methylobacterium suomiense* S2, *Methylobacterium thiocyanatum* S1 and *Methylobacterium zatmanii* S9 from sunflower. The studies on methylotrophic community are necessary to explore the complexity of interaction between these *Methylobacterium* and host plants. Twelve PPFM bacterial strains have been isolated and identified as *M. Variabile* and *M. aquaticum* using 16S rDNA sequencing. Sahin et al. (2008) have reported the taxonomical variability within the genus *Methylobacterium*.

Fig. 2 Phylogenetic profiling of methylotrophic bacterial communities using *maxF* obtained from NCBI GenBank database



Raja et al. (2008) have reported the *Methylobacterium* from phyllosphere of cotton, maize, sunflower, soybean, and mentha plants using culturable and 16S ribosomal RNA (rRNA) gene sequencing techniques. The pink pigmented facultative methylotrophs (PPFMs) isolated from leaf samples have been identified and reported as *Methylobacterium populi*, *Methylobacterium thiocyanatum*, *Methylobacterium suomiense*, *M. aminovorans*, and *Methylobacterium fujisawaense*. Jayashree et al. (2011a) have isolated methylotrophic bacterial communities from water samples of Coom and Adyar and soil samples in Tamil Nadu. Subhaswaraj et al. (2017) have reported the isolation and characterization of IAA and cytokinins producing epiphytic methylotrophs from the phyllosphere of *Brassica niagra* and identified as *Methylobacterium extorquens* MM2 using *maxF* gene analysis. In another study by Kaparullina et al. (2017a), the methylotrophic bacterial communities have been identified from herbs, shrub, and trees in Pushchino. *Methylobacterium* and other genera such as *Methylophilus*, *Methylobacillus*, *Hansschlegelia*, *Methylopila*, *Xanthobacter*

and *Paracoccus* have been identified using sequencing of the 16S rRNA genes.

Novel methylotrophs from diverse sources

A huge number of methylotrophic microbes, belonging to different classes and families have been reported from diverse habitats worldwide. These novel methylotrophs have been isolated from diverse habitats such as acidic soil, arid soil, air, freshwater, leaf surface and rhizospheric soil (Table 1).

Genome sequencing of methylotrophic bacteria

In the last few decades, the genome sequencing has been done for methylotrophic bacterial isolates from diverse habitats worldwide (Table 2). The complete genome information of various methylotrophic bacterial strains are available, such

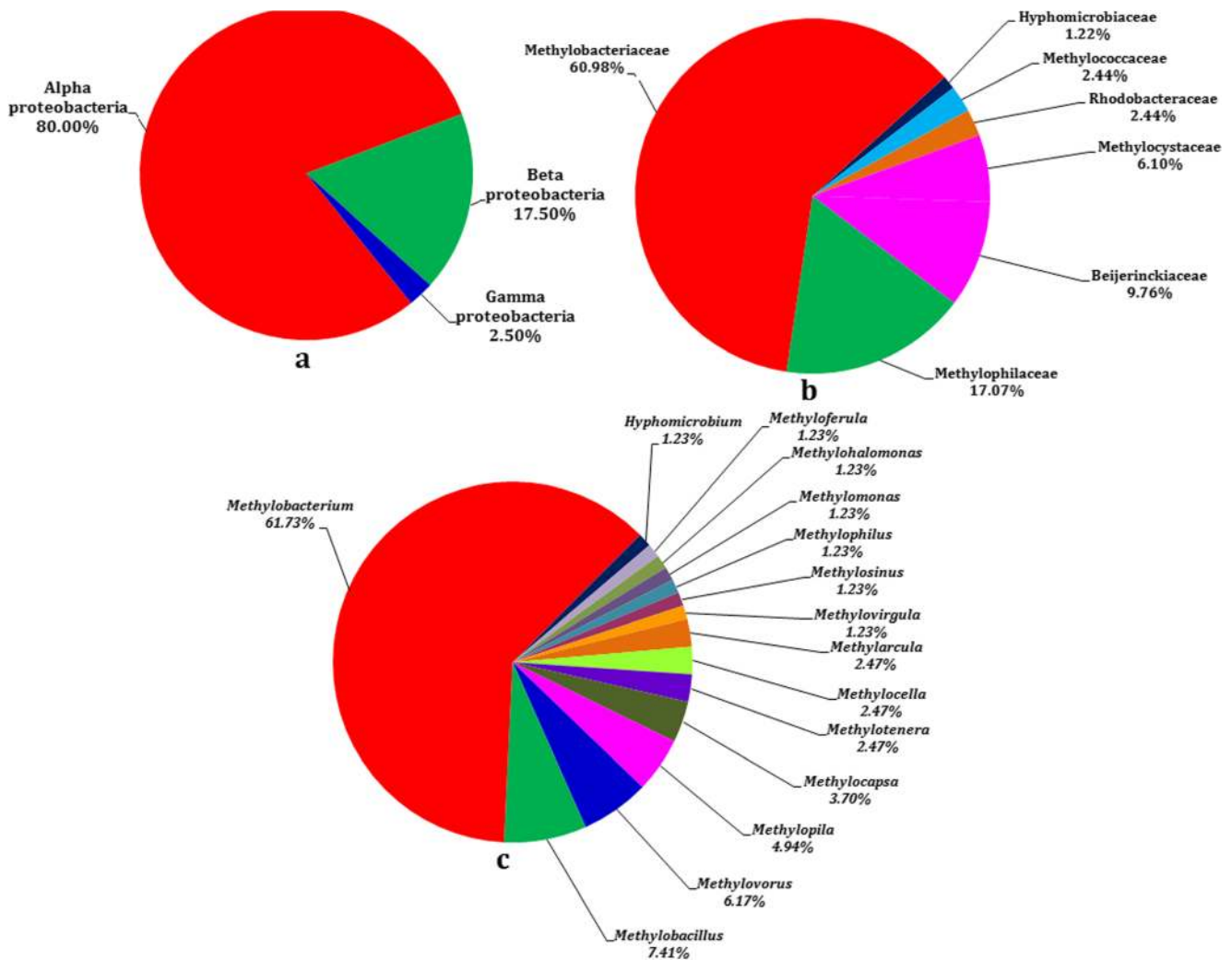


Fig. 3 **a** Abundance of methylotrophic bacterial communities belonging to different classes, **b** methylotrophic bacterial communities belonging to different families, **c** Distribution and abundance of different predominant genera of methylotrophic bacterial communities isolated from diverse habitats worldwide. **Sources:** Low temperature (Romanovskaia et al. 2005; Sapp et al. 2018; Schouten et al. 2000; Yadav 2015, 2017d); High temperature (Amin et al. 2017; Bodrossy et al. 1997, 1999; Rekadwad 2014; Trotsenko et al. 2009; Verma et al. 2016b); Hyper saline (Doronina et al. 2003b, 2013, 2000b; Poroshina et al. 2013; Shmareva et al. 2018); Drought (Kerry et al. 2018; Sivakumar et al. 2017; Verma et al. 2014; Veyisoglu et al. 2013); Acidic habitats (Dedysh et al. 2002, 2000; Dunfield et al. 2003; Röling et al. 2006; Verma et al. 2013;

Vorob'ev et al. 2009; Vorobev et al. 2011); Alkaline habitats (Doronina et al. 2003a, 2005, 2003b; Shmareva et al. 2018; Trotsenko et al. 2007); Phyllosphere (Balachandar et al. 2008; Kang et al. 2007; Madhaiyan et al. 2014; Madhaiyan and Poonguzhali 2014; Madhaiyan et al. 2009, 2012; Raja et al. 2008; Subhaswaraj et al. 2017; Tani and Sahin 2013; Tani et al. 2012a, b; Wellner et al. 2013, 2012); Rhizospheric (Cao et al. 2011; Doronina et al. 1998, 2002; 2000c; Gallego et al. 2005c; Idris et al. 2006; Kouno and Ozaki 1975; Urakami et al. 1993; Wood et al. 1998; Yadav and Yadav 2018a, b); Endophytic (Jourand et al. 2004; Prombunchachai et al. 2017; Sy et al. 2001; Van Aken et al. 2004); Drinking water (Gallego et al. 2005b, 2006; Kato et al. 2008)

as *Methylobacterium populi* BJ001 (Van Aken et al. 2004), *Methylovorus glucosetrophus* SIP3–4 (Lapidus et al. 2011), *Methylobacterium extorquens* CM4 (Marx et al. 2012), *Methylobacterium nodulans* ORS 2060 (Marx et al. 2012), *Methylobacterium mesophilicum* SR1.6/6 (Marinho Almeida et al. 2013), *Methylobacterium aquaticum* MA-22A (Tani et al. 2015), *Methylobacterium radiotolerans* JCM 2831 (Eevers et al. 2015), *Methyloferula stellata* AR4 (Dedysh et al. 2015b), *Methylotenera mobilis* JLW8 (McTaggart et al. 2015), *Methylotenera versatilis* 301 (McTaggart et al. 2015),

Methylobacterium indicum SE2.11 (Chaudhry et al. 2016) and *Methylobacterium* sp. AMS5 (Minami et al. 2016). A number of informations can be deciphered from the complete genome sequence of novel methylotrophs.

The complete genome of three representatives viz. *Methylovorus glucosetrophus* SIP3–4, *Methylotenera versatilis* 301 and *Methylotenera mobilis* JLW8, of *Methylophilaceae* family have been isolated from Lake Washington, Seattle, WA (Lapidus et al. 2011). The PPFMs in the Rhizobiales are widespread in the environment, and

Table 1 Biodiversity of novel methylotrophs reported from diverse habitats worldwide

Novel Methylotrophs	C-Source	Habitats	References
<i>Methylobacterium frigidaeris</i> IER25–16 ^T	CH ₃ OH	Air conditioning	Lee and Jeon (2018)
<i>Methylobacillus methanolivorans</i> Z ^T	CH ₃ OH	Activated sludge	Kaparullina et al. (2017b)
<i>Methylocapsa palsarum</i> NE2 ^T	CH ₄ / CH ₃ OH	Palsa soil	Dedysh et al. 2015a)
<i>Methylobacterium phyllostachyos</i> BL47 ^T	CH ₃ OH	Bamboo leaf	Madhaiyan and Poonguzhali (2014)
<i>Methylobacterium pseudosasicola</i> BL36 ^T	CH ₃ OH	Bamboo leaf	Madhaiyan and Poonguzhali (2014)
<i>Methylobacterium brachythecii</i> 99b ^T	CH ₃ OH	Bryophytes	Tani and Sahin (2013)
<i>Methylobacterium haplocladii</i> 87e ^T	CH ₃ OH	Bryophytes	Tani and Sahin (2013)
<i>Methylobacterium tarhaniae</i> N4211 ^T	CH ₃ OH	Arid soil	Veyisoglu et al. (2013)
<i>Methylobacterium thuringiense</i> C34 ^T	CH ₃ OH	Leaf surfaces	Wellner et al. (2013)
<i>Methylobacterium trifolii</i> TA73 ^T	CH ₃ OH	Leaf surfaces	Wellner et al. (2013)
<i>Methylobacterium cerastii</i> C44	CH ₃ OH	Leaf surfaces	Wellner et al. (2012)
<i>Methylobacterium gnaphalii</i> 23e ^T	CH ₃ OH	Cudweed	Tani et al. (2012a)
<i>Methylobacterium gossipiicola</i> Gh-105 ^T	CH ₃ OH	Cotton leaf	Madhaiyan et al. (2012)
<i>Methylobacterium oxalidis</i> 35a ^T	CH ₃ OH	<i>Oxalis corniculata</i>	Tani et al. (2012b)
<i>Methylotenera versatilis</i> 301 ^T	CH ₃ NH ₂	Lake Washington	Kalyuzhnaya et al. (2012)
<i>Methylobacterium marchantiae</i> JT1 ^T	CH ₃ OH	liverwort Thallus	(Schauer et al. (2011)
<i>Methylobacterium soli</i> YIM 48816 ^T	CH ₃ OH	Soil	Cao et al. (2011)
<i>Methyloferula stellata</i> AR4 ^T	CH ₄ / CH ₃ OH	Acidic <i>Sphagnum</i>	Vorobev et al. (2011)
<i>Methylovorus menthalis</i> VKM B-2663 ^T	CH ₃ OH	Corn mint	Doronina et al. (2011)
<i>Methylocapsa aurea</i> KYG ^T	CH ₄	Forest Soil	Dunfield et al. (2010)
<i>Methylovirgula ligni</i> BW863 ^T	CH ₃ OH	Beechwood	Vorob'ev et al. (2009)
<i>Methylobacterium phyllosphaerae</i> B27 ^T	CH ₂ O	Leaf tissues of rice	Madhaiyan et al. (2009)
<i>Methylobacterium brachiatum</i> B0021 ^T	CH ₃ OH	freshwater	Kato et al. (2008)
<i>Methylobacterium gregans</i> 002-074 ^T	CH ₃ OH	freshwater	Kato et al. (2008)
<i>Methylobacterium komagatae</i> 002-079 ^T	CH ₃ OH	freshwater	Kato et al. (2008)
<i>Methylobacterium persicinum</i> 002-165 ^T	CH ₃ OH	freshwater	Kato et al. (2008)
<i>Methylobacterium tardum</i> RB677 ^T	CH ₃ OH	freshwater	Kato et al. (2008)
<i>Methylobacterium iners</i> 5317S-33 ^T	CH ₃ OH	Air sample	Weon et al. (2008)
<i>Methylobacterium aerolatum</i> 5413S-11 ^T	CH ₃ OH	Air sample	Weon et al. (2008)
<i>Methylobacterium oryzae</i> CBMB20 ^T	CH ₃ OH	Rice	Madhaiyan et al. (2007a)
<i>Methylobacterium platani</i> PMB02 ^T	CH ₃ OH	<i>Platanus leaf</i>	Kang et al. (2007)
<i>Methylobacterium salsuginis</i> MR ^T	CH ₂ O	Sea water	Wang et al. (2007)
<i>Methylobacterium jeotgali</i> S2R03-9 ^T	CH ₄	Seafood	Aslam et al. (2007)
<i>Methylobacterium goesingense</i> iEII3	CH ₃ OH	Soil	Idris et al. 2006)
<i>Methylotenera mobilis</i> JLW8 ^T	CH ₃ NH ₂	Lake Washington	Kalyuzhnaya et al. (2006)
<i>Methylobacterium adhaesivum</i> AR27 ^T	CH ₃ OH	drinking water	Gallego et al. (2006)
<i>Methylobacterium aquaticum</i> GR16 ^T	CH ₃ OH	Water	Gallego et al. (2005a)
<i>Methylobacterium hispanicum</i> GP34 ^T	CH ₃ OH	Water	Gallego et al. (2005a)
<i>Methylobacterium variabile</i> GR3 ^T	CH ₃ OH	soil	Gallego et al. (2005c)
<i>Methylobacterium isbiliense</i> AR24 ^T	CH ₃ OH	drinking water	Gallego et al. (2005b)
<i>Methylobacillus pratensis</i> F31 ^T	CH ₃ OH	Meadow grass	Doronina et al. (2004)
<i>Methylobacterium nodulans</i> ORS 2060 T	CH ₄	<i>Crotalaria</i>	Jourand et al. (2004)
<i>Methylobacterium podarium</i>	CH ₃ OH	Human foot	Anesti et al. (2004)
<i>Methylobacterium populi</i> BJ001 ^T	CH ₃ OH	<i>Populus</i>	Van Aken et al. (2004)
<i>Methylobacterium nodulans</i> 2060 T	CH ₃ OH	Legume root	Jourand et al. (2004)

Table 1 (continued)

Novel Methylo trophs	C-Source	Habitats	References
<i>Methylocella silvestris</i> BL2 ^T	CH ₄	Acidic forest Soil	Dunfield et al. (2003)
<i>Methylobacterium lusitanum</i> RXM ^T	CH ₃ OH	Sewage	Doronina et al. (2002)
<i>Methylobacterium suomiense</i> , F20 ^T	CH ₃ OH	Soil	Doronina et al. (2002)
<i>Methylocapsa acidiphila</i> B2 ^T	CH ₄	Acidic Sphagnum	Dedysh et al. (2002)
<i>Hyphomicrobium chloromethanicum</i> CM2 ^T	CH ₃ Cl	Petroleum soil	McDonald et al. (2001)
<i>Methylobacterium chloromethanicum</i> CM4 ^T	CH ₃ Cl	Petroleum soil	McDonald et al. (2001)
<i>Methylobacterium dichloromethanicum</i>	CH ₂ Cl ₂	Water	Doronina et al. (2000c)
<i>Methylocella palustris</i> KT	CH ₄	Acidic soil	Dedysh et al. (2000)
<i>Methylovorus mayi</i>	CH ₃ OH	Maize	Doronina et al. (2000a)
<i>Methylopila helvetica</i> VKMB-189	CH ₂ Cl ₂	Soil	Doronina et al. (2000c)
<i>Methylarcula marina</i> h1 ^T	CH ₃ NH ₂	Sea estuary	Doronina et al. (2000b)
<i>Methylarcula terricola</i> h37 ^T	CH ₃ NH ₂	Black Sea	Doronina et al. (2000b)
<i>Methylobacterium thiocyanatum</i>	CH ₃ OH	Soil	Wood et al. (1998)
<i>Methylopila capsulata</i> IM1 ^T	CH ₃ OH	soil	Doronina et al. (1998)
<i>Methylobacterium aminovorans</i> TH-1	CH ₃ OH	Soil	Urakami et al. (1993)
<i>Methylovorus glucosotrophus</i> 6B1	CH ₃ OH	waste water	Govorukhina and Trotsenko (1991)
<i>Methylobacillus glycogens</i> T-11	CH ₃ OH	Decaying tomato	Yordy and Weaver (1977)
<i>Methylobacterium organophilum</i> XX	CH ₄	Lake	Patt et al. (1976)

many plant growth-promoting substances *Methylobacterium* have been characterized (Kwak et al. 2014). Some endophytic methylo trophs have been reported from rice ecosystem and soybean stem. The whole genome sequence of rice endophyte *Methylobacterium oryzae* CBMB20^T has been done by Kwak et al. (2014) whereas, the complete genome sequence of soybean endophyte *Methylobacterium* sp. AMS5 was reported by Minami et al. (2016). The complete genomic information of methylo trophic communities is useful to understand plant microbe-interaction and mechanism of plant growth promotion and adaptations of methylo trophic communities under diverse abiotic stress conditions (Table 2).

Plant growth promoting attributes of methylo trophs

The plant associated methylo trophs can promote the plant growth, enhance crop productivities and help adaption in diverse abiotic stresses of heat, pH and salinity. A huge diversity of methylo trophic bacterial community has been sorted out from different plants as epiphytic, endophytic and rhizospheric and from diverse extreme habitats of high/ low temperature, salinity, drought, acidic and alkaline soil. The methylo trophs have been shown to PGP directly, e.g. by nitrogen-fixation; P, K and Zn-solubilization; production of

Fe-chelating compounds; production of cytokinin, auxin and gibberellins and plant hormones and ACC deaminase activities. Several methylo trophs support PGP indirectly, via production of ammonia, HCN, siderophores, secondary metabolites, extra cellular hydrolytic enzymes and antagonistic substances, which inhibits the growth of different plant pathogen (Verma et al. 2017a, b; Yadav 2017; 2018a; b) (Table 3). The methylo trophic microbes when inoculated and bio-inoculants of biofertilizers, they promote the growth of plants in a number of ways through increased biomass, chlorophyll, germination rates, hydraulic activity, leaf area; nitrogen content, protein content; Fe content, Zn content, yield and tolerance to abiotic stresses like draught, temperature, salinity, pH etc., thus the diverse groups of methylo trophic communities enhanced crops productivities and soil fertility through one or more mechanisms for sustainable agriculture as long-term eco-friendly technology.

Production of phytohormones and Fe-chelating compounds

Plant-associated methylo trophs produce PGP phytohormones such as auxins, gibberellins and cytokinin. The gibberellins production is most typical for the rhizospheric methylo trophs whereas, auxins production is common to all the plant associated methylo trophs. Among indole derivative auxins, indole-

Table 2 Genome sequencing of methylotrophs isolated from diverse habitats worldwide

Methylotrophs	Size (Mb)	GC%	Number of Proteins	Number of Genes	Reference
<i>Methylobacillus flagellatus</i> KT	2.97	55.7	2715	2815	NCBI
<i>Methylobacillus glycogenes</i> JCM 2850	3.25	53.4	2433	634	NCBI
<i>Methylobacillus rhizosphaerae</i> Ca-68	2.37	52.4	2277	2356	NCBI
<i>Methylobacterium aquaticum</i> MA-22A	5.35	71.1	4674	4913	Tani et al. (2015)
<i>Methylobacterium brachiatum</i> 3.1 M4	5.81	69.8	5511	5583	NCBI
<i>Methylobacterium extorquens</i> CM4	5.78	68.2	5156	5400	Marx et al. (2012)
<i>Methylobacterium frigidaeris</i> IER25–16	6.4	70.5	6433	6964	NCBI
<i>Methylobacterium gossipiicola</i> Gh-105	4.52	68.7	4224	4291	NCBI
<i>Methylobacterium indicum</i> SE2.11	6.93	70.5	5677	6404	Chaudhry et al. (2016)
<i>Methylobacterium mesophilicum</i> SR1.6/6	6.21	69.5	5945	6052	Marinho Almeida et al. (2013)
<i>Methylobacterium nodulans</i> ORS 2060	7.77	68.9	7020	7471	Marx et al. (2012)
<i>Methylobacterium oryzae</i>	6.29	69.8	5530	5771	Kwak et al. (2014)
<i>Methylobacterium phyllosphaerae</i> CBMB27	6.08	69.8	5355	5548	NCBI
<i>Methylobacterium phyllostachyos</i> BL47	6.02	68.7	5790	5863	NCBI
<i>Methylobacterium platani</i> PMB02	7.02	71.1	6062	6402	NCBI
<i>Methylobacterium populi</i> BJ001	5.8	69.4	5240	5427	Van Aken et al. (2004)
<i>Methylobacterium pseudosasicola</i> BL36	6.85	68.4	6795	6870	NCBI
<i>Methylobacterium radiotolerans</i> JCM 2831	6.08	71.5	5600	5756	Eevers et al. (2015)
<i>Methylobacterium rhodinum</i> JCM 2811	3.82	67.9	–	–	NCBI
<i>Methylobacterium salsuginis</i> CC 1.6474	5.32	69.6	5012	5082	NCBI
<i>Methylobacterium</i> sp. AMS5	5.44	68.5	4670	4917	Minami et al. (2016)
<i>Methylobacterium tarhaniae</i> DSM 25844	6.74	70.4	5746	6174	NCBI
<i>Methylobacterium thiocyanatum</i>	3.9	67.3	–	–	NCBI
<i>Methylobacterium variabile</i> DSM 16961	7.43	70.7	6441	6913	NCBI
<i>Methylobacterium zatmanii</i>	1.870	47.91	–	–	NCBI
<i>Methylocapsa acidiphila</i> B2	3.92	61.9	3520	3656	NCBI
<i>Methylocapsa aurea</i> KYG T	0.7	61.3	647	669	NCBI
<i>Methylocapsa palsarum</i> NE2	4.11	61.8	3820	3885	NCBI
<i>Methyloferula stellata</i> AR4	4.24	59.6	3877	3961	Dedysh et al. (2015b)
<i>Methylotenera mobilis</i> JLW8	2.55	45.5	2326	2396	McTaggart et al. (2015)
<i>Methylotenera versatilis</i> 301	3.06	42.6	2762	2842	McTaggart et al. (2015)
<i>Methylovorus glucosetrophus</i> SIP3–4	3	54.9	2795	2867	Lapidus et al. (2011)

acetic acid (IAA) is the most well characterized from methylotrophic bacteria and other predominant genera such as *Arthrobacter*, *Bacillus*, *Pseudomonas*, *Serratia*, *Burkholderia*, and *Azospirillum*. The methylotrophic microbial communities producing IAA, gibberellins and cytokinins may potentially be used to promote plant growth under normal as well as abiotic stress conditions. Phytohormones are produced by a number of methylotrophs; to name a few: *Methylobacterium extorquens* IIWP-43, *Methylobacterium extorquens* MP1, *Methylobacterium mesophilicum* B-2143, *Methylobacterium mesophilicum* HHS1–36, *Methylobacterium mesophilicum* IIWP-45,

Methylobacterium mesophilicum NIAW1–41, *Methylobacterium phyllosphaerae* HHS2–67, *Methylobacterium radiotolerans* HHS1–45, *Methylobacterium radiotolerans* IHD-35, *Methylobacterium* sp. ABR-48, *Methylobacterium* sp. CBMB20, *Methylobacterium* sp. Mb10, *Methylobacterium* sp. NIAW2–37, *Methylobacterium* sp. THD-35 and *Methylobacterium zatmanii* MS4 (Chanratana et al. 2017; Ivanova et al. 2001; Meena et al. 2012; Omer et al. 2004; Pattnaik et al. 2017; Trotsenko et al. 2001; Verma et al. 2015).

Ivanova et al. (2001) have reported the isolation of obligate and facultative methylotrophic bacteria, having ability to

Table 3 Stress adaptive methylotrophs with multifarious PGP attributes for alleviation of diverse abiotic stresses in plants (P- Phosphate solubilisation; IAA- Indol acetic Acid production; Sid- Siderophores production; GA-Gibberellic acid production; ACC- ACC deaminase production; N₂F-N₂ Fixation)

Methylotrophs	P	IAA	Sid	ACC	GA	N ₂ F	Reference
<i>Methylobacillus arboreus</i> Iva	+	–	–	–	–	–	Agafonova et al. (2013)
<i>Methylobacterium extorquens</i> G10	+	–	–	–	–	–	Agafonova et al. (2013)
<i>Methylobacterium extorquens</i> IIWP-43	+	+	+	–	–	–	Verma et al. (2014)
<i>Methylobacterium extorquens</i> MP1	–	+	–	–	–	–	Pattnaik et al. (2017)
<i>Methylobacterium fujisawaense</i>	–	–	–	+	–	–	Madhaiyan et al. (2006a)
<i>Methylobacterium lusitanum</i> MSF 32	+	–	–	–	–	–	Jayashree et al. (2011b)
<i>Methylobacterium mesophilicum</i> AR5.1	–	–	+	–	–	–	Lacava et al. (2008)
<i>Methylobacterium mesophilicum</i> B-2143	–	+	–	–	–	+	Ivanova et al. (2001)
<i>Methylobacterium mesophilicum</i> HHS1–36	–	+	+	+	+	–	Verma et al. (2015)
<i>Methylobacterium mesophilicum</i> IIWP-45	+	+	+	–	–	–	Verma et al. (2014)
<i>Methylobacterium mesophilicum</i> NIAW1–41	+	+	+	+	–	–	Verma et al. (2016b)
<i>Methylobacterium nodulans</i> 2060 T	–	–	–	–	–	+	Jourand et al. (2004)
<i>Methylobacterium oryzae</i> CBMB20	–	–	–	+	–	–	Chinnadurai et al. (2009)
<i>Methylobacterium oryzae</i> CBMB20 ^T	–	–	–	+	–	–	Madhaiyan et al. (2007a)
<i>Methylobacterium phyllosphaerae</i> HHS2–67	–	+	+	+	+	–	Verma et al. (2015)
<i>Methylobacterium populi</i> TNAU1	–	–	–	+	–	–	Raja et al. (2008)
<i>Methylobacterium radiotolerans</i> COLR1	–	–	–	+	–	–	Chinnadurai et al. (2009)
<i>Methylobacterium radiotolerans</i> HHS1–45	–	+	+	+	+	–	Verma et al. (2015)
<i>Methylobacterium radiotolerans</i> IHD-35	+	+	+	–	–	–	Verma et al. (2014)
<i>Methylobacterium</i> sp. ABR-48	–	+	–	–	–	–	Yadav et al. (2015a)
<i>Methylobacterium</i> sp. CBMB20	–	+	–	–	–	+	Lee et al. (2006)
<i>Methylobacterium</i> sp. HHS2–69	–	–	+	+	+	–	Verma et al. (2015)
<i>Methylobacterium</i> sp. Mb10	–	+	–	–	–	–	Omer et al. (2004)
<i>Methylobacterium</i> sp. NIAW2–37	+	+	+	+	–	–	Verma et al. (2016b)
<i>Methylobacterium</i> sp. THD-35	+	+	+	–	–	+	Verma et al. (2013)
<i>Methylobacterium</i> sp. WP1	–	–	–	+	–	–	Chinnadurai et al. (2009)
<i>Methylobacterium zatmanii</i> MS4	–	+	–	–	–	–	Pattnaik et al. (2017)
<i>Methylopila musalis</i> MUSA	+	–	–	–	–	–	Agafonova et al. (2013)
<i>Methylovorus menthalis</i> MM	+	–	–	–	–	–	Agafonova et al. (2013)

produce plant growth promoter IAA (3–100 µg/mL). Omer et al. (2004) reported the presence of IAA in supernatants of PPFMs microbial cultures, three out of the 16 isolates tested showed a positive reaction in a colorimetric assay. The presence was further unambiguously confirmed by high-performance liquid chromatography in combination with NMR. The IAA production was significantly stimulated by L-tryptophan. These results prove that PPFM bacteria are able to produce the plant hormone IAA.

Pink-pigmented facultative methylotrophs are prevalent aerobic bacteria colonizing the phyllosphere of various plant species (Pattnaik et al. 2017). PPFMs have the ability to utilize plant-derived methanol as an energy substrate when plants are being colonized under stress.

PPFMs were isolated from the phyllosphere of peach (*Prunus persica* L.) and strawberry (*Fragaria ananassa* L.) by the leaf imprint method. The 16S rRNA gene sequences demonstrated that the isolates MP₁ and MS₄ were *Methylobacterium extorquens* and *Methylobacterium zatmanii*, respectively. High-performance thin-layer chromatographic analysis indicated production of indole acetic acid by *M. extorquens* MP₁ and *M. zatmanii* MS₄. The amount of IAA produced was 10.353 and 8.473 µg·mL⁻¹ for *M. extorquens* MP₁ and *M. zatmanii* MS₄, respectively. The increased production of IAA and subsequent enhancement in growth-promoting traits indicates that methylotrophs from diverse plant species can be used to improve early plant development in tomato under controlled conditions.

Lacava et al. have reported the isolation of *Methylobacterium* spp., as endophyte from citrus plant; which can produce iron chelating compounds (Lacava et al. 2008). The Fe-chelating compounds production of *Methylobacterium* strains were tested using chromeazurol agar assay test (CAS), Csáky test (hydroxamate-type) and Arnow test (catechol-type). All 37 strains of *Methylobacterium* sp. tested were CAS-positive for Fe-chelating compounds production. *Methylobacterium* sp. produced hydroxamate-type, but not catechol-type siderophores. In vitro growth of *Xfp* was stimulated by the presence of supernatant siderophores of endophytic *Methylobacterium mesophilicum*. A number of studies have been reported mentioning the siderophores production by methylotrophic bacteria such as *Methylobacterium extorquens* IWP-43, *Methylobacterium mesophilicum* AR5.1, *Methylobacterium mesophilicum* HHS1–36, *Methylobacterium mesophilicum* IWP-45, *Methylobacterium mesophilicum* NIAW1–41, *Methylobacterium phyllosphaerae* HHS2–67, *Methylobacterium radiotolerans* HHS1–45, *Methylobacterium radiotolerans* IHD-35, *Methylobacterium* sp. HHS2–69, *Methylobacterium* sp. NIAW2–37 and *Methylobacterium* sp. THD-35 (Lacava et al. 2008; Verma et al. 2014, 2016b, 2015).

N₂-fixation by methylotrophic microbes

Nitrogen is the major limiting factor for plant growth, the application of N₂-fixing microbes as biofertilizers has emerged as one of the most efficient and environmentally sustainable methods for increasing the growth and yield of crop plants under the natural and abiotic stress conditions. N₂-fixation by methylotrophic microbes is one of the possible biological alternatives to N-fertilizers and could lead to more productive and sustainable agriculture and act as ecofriendly technology. Many plant associated methylotrophs have been reported to fix N₂ for availability to the host plants. A variety of nitrogen fixing methylotrophs *Methylobacterium mesophilicum* B-2143, *Methylobacterium nodulans* 2060 T, *Methylobacterium* sp. CBMB20 and *Methylobacterium* sp. THD-35 have been isolated from the rhizosphere of various crops, which contribute fixed nitrogen to the associated plants (Jourand et al. 2004; Lee et al. 2006; Madhaiyan et al. 2015, 2014; Raja et al. 2006; Rekadwad 2014; Sy et al. 2001).

Sy et al. (2001) isolated N₂-fixing *Methylobacterium nodulans* a facultative methylotroph from *Crotalaria* legumes. Rekadwad (2014), isolated N₂-fixing methylotrophs from mud near hot springs, Unkeshwar, Maharashtra, India and which has been identified as *Methylobacterium organophilum* using morphological and biochemical tests. The isolated methylotrophic bacteria were found to enhance plant growth and yield when inoculated with *Vigna radiata*. Raja et al. (2006), reported 11 nitrogen fixing methylotrophic microbes out of 250 *Methylobacterium* studied. In another study by Madhaiyan et al. (2014), *Methylobacterium* sp. L2–4 is

reported as nitrogen fixing *Methylobacterium* isolated from leaf *Jatropha curcas*.

P-solubilization

Phosphorus (P) is major essential macronutrients for plant growth and development. The Methylotrophs have capabilities to solubilise inorganic form of soil P and make it available to the host plants. Some methylotrophic bacteria can convert insoluble phosphorus to soluble orthophosphate and make available to the plants in rhizosphere region (Kumar et al. 2016). The rhizospheric methylotrophic microbial communities possessing P-solubilizing attributes could be used as bioinoculants or biofertilizers and act as ecofriendly bioresources for replacements of chemical phosphorus fertilizers. P-solubilization by methylotrophic communities is common PGP traits which help the crops for plant growth and development under the normal as well as abiotic stress conditions. A vast number of PGP methylotrophs with P-solubilizing ability have been sorted out including the members such as *Methylobacillus arboreus* Iva, *Methylobacterium extorquens* G10, *Methylobacterium extorquens* IWP-43, *Methylobacterium lusitanum* MSF 32, *Methylobacterium mesophilicum* IWP-45, *Methylobacterium mesophilicum* NIAW1–41, *Methylobacterium radiotolerans* IHD-35, *Methylobacterium* sp. NIAW2–37, *Methylobacterium* sp. THD-35, *Methylopila musalis* MUSA and *Methylovorus menthalis* MM (Agafonova et al. 2013; Jayashree et al. 2011b; Verma et al. 2013, 2014, 2016b). Microbial strains solubilize Phosphorus, probably by producing the organic acids such as acetate, ketogluconate, oxalate, citrate, glycolate, succinate, gluconate, lactate and tartarate (Stella and Halimi 2015; Yadav et al. 2015b).

P-solubilizing activity was found in 14 strains of plant-associated aerobic methylotrophic bacteria belonging to the five genera *Methylophilus*, *Methylobacillus*, *Methylovorus*, *Methylopila* and *Methylobacterium* with 12 distinct species *Methylobacillus arboreus*, *Methylobacterium extorquens*, *Methylobacterium extorquens*, *Methylobacterium nodulans*, *Methylophilus flavus*, *Methylopila capsulata*, *Methylopila capsulate*, *Methylopila musalis*, *Methylopila turkiensis*, *Methylovorus fructose*, *Methylovorus mays*, *Methylovorus menthalis* (Agafonova et al. 2013). The growth of *Methylobacterium* on medium with methanol as the carbon and energy source and insoluble tricalcium phosphate as the phosphorus source was accompanied by a decrease in pH due to the accumulation of up to 7 mM formic acid as a methanol oxidation intermediate and by release of 120–280 μM phosphate ions, which can be used by both bacteria and plants. Thirteen PO₄-solubilization PPFM isolates were reported from Adyar and Cooum river, Chennai and forest soil Tamilnadu, India (Jayashree et al. 2011b) and they were identified as *Methylobacterium extorquens*, *Methylobacterium*

komagatae, *Methylobacterium gregans*, and *Methylobacterium organophilum*. The higher phosphate solubilization was observed in four strains 202 mg l⁻¹ by MSF 34, 279 mg l⁻¹ by *Methylobacterium komagatae*, 301 mg l⁻¹ by MDW 80 and 415 mg l⁻¹ by MSF 32, after 7 days of incubation.

In research by Verma et al. (2013), the acid tolerant methylotrophic P-solubilizing bacteria have been isolated from wheat growing in acidic soil of southern hill zone of India and found that *Methylobacterium* sp. IARI-THD-35 and *Methylobacterium radiotolerans* IARI-THW-31 solubilized $3.6.35 \pm 1.0$ and 21.35 ± 1.0 $\mu\text{g mg}^{-1} \text{day}^{-1}$ respectively under the abiotic stress of low pH. The Acidolerant methylotrophic microbes may have application as bioinoculants or biofertilizers and biocontrol agents in crops growing under acidic conditions. In another study by Verma et al. (2014) the thermotolerant methylotrophic microbes have been isolated from wheat growing in sub-arid region as central zone of India. The P-solubilizing attributes were found in three *Methylobacterium* as *Methylobacterium extorquens* IARI-IIWP-43 (23.6 ± 1.0 $\mu\text{g mg}^{-1} \text{day}^{-1}$), *Methylobacterium mesophilicum* IARI-IIWP-45 (12.6 ± 1.5 $\mu\text{g mg}^{-1} \text{day}^{-1}$) and *Methylobacterium radiotolerans* IARI-IHD-35 (14.6 ± 1.2 $\mu\text{g mg}^{-1} \text{day}^{-1}$) under abiotic stress of high temperature. These promising isolates showing a range of useful PGP attributes may be explored for agricultural applications. The biodiversity of wheat associated bacteria were deciphered from peninsular zone of India for their potential application for plant growth under the high temperature conditions (Verma et al. 2016b). Among the 264 bacterial isolates, two *Methylobacterium* were found to solubilize phosphorus as *Methylobacterium* sp. IARI-NIAW2-37 (41.6 ± 0.1 mg l⁻¹) and *Methylobacterium mesophilicum* IARI-NIAW1-41 (43.2 ± 1.1 mg l⁻¹) isolated from wheat.

Alibrandi et al. (2018) isolated several *Methylobacterium* exhibiting both PGP and antimicrobial activities from seed endosphere of *Anadenanthera colubrine*. The isolates were able to solubilize organic phosphate and can grow without inducing a colour change, thus suggesting an enzymatic mechanism of phosphate solubilisation. The activities have been shown by four strains namely *Methylobacterium indicum* SE2. 11, *Methylobacterium extorquens* IAM 12631, *Methylobacterium hispanicum* DSM 16372 and *Methylobacterium rhodesianum* DSM 5687.

ACC deaminase activity

Ethylene is one of the most important plant hormones which is usually found in the gaseous form and is produced endogenously. It is efficient at low concentrations controlling various activities such as growth, cellular metabolism and even senescence. The methylotrophic bacteria possess an enzyme ACC deaminase which converts ACC, the immediate precursor of

ethylene to α -ketobutyrate and ammonium thus lowering the concentration of the ethylene during the stress conditions and stimulating the growth of the plants. The ACC deaminase activity has been reported in *Methylobacterium fujisawaense* (Madhaiyan et al. 2006a), *Methylobacterium mesophilicum* HHS1-36 (Verma et al. 2015), *Methylobacterium mesophilicum* NIAW1-41 (Verma et al. 2016b), *Methylobacterium oryzae* CBMB20 (Chinnadurai et al. 2009), *Methylobacterium oryzae* CBMB20^T (Madhaiyan et al. 2007a), *Methylobacterium phyllosphaerae* HHS2-67 (Verma et al. 2015), *Methylobacterium populi* TNAU1 (Raja et al. 2008), *Methylobacterium radiotolerans* COLR1 (Chinnadurai et al. 2009), *Methylobacterium radiotolerans* HHS1-45 (Verma et al. 2015), *Methylobacterium* sp. HHS2-69 (Verma et al. 2015), *Methylobacterium* sp. NIAW2-37 (Verma et al. 2016b) and *Methylobacterium* sp. WP1 (Chinnadurai et al. 2009). Joe et al. (2014), reported *Azospirillum brasilense* CW903 and *Methylobacterium oryzae* CBMB20 showing ACC deaminase activity reduced ethylene levels in plants. Rhizobial strains possessing ACC deaminase activity have been known to be 40% more proficient in forming nitrogen-fixing nodules as compared to strains lacking this activity (Ma et al. 2004, 2003). The phytohormone ethylene plays an important role in PGP and development including fruit ripening, germination, leaf and flower senescence and abscission, root-hair initiation, nodulation and response to wide variety of stresses (Abeles et al. 1992).

Madhaiyan et al. (2006a), reported the presence of ACC deaminase in *Methylobacterium fujisawaense* and its lowering of ethylene levels and promotion of root elongation in canola seedlings under gnotobiotic conditions. Chinnadurai et al. (2009), isolated epiphytic *Methylobacterium radiotolerans* from rice and characterized for their PGP attributes of ACC deaminase and its role in regulating plant ethylene level. Foliar spray of ACC deaminase enhanced the shoot and root length of rice under the gnotobiotic condition. The possible interaction of the plant hormones auxin and ethylene and the role of 1-aminocyclopropane-1-carboxylate (ACC) deaminase containing bacteria on ethylene production in canola (*Brassica campestris*) in the presence of inhibitory concentrations of growth regulators were investigated by Madhaiyan et al. (2007b). In another research of Madhaiyan et al. (2007a), A pink-pigmented, facultatively methylotrophic bacterium, strain CBMB20^T, isolated from stem tissues of rice, was analysed by a polyphasic approach. Verma et al. (2015), isolated and characterized the ACC deaminase in *Methylobacterium mesophilicum* IARI-HHS1-36, *Methylobacterium radiotolerans* IARI-HHS1-45, *Methylobacterium* sp. IARI-HHS2-69 and *Methylobacterium phyllosphaerae* IARI-HHS2-67 from wheat (*Triticum aestivum*) from the northern hills zone of India. Prombunchachai et al. (2017) evaluated the production

of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase enzyme from endophytic *Methylobacterium radiotolerans* ED5–9. Activity of ACC deaminase enzyme was observed at 365.05 ± 90.51 nmol of α -ketobutyrate/mg of protein/h. The ACC deaminase determines the ability of bacteria to increase the resistance of plants to various types of stress. The genes of ACC deaminase (*acdS*) and the closely related enzyme D-cysteine desulfhydrase (*dcdD*) were searched in type strains of various representatives of the genus *Methylobacterium* by Ekimova et al. (2018).

Abiotic stress and microbial responses

Under stressed conditions, the microbes change their physiology and metabolic activities according to the environment. These environmental stimuli induce the methylotrophic physiology in response to various stress environments. This is therefore called as microbial stress responses (Boylan et al. 1993; Gaidenko and Price 1998). Biotic and abiotic factors have major impact on a plant that lead to significant losses in crop productivity. Several abiotic factors are responsible for changes in environmental balance that ultimately affecting the plant productivity. Agriculture sector is mostly affected by numerous abiotic factors such as water stress, salinity stress, temperature stress and drought stress. The microbial entities present on earth are most abundant and fundamental living system, present naturally in soil ecosystem. The microbial life is affecting plant growth development as interacting with plant as a part of their metabolism in soil. To fight against abiotic stresses, microbial system associated with plants is providing basic defence to plants combating diseases by providing essential nutrients (Turner et al. 2013) (Fig. 4).

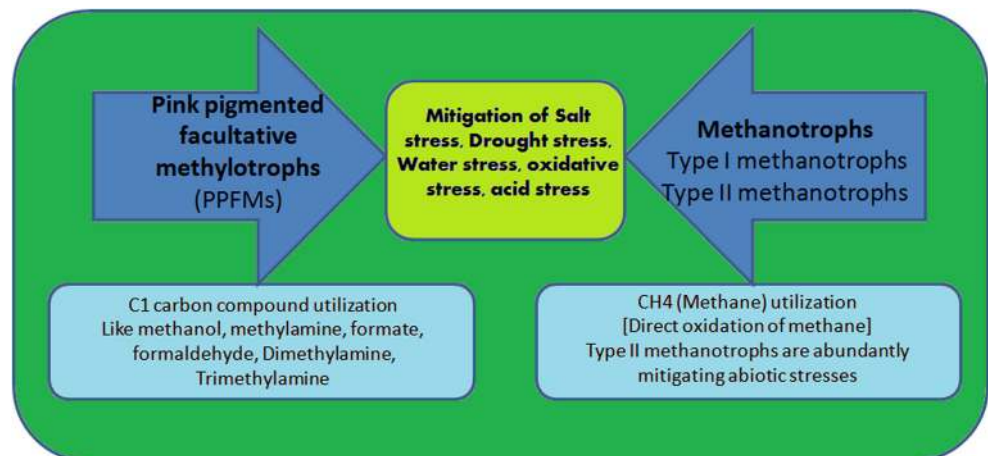
To avoid and to accommodate under abiotic stress condition, plants are fighting with their intrinsic metabolic activities for the improvement of plant growth and development. Moreover, microorganisms are those cosmopolitan natural

inhabitants, helping plants to mitigate abiotic stresses by exploring their metabolic capabilities. In the natural ecosystem, microbial interaction with plant is beneficial that enhances the local and systemic metabolic mechanisms providing strength to plant system under unfavourable conditions. This beneficial interaction comprises a very tedious plant cellular mechanism. A number of molecular and biochemical approaches are being used to resolve and to understand the complex pathways and processes inside the cell. The understanding of complex cellular processes along with physiological aspects provides the interpretation of plant-microbe association and defence mechanism against abiotic stresses. Further it is required to look into deeper insights to understand the mitigation mechanism of abiotic stresses in crop plants for their translation in enhance crop productivity. This is achieved by various ‘multi-omics’ approaches such as genomics, proteomics, transcriptomics and metabolomic studies on crop-microbe interaction and their impact on external environment (Meena et al. 2017). Microbial system interacting with plants induces various local and systemic responses, triggering plant metabolic activities to sustain and to accommodate them under unfavourable abiotic stress condition (Nguyen et al. 2016). Apart from epiphytic microorganisms, endophytic bacteria and fungi are also reported to survive in extreme climatic condition within healthy crop plants inside the tissues and enhance plant growth and development under stress environment such as drought, salinity, heat and nutrient deficient environment (Fig. 4). The endophytic microbial communities are reported to utilise their molecular mechanism for increasing stress tolerance along with antioxidant activities like reactive oxygen species scavenging (Rana et al. 2018; Lata et al. 2018).

Salt stress tolerance and mitigation

One very important group of methylotrophs i.e. PPFM is reported to survive in extreme saline environment and colonization of methylotroph strain with plant root was

Fig. 4 Abiotic stress mitigation by methylotrophic bacterial community



analysed. Egamberdieva et al. (2015) has shown that Methylophilic strain *Methylobacterium mesophilicum* has the ability to survive in higher saline condition and was able to colonize plant roots and shoot under extreme salt and drought environment. In a gnotobiotic sand system, the survival of bacterial strain along with different salt concentrations added was investigated and analysed in a pot experiment. Even in saline soil, *Methylobacterium mesophilicum* strain was well enough to colonize plant root and shoot. In salt-free environment the bacterial population was observed to be 6.4×10^4 while under saline environment it was found to be 2.6×10^4 CFU/g root. In the study, the *Methylobacterium* strain was found to be antibiotic resistant also and that may be a probable reason for facilitating microbial colonization with plants such as cucumber, tomato and paprika (Egamberdieva et al. 2015).

In a very interesting report, Gourion et al. (2008) demonstrated the necessity of PhyR (for phyllosphere-induced regulator) coding gene expression in *Methylobacterium extorquens* AM1 for the stress tolerance of most of the plants under multiple stress conditions such as oxidative stress, osmotic stress, drought stress water stress and others. They emphasised that during *Methylobacterium*-plant interaction in various stress environment, the protein coding PhyR gene is synthesized more that is facilitating the microbial colonization with the plant. This microbial colonization further induces the tolerance in plant cells by triggering several protecting metabolic machinery (Gourion et al. 2008). During induction of physiological pathways inside the plants, several proteins were expressed and synthesised such as catalase (KatA), lactoylglutathione lyase (GloA), a heat shock protein (Hsp20) and DNA protection protein (Dps).

A tolerance towards acidic environment was observed by Dedysh et al. (2004), which showed the isolation and identification of three different methanotrophic bacterial strains (T4^T, TCh1 and TY1). After molecular characterization these acid tolerant methylophilic strains were identified as *Methylocella* sp., *Methylocella palustris* and *Methylocella silvestris*, respectively. Out of these three, first strain T4^T was reported a novel strain as *Methylocella tundra* isolated from Sphagnum tundra peatlands in acidic environment (Table 4).

One of the earlier investigations reported extremophilic bacteria from sediment samples of soda lake Magadi in Kenya and the chloride–sulfate lakes in Kulunda Steppe (Russia). Study reported the isolation and identification of halophilic and salt tolerant obligate methylophilic strain (Sorokin et al. 2007). This obligate methylophilic strain was declared as a novel strain *Methylohalomonas lacus* gen. nov., sp. nov., HMT 1^T. From the sediment, two other restricted facultative methylophilic strains (AMT 1^T and AMT 3) were obtained that were identified as a member of family Ectothiorhodospiraceae.

For the sustainable agriculture system, various PGP microbes are being utilized since several years back (Kumar et al. 2015a, b, 2016; Madhaiyan et al. 2011; Yadav and Saxena 2018). In the recent investigation, it was found that the PGP methylophilic strain *Methylobacterium oryzae* CBMB20 was able to tolerate salt stress and desiccation, heat, UV irradiation, different temperature regimes, oxidative stress, starvation condition. In exposure to various NaCl concentrations, the ACC deaminase activity was also observed along with gradual and drastic reduction in aggregated and

Table 4 Methylophilic from diverse sources and their application in mitigation of abiotic stresses in plants

Methylophilic	Stress	Sources	Reference
Methanotrophs	Water	Upland soil	Von Fischer et al. (2009)
<i>Methylobacterium extorquens</i>	Multiple	Common Plants	Gourion et al. (2008)
<i>Methylobacterium mesophilicum</i>	Salt	Tomato	Egamberdieva et al. (2015)
<i>Methylobacterium mesophilicum</i>	Drought	Cucumber	Egamberdieva et al. (2015)
<i>Methylobacterium oryzae</i>	Salt	Paddy field	Chanratana et al. (2017)
<i>Methylobacterium</i> sp.	Drought	Coastal sage	Irvine et al. (2012)
<i>Methylocella tundrae</i>	pH	Tundra Peatlands	Dedysh et al. (2004)
<i>Methylomonas lacus</i>	Salt	Hypersaline lake	Sorokin et al. (2007)
<i>Methylohalomonas kenyaensis</i>	Salt	Hypersaline lake	Sorokin et al. (2007)
<i>Methylosinus trichosporium</i>	Water	Forest soil	Schnell and King (1996)
<i>Methylomonas rubra</i>	Water	Forest soil	Schnell and King (1996)
PPFMs	Drought	Tomato plant	Chanratana et al. (2017)
PPFMs	Drought	Tomato plant	Sivakumar et al. (2017)
Type I, II methanotrophs	Drought	Paddy field	Collet et al. (2015)
Type II methanotrophs	Water	Sphagnum mosses	Putkinen et al. (2012)

non-aggregated methylotrophic bacterial cells over increased salt concentrations (Chanratana et al. 2017).

Drought stress tolerance and mitigation

A major abiotic stress i.e. drought is considered as a great challenge for the growth and development of crop plants, inhibiting the proper seed germination and seedling growth under drought condition. Drought is considered as a limiting factor for the growth and development of crop plants in dry ecosystem (Brown et al. 1985; Daneshian and Zare 2005). Several study reported the involvement of bacterial communities (specially plant growth promoting bacteria) in alleviation of drought stress (Saikia et al. 2018; Ngumbi and Kloepper 2016; Yadav and Yadav 2018a, b). Like other bacterial communities, methylotrophs are very important group of microbes alleviating drought stress and facilitating proper plant growth and development.

The genus *Methylobacterium* is represented by a subpopulation of methylotrophs, PPFMs (Pink pigmented facultative methylotrophs) (Green and Bousfield 1983) and this subpopulation is very peculiar group of bacteria mitigating the unfavourable and adverse abiotic stress such as drought stress in agriculture. The application of PPFMs improves the plant growth and development (Hayat et al. 2010). They are very helpful in making agriculture sustainable by protecting plants against abiotic and biotic stresses (Van Loon et al. 1998).

In a recent research outcome, it was emphasized that PPFM (Pink pigmented facultative methylotrophs) along with other PGPR (Plant growth promoting rhizobacteria) helps in alleviating drought stress in tomato plant in early growth stage. Study reveals that, the co-inoculation of PGPR and PPFM improves the seed germination related characters along with stress tolerant index (Sivakumar et al. 2017). The PPFM (2%) in combination with PGPR enhanced the antioxidant activity also under drought stress. The impact of PPFMs and PGPRs in alleviation of drought stress was analysed by conducting a pot culture experiment with tomato plant varieties. The pot experiment was carried out with foliar spray of different plant growth regulators like salicylic acid, gibberellic acid and PPFMs. Data suggested that PPFMs foliar spray was able to mitigate drought stress significantly (Sivakumar et al. 2017).

In another study in California, the abiotic stress tolerance ability of PPFM was elaborated in which PPFM abundance was assessed in the root zone of five different invasive plant species, ranging from 10^2 to 10^5 CFU/g dry soil. In annual and biennial plant species the PPFM abundance was found more as compared to perennial plant species. The abundant root of coastal sage scrub plants colonised with PPFMs was influenced by surrounding and immediate plant communities. In this natural ecosystem PPFMs may be utilized as a good target for the alleviation of abiotic and biotic stress (Irvine et al. 2012). From air dried paddy field soil several methanotrophs

were reported in a recent investigation (Collet et al. 2015). The methanotrophic community and their resistance were examined in a dry paddy field soil stored for 1 to 18 years and their drought tolerance was documented. In this investigation, Type II methanotrophic community was found to be abundant as compared to Type I methanotrophs (Collet et al. 2015).

Water stress tolerance and mitigation

The water stress tolerance was observed well enough by the methanotrophic bacterial communities in several studies. One of the investigations revealed the effect of water stress mitigation by Type II MOB (Methanotrophs oxidizing bacteria) in Sphagnum mosses (Putkinen et al. 2012). It was concluded in a study Van Winden et al. (2010) that peatland water Table (WT) play an important factor influencing activity of methane oxidizing bacterial community in mosses. Due to natural fluctuation in WT level, the Sphagnum associated methanotrophs also get fluctuated i.e. either deactivated or reactivated. In the study it was emphasized that water serve as an important route for the methanotroph abundance in Sphagnum-methanotroph association. Peatland drainage can change the methanotroph community composition (Jaatinen et al. 2005) and Sphagnum coverage is reduced consequently affecting Mosses-Methanotrophs association (Yrjälä et al. 2011). An experiment conducted in upland (well drained, oxic) ecosystem described the decrease in methanotroph activity, suggesting that the diminished activity of methanotroph community resulted from water stress to methanotrophs but presence of some resistance strains also (Von Fischer et al. 2009).

In a chamber based approach soil methanotroph activity was measured on the basis of measures of soil diffusivity. The experiment showed that the rate of methane consumption is proportional to change in methanotroph activity and diffusivity. The field experiment over a seven week period represents soil moisture fell from 38% to 15% water-filled pore spaces, and diffusivity doubled as the larger soil pores drained of water. However, methane consumption was reduced by 40%, following a huge decrease (about 90%) in methanotroph activity, suggesting that the decline in methanotroph activity resulted from water stress to methanotrophs (Von Fischer et al. 2009). The fluctuations in the atmospheric methane utilization rate were documented under high water contents and low water contents situations. At a 25% soil water content and with 20.2 MPa water potential the maximum atmospheric methane consumption was reported. The uptake rates were highest at soil water content 38% with 20.03 water potential in the presence of 200 ppm initial methane. The experiment results showed that atmospheric and elevated methane consumption was decreased with decrease in water potential on addition of ionic solutes to soil. In soil samples, the methane consumption was not seen effective but

the methanotrophic isolates (*Methylosinus trichosporium* from a freshwater peat and *Methylomonas rubra* from an intertidal marine mudflat) have shown a great potential to survive and to consume methane in adverse water stress condition (Schnell and King 1996).

Conclusion and future scope

Generally, abiotic stresses have shown a reciprocal relationship with bacterial survival but a number of bacterial entities are reported to tolerate stresses by manipulating its physiology to accommodate. Here, in the current review it was emphasised to show the ability of a particular group of bacteria i.e. methylotrophs that how they cope with the stresses in the environment and how they can be utilised further as bioinoculants. Under abiotic stress condition such as salt stress, physiological changes occur inside the methylotrophic cells such as increased extracellular polysaccharides production, increased cell hydrophobicity, formation of biofilm and accumulation of osmolytes like proline. The changes facilitate the growth of methylotrophs in several harsh environments. The methanotrophic community comprises methanotrophs Type I and methanotrophs Type II methylotrophs, actively reported to tolerate stresses like drought and water. Interestingly, different methanotrophs were reported from the soil samples of a barren paddy field. This review is emphasizing not only the diversity of abiotic stress tolerant methylotrophic community but also their exploitation and application in future for the sustainability.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflicts of interest to this work.

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