Chapter 8
Phylogenetic Diversity of Epiphytic Pink-Pigmented Methylotrophic Bacteria and Role in Alleviation of Abiotic Stress in Plants

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Abstract Plant and methylotrophic bacterial interactions that improve plant growth and plant fitness are becoming a topic of very important considerable interest. Methylotropic bacteria are distributed in various diverse environments/colonize different habitats and utilize reduced one-carbon compounds as source of energy and play an important role in the biogeochemical cycle. Methylotrophic bacteria colonize in different parts of the plants like endophytes, epiphytes and in roots of plant rhizosphere. Pink-pigmented facultative methylotrophic (PPFM) bacteria present in the phyllosphere enhance plant growth by producing phytohormones such as IAA, Zeatin, Cytokinins, ACC deaminase and diverse secondary metabolites to overcome abiotic stress. Biological interactions of Methylotrophic bacteria enhance plant growth indirectly by increasing the nutrients uptake and beneficial in reduction of greenhouse effects to the environments. Pink-pigmented facultative methylotrophic bacteria colonize in phyllosphere of plants as epiphytes and utilize methanol as a sole carbon source of energy. In plant colonization, the occurrence and distribution of Methylotrophic bacteria may be influenced by various factors like plant genotype, geographical conditions or by interactions with associated microorganisms and phytohormones production which may result and lead to increased plant fitness.

Keywords Methylotrophic bacteria · PPFM · Plant growth promotion · Phyllosphere · Sustainable agriculture

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8.1 Introduction

Prolonged biological and chemical research have expanded our agricultural knowledge. Chemical fertilizer contains the most important elements of modern agriculture that provide the required nutrients, which are not present in the soil or other organic sources for crop improvement. The utilization and overexploitation of chemical fertilizers have an 'ecological footprint'. It reduces productivity and disturbs nutrients level in the soil, which further leads to a deterioration in quality of the soil and causes various plant diseases. The excessive use of chemical fertilizers in the field depletes non-renewable resources and dangerous to soil fertility and environments (Dubey et al. 2012). In general, the association of *Methylobacterium* spp. and host plants may be or epiphytic or endophytic in nature (Kumar et al. 2019b; Jourand et al. 2004; Omer et al. 2004b; Lacava et al. 2004). *M. nodulans* and *M. radiotolerans* interact with host plants and fix nitrogen fixation and nodule formation (Sy et al. 2001; Menna et al. 2006), whereas some *Methylobacterium* species are involved in the production of phytohormones (Meena et al. 2006) or interact with plant pathogens (Lacava et al. 2004), promoting plant growth (Madhaiyan et al. 2006b; Tani et al. 2012) and higher rate of photosynthetic activity (Cervantes et al. 2004).

Methylobacterium spp. are in connection with more than 70 plant species that actively colonize in different parts of the plants like branches, roots and leaves. Several studies have reported earlier that *Methylobacterium* spp. are identified as endophytes of various plants, such as citrus fruits, pine, cotton, eucalyptus, strawberries, peanuts, hemp, Catharanthus roseus, mangroves and tobacco.

Methylobacterium spp. are well known to be not phytopathogenic bacteria and reported that few *Methylobacterium* spp. produce enzyme pectinase and cellulose, which may cause systemic resistance during plant colonization of methylotrophs strains. In addition to phytohormone production, *Methylobacterium* spp. are capable of producing valuable biotechnological potential product like bioplastic, which are biodegradable and ecofriendly in nature. Polyhydroxyalkanoate (PHA) and polyhydroxybutyric acid (PHB) are biopolymers that are genetically modified strains like *M. extorquens* to increase higher amount of PHB and PHA production by utilizing methanol as substrate (Hofer et al. 2011).

Methylotropic bacteria colonize in different parts of the host plant as endophytes, epiphytes in the phyllosphere and produce diverse secondary metabolites as biocontrol agents to defense against phytopathogens. This chapter mainly deals with *Methylobacterium* spp. diversity, biotechnological importance of pink-pigmented facultative methylotrophic (PPFM) bacteria and various potential applications in agriculture as biofertilizers, co-inoculants and its role in biogeochemical cycle. This chapter also covers diversity of methylotrophs, genomics, metabolic potential of pink-pigmented facultative methylotrophic bacteria in the plant phyllosphere and role in alleviation of abiotic stress to the host plants.

8.2 Diversity and Metabolism of Methyotrophs

Methylotrophs are classified and subdivided into three subgroups on the basis of their metabolic activity like carbon-substrate utilization: (1) Obligate methylotrophs utilize single carbon compounds as sole source of energy (2) Restricted facultative methylotrophs utilize a limited range of complex carbon compounds apart from C1 compounds and (3) methylotrophs utilize and grow in medium with complex carbon compounds are called less-restricted facultative (Jenkins et al. 1987). Three distinct genera such as *Methylophilus* (Jenkins et al. 1987), *Methylobacillus* (Urakami and Komagata 1986; Yordy and Weaver 1977), and *Methylovorus* (Govorukhina and Trotsenko 1991) of betaproteobacteria are classified and considered as restricted facultative methylotrophs, whereas genus *Methylobacterium* is considered and well known as less-restricted facultative methylotrophs in the Alphaproteobacteria. Recently, Taubert et al. (2016) identified and reported an additional active group of the methylotrophic community. A common one-carbon (C1) substrate for many methylotrophic bacteria is methanol, whereas subgroups of these bacteria have the ability to use methane, methanesulfonate, other methylated sulphur species, methylated amines and the halogenated hydrocarbons chloromethane, bromomethane and dichloromethane, either in addition to methanol or exclusively methane, methanesulfonate, other methylated sulphur species, methylated amines and the halogenated hydrocarbons chloromethane, bromomethane, and dichloromethane as sole source or in addition with methanol as source of energy. The association of Methylobacterium spp. and host plants may be or epiphytic, phlylosphere, rhizosphere or endophytic in nature and produce phtohormones, nitrogen fixation, abiotic stress tolerance and maintain biogeochemical cycles (Kumar et al. 2019b) (Figs. 8.1 and 8.2).

8.3 Methylotrophic Community in the Phyllosphere

The distribution and diversity of phyllosphere microorganisms are influenced by various factors like nutrient availability, stress resistance, motility, growth, bacterial traits and metabolic activity (Bulgarelli et al. 2013; Yadav 2018; Yadav et al. 2017c, 2019). In addition, climate, plant genotype and geography are the major driving forces for methylotrophic bacterial population in the phyllosphere region of plants (Redford et al. 2010; Siefert et al. 2014 and Knief et al. 2010). Knief et al. (2010) reported efficient methylotrophic bacterial colonization, competitiveness and survival are closely linked to bacterial phylogeny and metabolic diversity of microorganisms of *Arabidopsis thaliana* in the phyllosphere. Knief et al. (2010) studied and reported that *Methylobacterium* community composition had strong effects and it varies based on culture-independent metagenome sequencing

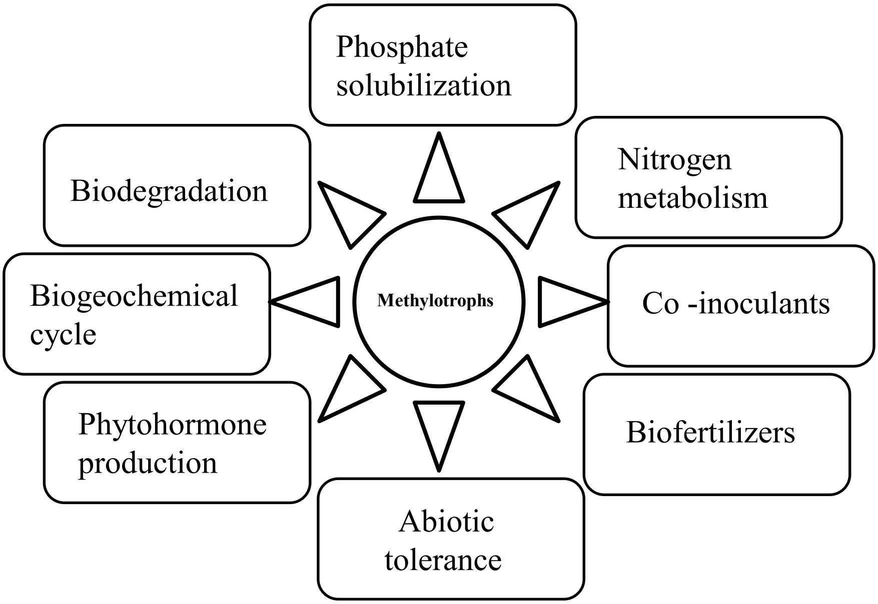

Fig. 8.1 Diverse role of methylotrophic bacteria application

analysis of leaves from *Medicago truncatula, Arabidopsis thaliana* and surrounding plant species at different locations. In *Medicago truncatula*, efficient colonization of phyllosphere Methylotrophs was observed due to the advantage of utilizing methanol as a source of energy and as a solitary carbon substrate (Sy et al. 2005). The association and interactions of different methylotrophic species like *M. mesophilicum, M. radiotolerans* and *M. fujisawaense* reported as strong colonizers with plant species were observed (Mizuno et al. 2013). In phyllosphere, methylotrophic microbes are present in huge numbers and under competitive conditions or during plant colonization, methylotrophic bacteria use plant-derived methanol as a substrate for energy and used for efficient colonization in the phyllosphere region (Abanda-Nkpwatt et al. 2006; Fall and Benson 1996; Sy et al. 2005). Colonization pattern of plant root and leaf surfaces was observed by using of green-fluorescent-marked strain of *Methylobacterium suomiense* (Poonguzhali et al. 2008) (Fig. 8.3).

8.4 Epiphytic PPFM Methylotrophs in the Phyllosphere

Epiphytic Pink-Pigmented Facultative Methylotrophs (PPFMs) are phylogenetically diverse and belong to the genus *Methylobacterium.* PPFMs utilize one-carbon compounds such as methanol, formate, formaldehyde and other multicarbon substrates as a sole source of energy. Pink-Pigmented Facultative Methylotrophs (PPFMs) belong

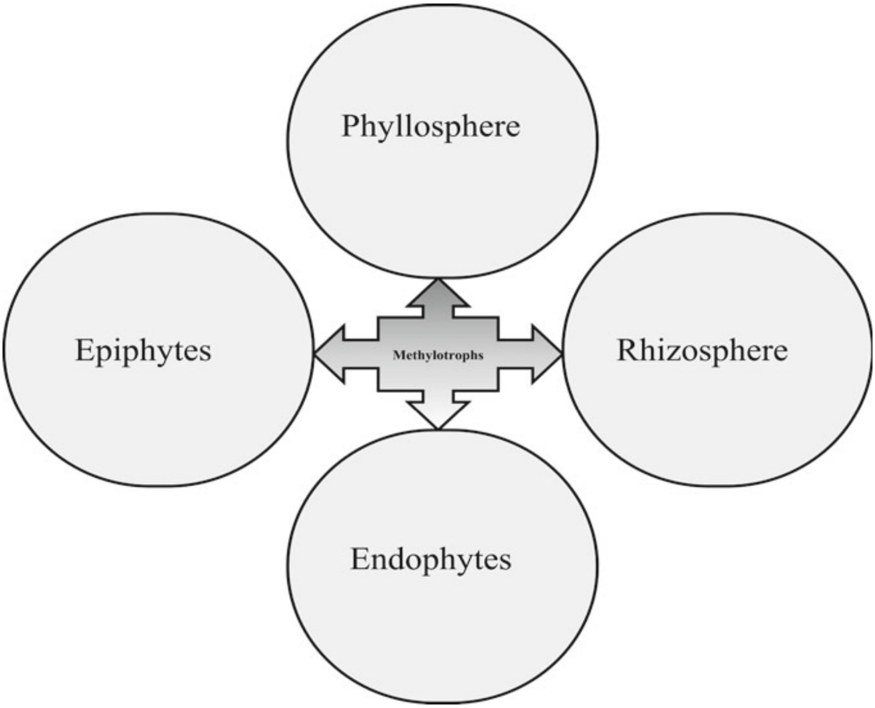

Fig. 8.2 Distribution role of methylotrops associated with different parts of the plants

to *Proteobacteria*, order Rhizobiales and Methylobacteriaceae family (Green and Bousifield 1982). PPFM is found in diverse habitats ubiquitous in nature including phyllosphere, rhizosphere, dust, freshwater, sediments and Lakes (Corpe and Rheem 1989; Green and Bousifield 1982). *Methylobacterium* spp. are generally distributed as epiphytes representing a significant bacterial population on plant leaves and in phyllosphere region of numerous plants (Hirano and Upper 1991; Holland and Polacco 1994). The colonization of *Methylobacterium* in a mucilaginous layer of plant tissues is the first step in colonization of microbes in the plant phyllosphere region (Andreote et al. 2006; Rossetto et al. 2011; Verma et al. 2017; Yadav et al. 2018c). The presence of methanol dehydrogenase (*mxaF*) gene in the genome of Pink-Pigmented Facultative Methylotrophic bacteria oxidizes methanol as an energy source (Anthony et al. 1994). In phyllosphere region of some plants, methane and methanol are emitted in the aerial part and serve as a habitat for distribution of methylotrophic bacterial population were reported earlier (Corpe and Basile 1982). Pink-Pigmented Facultative Methylotrophs were isolated using methanol-based mineral medium using methanol as an exclusive carbon and energy source (Corpe 1985).

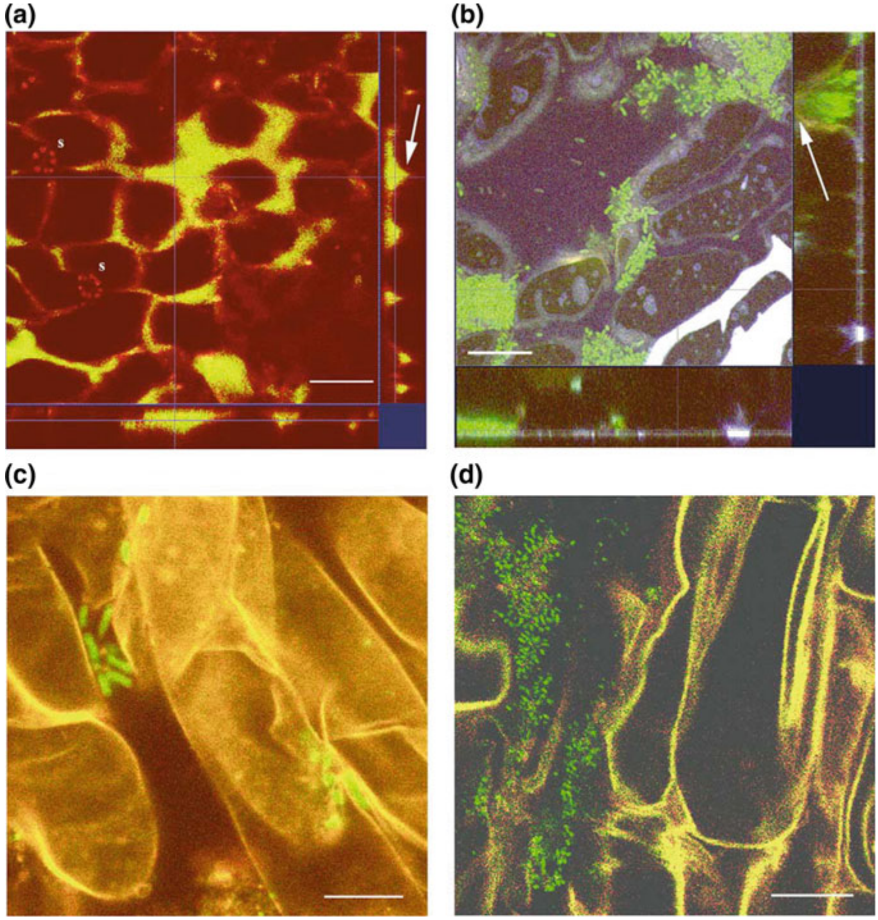

Fig. 8.3 Colonization of methylotrophic bacteria using green-fluorescent-marked strain of *Methylobacterium suomiense*

8.5 Genomics of PPFM Bacteria

The genotype of PPFM bacteria or interactions of associated microorganisms influence bacterial colonization and distribution in the host plant either directly or indirectly (Dourado et al. 2012).

8.6 Genetic Diversity of Methylotrophs

In general, Methylotrophic bacteria appears pink-pigmented in colours due to biosynthetic potential of carotenoids in the bacterium (VanDien et al. 2003). Methylotrophs are rod shaped aerobic in nature and able to grow in medium containing methanol and methylamine as carbon(C1) source for its metabolic activity (Toyama et al. 1998). The most significant characteristic feature of this group is the ability to oxidize and utilize methanol as a substrate by using the enzyme methanol dehydrogenase enzyme (MDH). PPFMs strains were isolated through leaf impression technique from phyllosphere of three different crops, which were further confirmed based on genomic DNA isolation of the isolates and PCR amplification of partial *mxaF* gene (550 bp sized partial *mxaF* gene). In metabolism of methylotrophic bacteria, the enzyme methanol dehydrogenase (MDH), the *mxa*F gene encode for encodes the large subunit, which helps to understand *Methylobacterium* niche-specific plant association (Dourado et al. 2012).

The enzyme methanol dehydrogenase (MDH) oxidizes methanol into formaldehyde metabolism, which starts in the periplasm of methylotrophic bacterium (Zang et a 2003). *The mxa*F and *mxa*I genes encodes for large, small subunits and cytochrome C primary electron acceptor for methanol dehydrogenase are encoded by *mxa*G gene (Mcdonald and Murrell 1997). Methanol dehydrogenase enzyme is mainly composed of two small (8.5 kDa) and two large (66 kDa) subunits. The large subunit (MxaF) is important for the functional activity of methanol dehydrogenase (Skovran et al. 2011). Random amplified polymorphic DNA (RAPD) is a unique molecular fingerprinting technique which was commonly used to distinguish between closely related bacterial strains at species level (Mazurier et al. 1992; Williams et al. 1990).

Van Aken et al. (2004) investigated and reported metabolic and genetic diversity of PPFM bacteria in the phyllosphere region of maize, cotton and sunflower to understand the PPFMs diversity within a particular plant species and different plant species using RAPD molecular fingerprinting and profiling carbon-substrate utilization pattern. Vuilleumier et al. (2009) reported variations in the numbers of insertion elements (IS) and in the organization of the genes have been identified in two different *Methylobacterium* (AM1 and DM4) strains associated with methanol metabolism. *Methylobacterium* bacterial strains have been sequenced and reported *M. extorquens PA1 as an* as a competitive colonizer of the phyllosphere region of *Arabidopsis thaliana* plants (Knief et al. 2010).

8.7 Methylotrophic as Plant Growth Promoters

Methylotrophs promote plant growth through beneficial interactions with plants by producing phytohormones and indirectly by increasing the availability of nutrients (Lidstram and chistordava 2002; Koenig et al. 2002). Methylotrophs colonize in various parts of the plant and produce phytohormones like auxins, cytokinin and zeatin. Plant growth substance promotes growth of both shoot and root system (Verma et al. 2013, 2014, 2015, 2016; Yadav et al. 2016). Doronina et al. (2001) reported aerobic methylotrophic bacteria produce auxins range from 20 mg/ml in the culture medium. In methylotrophic bacteria, biosynthesis of IAA was initiated from tryptophan as precursor and addition of tryphtophan enhances the synthesis of IAA (Schneider and

Wightman 1974). The biosynthesis of IAA through IPA pathway, which involves the transfer of amino group from tryphtophan to IPS, which is catalyzed by aromatic aminotransferases and then to IAA in methylotrophic bacteria. The enzyme aminotransferase activity was observed and identified in several methylotrophic bacteria (Ivanova et al. 2001).

The genes responsible for enzymes such as amine oxidase, aldehyde dehydrogense, N-acyl transferase and amidase were related to auxins biosynthesis and identified in methylotrophic bacteria (Kwak 2014; Madhaiyan et al. 2006c; Tani et al. 2012). Schauer and Kutschera (2011) reported a novel *Methylobacterium funariae* produced phytohormone like auxin and cytokinin were isolated from phyllosphere region of common mosses. In phyllosphere region, inoculation with *Methylobacteriu*m produced phytohormone IAA, which indirectly alter IAA concentrations in the plant and stimulate the plant growth (Lee et al. 2006). Pink-pigmented facultative bacteria were widely distributed and colonize in the phyllosphere of medicinal, agricultural crops and wild plants in Ukraine region (Romanovskaya et al. 1998). Lee et al. (2004) reported phytohormone IAA from methylotrophic isolates such as *Methylotrophic extorquens* and *Methylotrophic fujisawaense* isolated from the phyllosphere region of rice.

8.7.1 Production of Phytohormones by PPFM

Anitha (2010) reported Pink Pigmented Facultative Methylotrophic bacteria (PPFMs) was isolated from phyllosphere of soybean and groundnut producing phytohormone IAA and enhance plant growth. Keerthi et al. (2015) reported PPFM were used as biofertilizers in green grams isolated from phyllosphere environment. Tani et al. (2015) reported methylotrophic sp. producing both IAA and cytokinin associated with red pepper. Cytokinins are plant growth hormones, which regulate many physiological processes in plants such as to stimulate plant cell division, activate dormant buds, remove apical domination and induce seed germination. Ivanova et al. (2000) reported *M. mosophilicum* isolated from phyllosphere of rye grass lium perenne were able to synthesize cytokinins using biotest with the *Amaranthus candatus* L. seedlings. Holland (1997) reported application of exogenous methanol to the host plant, which stimulates the growth of PPFM bacteria by producing phytohormone cytokinins. In addition to the cytokinin PPFM bacteria isolated from different crops like soybean, barley, maize and Arabidopsis plant contain phytohormone zeatin and zeatin rhiboside (Long et al. 1996). The presence of phytohormone cytokinins and zeatin in the culture liquids of methylotropic bacteria is confirmed through chromotagraphic and enzyme immuno assay analysis (Ivanova et al. 2000). Epiphytic pink-pigmented methylotrophic bacteria produce cytokinin, stimulate germination and growth of wheat (*Triticum aestivum*) seedling was reported Meena et al. (2012). Phytohormone production by methylotrophic bacteria associated with different crops (Table 8.1).

Table 8.1 Phytohormone production by methylotrophic bacteria associated with different crops

Crop plants	Crop associated Methylotrophs	Biofertilizer/Phytohormones production	References
Groundnut	Pink-pigmented facultative methylotroph	IAA production	Anitha (2010)
Green Gram	Pink-pigmented facultative methylotroph	Biofertilizer	Keerthi et al. (2015)
Soybean	Pink-pigmented facultative methylotroph	IAA production	Anitha 2010)
Red Pepper	*Methylobacterium* sp.	IAA and cytokinin production	Tani et al. (2015)
Rice	*Methylobacterium extorquens, Methylobacterium fujisawaense*	IAA production	Lee et al. (2004)
Wheat	*Methylobacterium* sp.	Cytokinin production	Meena et al. (2012)

8.8 PPFM as Biofertilizers

The spraying of PPFM on plants with 20% methanol leads to twofold increase in the PPFM population and increase in soybean plants, when compared to control plants (Nishio et al. 1977; Kumar et al. 2019a; Yadav et al. 2018a, b). Jayajyothi et al. (2014) reported foliar spray of pink-pigmented methylotrophic bacteria and Pseudomonas strains, in addition with biofertilizer enhance the microbial population and increase the nutrient uptake to the plants. Abd El Gawad et al. (2015) studied and reported enhanced growth, antioxidant activities and increased yield in snap bean crops based in field experiments in different seasons using PPFM bacterial isolates. Foliar spray or irrigation of PPFM bacteria along with methanol, ethanol or even both showed improvement in plant growth of cotton, sugarcane and strawberry plants (Madhaiyan et al. 2005; Yavarpanah et al. 2015). Ivanova et al. (2001) reported application of methanol spray on leaf surfaces to promote the growth of plants by producing phytohormones like cytokinin and auxin by PPFM bacteria. Madhaiyan et al. (2006a, b) investigated and reported higher yields of sugarcane (Saccharum officinarum L.), cotton (Gossypium hirsutum L.) were observed through foliar spray of PPFM along with methanol, which increases phytohormone production. Chauhan et al. (2010) also reported that the application of fertilizers with PPFM as foliar spray leads to higher crop yields. ICAR (2013) advocated application of PPFMs as biofertilizers can protect crops from drought stress conditions.

8.9 PPFM in the Nitrogen Metabolism

Nitrogen is considered as one of the essential nutrients required for plant growth, but the availability of nitrogen from the atmosphere was limited for the metabolism of plants (Kour et al. 2019a, b). In nitrogen fixation, the conversion of atmospheric nitrogen into ammonia takes place for the nutrient availability to the plants. The nitrogenase enzyme was involved in the biological reduction of nitrogen to ammonia which was carried out by a few prokaryotic organisms (Menna et al. 2006). PPFM are involved in the nitrogen metabolism of colonized plants indirectly. Soybean plants have several urease isoenzymes: the Eu1 urease located in beans, the Eu4 urease located in all plant tissues and the Eu2 and Eu3 ureases, which are necessary for the normal urease activity of soybean plants. In the soybean plants with the mutant *eu3-e1/eu3-e1* gene, urea was accumulated in the plant tissues because of impaired urease activity. The colonization of such plants by PPFM did not restore their urease activity. At the same time, the colonization of the double *eu1-sun/eu1-sun, eu4/eu4* soybean mutants by PPFM led to the restoration of their urease activity to a level of 20–40% of that of the wildtype plants, due to the PPFM urease (Holland and Polacco 1992).

8.10 PPFM as Bio-inoculants and Co-inoculants

Meena et al. (2012) reported application of methylotrophs as bio-inoculants for seed coating or as seed inoculation enhances seed germination. Methylotrophs are capable of promoting plant growth with different groups of bacteria as co-inoculants, which results in higher yield in pot and crop field conditions Poonguzhali et al. (2008). Meena et al. (2012) suggested development of bio-inoculants and co-inoculation of methylotrophic bacteria results in increased production of cytokinins and higher crop yield. Meenakshi and Savalgi (2009) reported co-inoculation of methylotrophs with *B. japonicum* as foliar spray consequences raise in number of nodules, when compared to seeds with single *B. japonicum* as control. In addition, foliar spray of bio-inoculants with methylotrophs leads to increase in chlorophyll content to the host plants. Nalayani et al. 2014 reported foliar application of different types of microbial consortia strains Pseudomonas, Bacillus and Azospirillum with PPFM results in higher yield of cotton plants.

8.11 PPFM in Abiotic Stress Tolerance

The phyllosphere methylobacteria are highly resistant to UV dehydration, freezing on hygroscopic carriers and ionizing radiation and elevated temperatures. The phyllosphere epiphytic methylotrophic PPFM may remain viable after UV irradiation with higher doses that are lethal to bacterial strains like *Pseudomonas, Enterococci* and *Methanotrophs* (Romanovskaya et al. 1998; Yadav et al. 2017a, b, d; Yadav and Saxena 2018). Plants can regulate phytohormones production during unfavourable conditions and in stressed environments to overcome from biotic or abiotic stresses (Salamone et al. 2005). Ethylene is a plant growth hormone essential for plants, which is produced during various physiological changes in plants and endogenously by plants (Khalid et al. 2006). Saleem et al. (2007) reported earlier ethylene as a plant growth regulator and identified as a stress-related hormone. Saleem et al. (2007) also reported the production of ethylene during unfavourable conditions or stress conditions, the invivo accumulation of ethylene is drastically increased, which negatively alters the overall growth of plant. The overall increased concentration of ethylene may lead to reduced performance of the crop.

Ethylene is a stress associated hormone related to auxin biosynthetic pathway and an increased level of ethylene in plants leads to deleterious effects like plant growth, accelerating abscission, ageing, inhibiting root elongation and senescence. In ethylene biosynthetic pathway, aminocyclopropane-1-carboxylic acid (ACC) is the precursor of the ethylene hormone converted from S-adenosylmethionine (SAM) and to ethylene by ACC synthase (ACS) and ACC oxidase (ACO), enzymes that are transcriptionally regulated separately by both biotic and abiotic factors. ICAR et al. (2013) reported the beneficial application of *Methylobacterium* (PPFMs) as biofertilizer helps the crops to protect and overcome crops drought stress and during high-temperature conditions. PPFMs synthesize phytohormones, 1-aminocyclopropane-1-carboxylate (ACC) to overcome abiotic stress conditions by utilizing methanol produced from plant leaves as a source of carbon and energy (ICAR 2013).

Plant growth-promoting methylotrophic bacteria produce the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which indirectly stimulate growth by decreasing ethylene concentrations in plants (Glick 1995). Chinnadurai et al. (2009) revealed that phyllosphere methylobacteria distributed in the rice leaves produce the enzyme ACC deaminase, which control the ethylene concentrations level in the rice plant. In earlier investigations, *Methylobacterium* strains were identified and reported to have ACC deaminase activity and tested for their potential in plant growth-promoting traits in various crops. *Methylobacterium* spp. are not phytopathogenic in nature which help in plant growth promotion by decreasing environmental stress, immobilizing heavy metals, degrading toxic organic compounds and even inhibiting plant pathogens. *Methylobacterium* spp able to synthesize polymer degrading pectinase and cellulase, suggesting that they can indirectly induce systemic resistance during plant colonization.

8.12 Conclusion and Future Prospects

PPFMs isolates and other methylotrophs improve plant growth by controlling or by inhibiting phytopathogens. PPFMs inhibit several phytopathogens including *Fusarium oxysporum, Sclerotium rolfsii, Colletotrichum capsici, Xanthomonas campestris and Cercospora capsici* and serve as biocontrol agents. Methylotrophs are widely used as bio-inoculants as a foliar spray on plants and serve as an alternative to chemical fertilizers to enhance crop yield. The application of methylotrophs as foliar spray regulates plant growth directly or indirectly. Methylotrophs regulate and play a key role in biogeochemical cycle of soil ecosystem, making the soil more suitable for higher crop yield. In addition, several characteristic features of methylotrophs like nitrogen fixation, phytohormone production, nodulation and nutrient acquisition as a promising substitute for synthetic or chemical fertilizers. In conclusion, methylotrophic bacteria serve as an alternative of biological control, plant growth promotion by nitrogen fixation, phosphate solubilization, phytohormone production and ACC deaminase production, along with balanced carbon cycling. Beneficial methylotrophic can be used for effective organic farming in sustainable agriculture in the future.

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