**The Multifaceted Role of *Methylorubrum* in Plant Growth Promotion and Abiotic Stress**

**Abstract**

A myriad of microorganisms inhabit and interact with plants and play a significant role in improving overall productivity and sustainability. Among the microorganisms, bacteria contribute more in fostering plant growth and development. They are collectively known as Plant Growth Promoting bacteria (PGPRs). *Methylorubrum* is onesuch group of bacterial genera that has both plant growth promoting ability and abiotic stress mitigation. *Methylorubrum,* a member of alpha-proteobacteria, ubiquitous in nature,can able to colonize the entire plant system, gained significant importance in crop production due to their multifaceted abilities. Due to their pink pigmentation, members of *Methylorubrum* genusare collectively known as Pink Pigmented Facultative Methylotrophs (PPFM). They improve plant growth through mineral solubilisation, phytohormone production, ACC deaminase and siderophore production. *Methylorubrum* with potential applications in agriculture can be used as a biostimulant, biofertilizer and biocontrol agent. This review provides thoughtful insights into the multidimensional role of *Methylorubrum* in sustainable agriculture.

**Keywords:** *Abiotic Stress Mitigation; Methylorubrum; Plant Growth Promotion.*

**1. Introduction**

Crops face a myriad of environmental challenges, both biotic and abiotic stress, including extreme temperatures, salinity, drought, pest and disease incidence and nutrient deficiencies that significantly impede the growth and development of crops. Global warming along with an increase in population poses a global threat for food security. Due to climate variability, global food production has already decreased (Tito *et al.* 2018). As a result of global warming, irregular rainfall pattern, high and low temperature stress, drought stress, UV stress and elevated CO2 levels significantly reduces the crop growth and alters their physiology (Madhaiyan *et al.* 2007a; Jinal *et al.* 2019; Gopi *et al.* 2020). Due to intricate nature of stress tolerance, employing conventional breeding techniques to develop crops with strong stress resistance is impossible. To adapt the unfavourable stress conditions, plants developed sophisticated mechanisms to reduce the impacts. The mechanisms include physiological, biochemical, molecular changes that help plants to maintain cellular homeostasis and ensure their survival. In the recent years, the usage of plant growth-promoting microorganisms emerged as a sustainable approach to improve plant productivity and resilience under both normal and stress conditions (Vandenkoornhuyse *et al.* 2015).

Plants are not a single entity, a host of diverse group of microorganisms that provide both beneficial and detrimental effects through a diverse relationship, including commensal, symbiotic, parasitic, and mutualistic that shapes the productivity of crops (Krishnamoorthy *et al.* 2021, Rani *et al.* 2021). The group of microorganisms that can promote the plant growth are known as Plant Growth Promoting bacteria (PGPBs). Among these PGPBs, *Methylorubrum,* a genus of pink-pigmented, facultative methylotrophic, able to colonise phyllosphere are commonly known as pink pigmented facultative methylotrophs (PPFMs) (Fig.1). *Methylorubrum* has gained major attention due to their significant potential in mitigating abiotic stress and improving plant growth. These plant-associated microbes helps plants to withstand abiotic stress through several mechanisms, including ACC-Deaminase production, phytohormones (auxin, cytokinin) synthesis, and by producing free radical scavenging enzymes (Prittesh *et al.* 2020). In the face of climate change and increasing abiotic stress, role of *Methylorubrum* is crucial in improving plant growth and stress mitigation for sustainable agriculture practices. Due to their versatile capabilities, inoculating *Methylorubrum*, either alone or in combination is a useful tool to improve plant growth and yield. Maintenance of proper plant – microbiome interactions, minimizes the use of hazardous agrochemicals and fosters sustainable agriculture practices (Delmotte *et al.* 2009).

**Figure 1. Phyllospheric Colonisation by *Methylorubrum***



**2. Taxonomy**

In 2018, Green and Ardley divided *Methylobacterium* into two genus *Methylobacterium, Methylorubrum.* Based on phenotyoic traits, 16s rRNA, multilocus sequence analysis (MLSA), he included 11 species in the genus *Methylorubrum,* including *Methylorubrum extorquens, M. aminovorans , M. podarium, M. populi, M. pseudosasae, M. rhodesianum, M. rhodinum, M. salsuginis, M. suomiense, M. thiocyanatum* and *M. zatmanii*. (Green and Ardley, 2018).

**3. Ecology**

*Methylorubrum* is a genus of facultative methylotrophs with diverse ecological adaptability. They are ubiquitous in nature, able to thrive in diverse niches, including water, soil, plants, animals and contaminated environments (Madhaiyan *et al.* 2007b). Their ability to utilize one carbon compounds as carbon source helps them to survive in unfavourable conditions. The ability of *Methylorubrum,* to utilize single-carbon compounds like methanol, methylamine, their ecological adaptability and metabolic versatility make it as valuable component in sustainable agriculture, bioprocessing and pollution abatement (Schauer *et al.* 2011, Green *et al.* 1988). It plays a crucial role in global carbon cycle by recycling this single carbon compounds. Table. 1 list the diversity of *Methylorubrum* in various environments (Danko *et al.* 2021).

**Table. 1 Diversity of *Methylorubrum* in diverse environments**

|  |  |  |
| --- | --- | --- |
| Environment | Species | References |
| **Air** | *Methylobacterium extorquens* | (Green and Ardley 2018) |
| **Soil** | *Methylobacterium populi* | (Van Aken *et al.* 2004) |
|  | *Methylobacterium suomiense* f20 | (Doronina *et al.* 2002),  |
|  | *Methylobacterium pseudosasae* | (Madhaiyan and Poonguzhali 2014) |
| **Plants** | *Methylobacterium rhodinum* | (Green and Bousfield, 1983) |
| **Animals** | *Methylobacterium zatmanii* | (Green *et al.* 1988) (Carvajal *et al.* 2011) |
| **Contaminated soils** | *Methylobacterium suomiense* | (Doronina *et al.* 2002) |
|  | *Methylobacterium thiocyanatum* |  (Wood *et al.* 1998) |
| **Man-made structures (Buildings, tap water showers)** | *Methylobacterium zatmanii* | (Kelley *et al.* 2004) |
|  | *Methylobacterium extorquens* | (Szwetkowski and Falkinham Iii, 2020) |
| **Hydrocarbon contaminated sites** | *Methylobacterium populi* | (Ventorino *et al.* 2014) |
|  | *Methylobacterium thiocyanatum* | (Ventorino *et al.* 2014) |
| **Outer space** | *Methylobacterium extorquens* | (Novikova *et al.* 2006) |

**4. Metabolism of single-carbon compounds**

Methylotrophs are a group microorganisms have the ability to utilize single – carbon compound methanol, methylamine or formate as a primary carbon source (Anthony 1982). Methanol dehydrogenase (MDHs) is the key enzyme that catalyses the oxidation of methanol to generate formaldehyde with hydrogen ion and electron production (Zhang *et al.* 2017). This produced formaldehyde enters into the cell and assimilated through any one of the following pathways – (i) Serine Cycle, (ii) Ribulose monophosphate cycle, (iii) Xylulose monophosphate cycle (Zhang *et al.* 2017). In most of the cases, *Methylorubrum* employs serine cycle for the assimilation of formaldehyde through a series of complex biochemical reactions that converts formaldehyde into building blocks of cell and energy production. This pathway also helps *Methylorubrum* to produce vital nucleic acids, lipids, amino acids from single – carbon compound methanol. Through these metabolic capabilities, *Methylorubrum* thrives in diverse environments and establish beneficial interaction with plants fosters plant growth and enhance stress tolerance. This capability helps *Methylorubrum* to stand out among the other microorganisms. In addition to single carbon assimilation, they play a crucial role in mineral solubilisation and nutrient uptake of plants. Another important essential micronutrient of plants that plays a crucial role in physiological processes of plants is iron. Plant Growth Promoting microorganisms produce siderophores, a specific type of molecules that enhance the bioavailability of iron for uptake (Verma *et al.* 2017).

**5. Plant Growth-Promoting Mechanisms**

*Methylorubrum* employ diverse mechanisms both directly and indirectly, to promote plant growth and improve crop productivity (Madhaiyan *et al.* 2006). Some of the direct mechanisms includes auxin and cytokine production and mineral solubilisation. Phytohormones regulate the plant growth and development. By producing indole acetic acid (IAA), a type of auxin essential for cell elongation and root development it promotes plant growth. On the other hand, cytokinins promote cell division, rejuvenates cells and increase shoot proliferation and biomass (Verma *et al.* 2017).

The production of organic acids, such as gluconic acid and organic acids, through metabolism, helps the bacteria to solubilize the insoluble phosphorous from unavailable form to available form (Kwak *et al.* 2014). Iron is an important micronutrient for plant, which promotes plant photosynthesis and chlorophyll synthesis. *Methylorubrum* enhance iron absorption through the production of siderophores (Shi *et al.* 2012). Siderophores are iron-chelating organic compounds that binds with the unavailable form of iron and convert it into available form (Ahmed and Holmström 2014).

 *Methylorubrum* also suppress the phytopathogens, by producing antimicrobial compounds and volatile compounds that inhibits the multiplication and activity of various bacterial and fungal pathogens. They also induce systemic resistance in plants, by activating plant defence genes and the production of defence-related enzymes, such as peroxidase, chitinase, that helps plants to respond more effectively in the event of pathogen attacks. *Methylorubrum* species promote plant growth through both direct and indirect pathways (Kazan 2015).

5.1. Phytohormone Production and Regulation

* **Auxins:** *Methylorubrum* can synthesize auxins, such as indole-3-acetic acid, which plays an important role in cell elongation, root development, and apical dominance (Mano and Nemoto, 2012). Increased auxin levels stimulate cell division and differentiation, leading to enhanced root and shoot growth (Ivanova *et al.* 2001).
* **Cytokinins:** Some *Methylorubrum* strains produce cytokinins, which promote cell division, rejuvenate cells, and enhance nutrient mobilization in plants (Holland and Polacco 1992). Cytokinins interact with auxins to regulate various developmental processes.
* **Ethylene Regulation:** *Methylorubrum* can modulate ethylene levels in plants through the production of ACC deaminase (42, 139, 209). ACC deaminase breaks the 1-Aminocyclopropane-1-carboxylic acid (ACC), the precursor to ethylene into ammonia and alpha-ketoglutaric acid, thereby reduces ethylene levels and mitigates its inhibitory effects under stress conditions (Madhaiyan *et al.* 2006).

5.2. Nutrient Acquisition

* **Nitrogen Fixation:**

Nitrogen fixing microorganism has the ability to convert atmospheric nitrogen into ammonia (Singh *et al.* 1981). Use of this nitrogen fixing bacteria reduces the necessity of synthetic nitrogen fertilizers. *Methylorubrum rhodesianum* has the potential to convert atmospheric nitrogen into ammonia; thereby increasing the availability of nitrogen, crucial nutrient for plant growth (Sy *et al.* 2001).

* **Phosphate Solubilization**

Plants uptake phosphorous as orthophosphate ions, however, in soil, based on the pH, phosphorous exists in insoluble forms, such as calcium phosphate or aluminium/iron phosphate (Tang *et al.* 2023). Through the production of organic acid, acid and alkyl phosphatase, phytase enzyme *Methylorubrum* converts insoluble phosphorous into soluble organic form. Several phosphorous solubilising *Methylorubrum* strains were isolated and listed in the table 3. that highlights their role in sustainable agriculture.

* **Siderophore Production:**

Iron is an important micronutrient mainly available in two oxidation forms Fe3+ (soluble) and Fe2+ (insoluble) in soil (Shi *et al.* 2012). Ferric form of iron is insoluble, making iron acquisition a challenge for plants. Under iron-limiting conditions, microorganisms secrete siderophores, an iron-chelating compound that enhances the iron uptake. A number of strains that can produce siderophores are presented in the table 3.

**Table 2. Stress adaptive *Methylorubrum* with multifarious PGP attributes for alleviation of diverse abiotic stresses in plants (P- Phosphate solubilization; IAA- Indole acetic Acid production; Fe- Siderophores production; ACC- ACC deaminase production**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| ***Methylorubrum*** | **P** | **IAA** | **Fe** | **ACC** | **Reference** |
| *Methylorubrum populi TNAU 1* | - | - | - | + | (raja *et al.* 2006) |
| *Methylorubrum extorquens G10* | + | - | - | - | (agafonova *et al.* 2013) |
| *Methylorubrum extorquens IIWP - 43* | + | + | + | - | (agafonova *et al.* 2013) |

6. **Abiotic stresses**

 *Methylorubrum* genus have remarkable ability in mitigating several abiotic stresses, including high and low temperature stress, drought, salinity and heavy metal toxicity. Abiotic stresses significantly reduce the growth and development of plants that will cause major yield loss and productivity. Plants associated with beneficial microbiome, is the basic line of defence against any abiotic stresses, especially *Methylorubrum* association mitigates the unfavourable effects of all abiotic stress through several mechanisms. These mechanisms include increased accumulation of osmolytes and antioxidant enzymes, promotes nutrient uptake, protection against phytopathogens and alters the ethylene level through ACC-D production. Fig 2. depicts the potential of *Methylorubrum* in abiotic stress mitigation.

**Figure 2. Role of *Methylorubrum* in abiotic stress mitigation**

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6.1. Drought stress

Drought stress triggers a lot of physiological and biochemical changes in plants, including reduced water uptake, decreased photosynthesis, and increased oxidative stress. During abiotic stress, plants accumulate excess amount of ethylene and ROX; alters DNA, RNA, proteins, phytohormones accumulation, osmolytes content, stomatal closure and reduces transpiration (Silva *et al.* 2020).. There are several reports of *Methylorubrum* species such as *M. populi, M. aminovorans, M. extorquens* have been reported to help plants to survive under abiotic stress conditions.

6.2. Salinity stress

Regular irrigation of field with salt water and sea water intrusion develops saline conditions. There are three different salt affected conditions- saline, sodic and alkaline. Saline condition refers to increased accumulation of soluble salts. Alkalinity describes soil conditions characterised by increased accumulation of carbonate and bicarbonate ions. Sodic soils have increased accumulation of exchangeable sodium that affects water and air movement. All the critical growth stages of plant are highly susceptible to salt stress (Kumar *et al.* 2015, Sorty *et al.* 2016, Mishra *et al.* 2016). Salinity stress poses a significant threat to agriculture, particularly in arid and semi-arid regions. High salt concentrations in the soil can disrupt plant water uptake, nutrient balance, and enzyme activity. Accumulation of salts reduces the water potential in soil and causes water to move out of the plant cell to the soil (Egamberdieva *et al.* 2015).

6.3. UV stress

 Ozone layer depletion due to anthropogenic greenhouse gas emissions, increases UV expose, which have significant impact in plants. UV radiation cause DNA damage, reduces photosynthesis and improves oxidative stress (Sage *et al.* 2012). UV-B causes nucleoprotein damage. generates DNA photoproduct, oxidises the plant tissues and reduce their survival rate (Kosobryukhov *et al.* 2020). *Methylorubrum* protects plant through various protective mechanisms through astaxanthin pigments and ergothioneine accumulation, that can absorb UV radiation and thereby reduces damage (Bazela *et al.* 2014).

**7. Mechanism of abiotic stress mitigation by *Methylorubrum***

* **ACC Deaminase Production**

Ethylene at lower concentrations promotes root extension, whereas high concentration inhibits root elongation. Under abiotic stress conditions, endogenous level of ethylene increases significantly. Ethylene as a stress hormone, can intensify the negative effects of drought (Glick 1995). *Methylorubrum* helps plants to reduce ethylene levels and thereby maintains better growth and water use efficiency under drought conditions. Through the production of ACC deaminase, *Methylorubrum* reduces ethylene levels in plants by converting the precursor of ethylene ACC into ammonia and alpha-ketoglutarate (Hardoim *et al.* 2008).

* **Osmolytes accumulation**

Osmolytes are solutes that accumulate in plants to reduce cell damage caused by oxidative stress (Sharma *et al.* 2019). Glycine betaine, proline, polyamines and sugars are some examples of osmolytes that can reduce the osmotic pressure induced by abiotic stress conditions. Plants treated with *Methylorubrum* spp. have showed increase accumulation of osmolytes like glycine betaine, proline and sugars, which help plant to maintain osmotic balance under abiotic stress. Osmolytes protect cellular structures and enzymes from damage caused by dehydration (Chandrasekaran *et al.* 2017).

* **Stomatal Regulation**

Stomata are minute pores present in the leaf surface that regulate gas exchange and water loss. Guard cells control the opening and closure of stomata. In abiotic stress conditions, plants accumulate abscisic acid (ABA), which in turn closes the stomatal pore (Daszkowska-Golec and Szarejko, 2013). *Methylorubrum* plays a significant role in stomatal regulation through both direct and indirect strategies to maintain water balance and gas exchange. Production of ACC deaminase, reduces ethylene levels and enhances photosynthesis and water retention (Krishnamoorthy, 2020; Sivakumar *et al.* 2017). Accumulation of proline and glycine betaine maintains turgor pressure and osmotic stability. In direct mechanism, *Methylorubrum* releases volatile organic compounds that activate defense phytohormones like salicylic acid and jasmonic acid, in turn triggers the opening of stomata through OST1 signal cascade. It also modulates ion channels, transporters and signalling proteins through gene expression (Krishnamoorthy, 2020). Opening of stomata reduces the leaf temperature, thereby reduces the adverse of the drought (Rajagopalan, 1956).

* **Increased antioxidant enzyme activity**

Abiotic stress conditions enhance the production of reactive oxygen species (ROS), such as singlet oxygen, superoxide radical, hydrogen peroxide, and hydroxyl radical (Sivakumar *et al.* 2017). Low quantities of these ROS, can be easily balanced by antioxidant enzymes. However, in abiotic stress conditions, the level of these molecules increases and results in oxidative damage. Accumulation of ROS leads to oxidative damage, causes protein degradation, lipid peroxidation, membrane disruption. Antioxidant enzymes such as peroxidase, superoxide dismutase, catalase, ascorbate peroxidase neutralize the ROS. Application of *Methylorubrum* enhances plant defence by upregulating the antioxidant related genes and increase the antioxidant enzyme activity, thereby facilitates ROS detoxification (Chandrasekaran *et al.* 2017).

**8. Synergistic Effects and Multi-Stress Tolerance**

In natural environments, plants often face multiple stresses, application of *Methylorubrum* spp. with plant growth-promoting capabilities have several beneficial effects on plants.

* **Reduced reliance on synthetic chemical fertilizers:** Enhance nutrient availability and promotes plant growth, *Methylorubrum* reduces the application of synthetic fertilizers, minimizes environmental pollution and promoting soil health.
* **Improved crop yields:** *Methylorubrum* can enhance crop yields under both normal and stressful conditions, contributes to food security and economic benefits for farmers.
* **Sustainable stress management:** *Methylorubrum* reduces the deleterious effects of abiotic stresses, contributes to sustainable agriculture in the face of global warming and increasing environmental pressures (Chandrasekaran *et al.* 2017).

**9. Conclusion**

*Methylorubrum* spp. is a group of plant growth-promoting bacteria that plays a crucial role in sustainable agriculture. Accumulation of osmolytes like proline and glycine betaine maintains the cell turgor pressure and maintains the osmotic balance, increased activity of antioxidants reduces the deleterious effects of reactive oxygen species, production of phytohormones like auxin and cytokinin increase shoot and root growth. These abilities of *Methylorubrum* to produce phytohormones, enhancing nutrient availability, and improve stress tolerance make them, a multifaceted candidate to improve plant growth and stress resilience. *Methylorubrum* supports plant resilience against adverse conditions, contributing sustainable yield. This symbiotic relationship with plants can minimizes the reliance on chemical fertilizers and promotes eco-friendly crop management strategies.

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**References**

Agafonova, N. V., Kaparullina, E. N., Doronina, N. V. and Y. A. Trotsenko. 2013. Phosphate-solubilizing activity of aerobic methylobacteria. *Microbiology*, **82:** 864-867.[10.1134/S0026261714010020.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1134%5CS0026261714010020)

Ahmed, E. and S. J. Holmström. 2014. Siderophores in environmental research: roles and applications. *Microb. Biotechnol.,* **7(3):** 196-208.[10.1111/1751-7915.12117.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1111%5C1751-7915.12117)

Anthony, C., 1982. The biochemistry of methylotrophs.

Bazela, K., Solyga-Zurek, A., Debowska, R., Rogiewicz, K., Bartnik, E. and I. Eris. 2014. L-Ergothioneine protects skin cells against UV-induced damage—a preliminary study. *Cosmetics*, **1(1):** 51-60.[10.3390/cosmetics1010051.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.3390%5Ccosmetics1010051)

Carvajal, T. M., Tan, R. L. and A. C. Lee. 2011. Methylobacterium zatmanii, a pink pigmented facultative methylotrophic (PPFM) bacterium isolated from the human oral cavity. *Philippine J Syst Biol.*, **1:** 9.

Chandrasekaran, P., Sivakumar, R., Nandhitha, G., Vishnuveni, M., Boominathan, P. and M. Senthilkumar. 2017. Impact of PPFM and PGRs on seed germination, stress tolerant index and catalase activity in tomato (*Solanum lycopersicum* l) under drought. *Int. J. Curr. Microbiol. App. Sci*, **6(6):** 540-549. [10.20546/ijcmas.2017.606.064.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.20546%5Cijcmas.2017.606.064)

Danko, D., Malli Mohan, G. B., Sierra, M. A., Rucker, M., Singh, N. K., Regberg, A. B., Bell, M.S., O’Hara, N. B., Ounit, R., Mason, C. E. and K. Venkateswaran. 2021. Characterization of spacesuit associated microbial communities and their implications for NASA missions. *Front. Microbiol.,* **12:** 608478. [10.3389/fmicb.2021.608478.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.3389%5Cfmicb.2021.608478)

Daszkowska-Golec, A. and I. Szarejko. 2013. Open or close the gate–stomata action under the control of phytohormones in drought stress conditions. *Front. Plant Sci.,* **4:** 138.[10.3389/fpls.2013.00138.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.3389%5Cfpls.2013.00138)

Delmotte, N., Knief, C., Chaffron, S., Innerebner, G., Roschitzki, B., Schlapbach, R., von Mering, C. and J. A. Vorholt. 2009. Community proteogenomics reveals insights into the physiology of phyllosphere bacteria. *Proceedings of the National Academy of Sciences*, **106(38):** 16428-16433. [10.1073/pnas.0905240106.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1073%5Cpnas.0905240106)

Doronina, N. V., Trotsenko, Y. A., Kuznetsov, B. B., Tourova, T. P. and M. S. Salkinoja-Salonen. 2002. Methylobacterium suomiense sp. nov. and Methylobacterium lusitanum sp. nov., aerobic, pink-pigmented, facultatively methylotrophic bacteria. *Int. J. Syst. Evol. Microbiol.,* **52(3):** 773-776.[10.1099/00207713-52-3-773.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5C00207713-52-3-773)

Egamberdieva, D., Wirth, S., Alqarawi, A. A. and E. Abd\_Allah. 2015. Salt tolerant Methylobacterium mesophilicum showed viable colonization abilities in the plant rhizosphere. *Saudi J. Biol. Sci.,* **22(5):** 585-590.[10.1016/j.sjbs.2015.06.029.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.sjbs.2015.06.029)

Glick, B.R., 1995. The enhancement of plant growth by free-living bacteria. *Can. J. Microbiol.* 41(2): 109-117.[10.1139/m95-015.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1139%5Cm95-015)

Gopi, K., Jinal, H. N., Prittesh, P., Kartik, V. P. and N. Amaresan. 2020. Effect of copper-resistant Stenotrophomonas maltophilia on maize (Zea mays) growth, physiological properties, and copper accumulation: potential for phytoremediation into biofortification*. Int. J. Phytoremediation.,* **22(6):** 662-668.[10.1080/15226514.2019.1707161.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1080%5C15226514.2019.1707161)

Green, P. N. and J. K. Ardley. 2018. Review of the genus Methylobacterium and closely related organisms: a proposal that some Methylobacterium species be reclassified into a new genus, Methylorubrum gen. nov. *Int. J. Syst. Evol. Microbiol.,* **68(9):** 2727-2748. [10.1099/ijsem.0.002856.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5Cijsem.0.002856)

Green, P. N., Bousfield, I. J. and D. Hood. 1988. Three new Methylobacterium species: M. rhodesianum sp. nov., M. zatmanii sp. nov., and M. fujisawaense sp. nov. *Int. J. Syst. Evol. Microbiol*., **38(1):** 124-127.[10.1099/00207713-38-1-124.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5C00207713-38-1-124)

Green, P. N. and I. J. Bousfield. 1983. Emendation of Methylobacterium Patt, Cole, and Hanson 1976; Methylobacterium rhodinum (Heumann 1962) comb. nov. corrig.; Methylobacterium radiotolerans (Ito and Iizuka 1971) comb. nov. corrig.; and Methylobacterium mesophilicum (Austin and Goodfellow 1979) comb. nov. *Int. J. Syst. Evol. Microbiol.,* **33(4):** 875-877.[10.1099/00207713-33-4-875.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5C00207713-33-4-875)

Hardoim, P. R., van Overbeek, L. S. and J. D. van Elsas. 2008. Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol.,* **16(10):** 463-471.[10.1016/j.tim.2008.07.008.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.tim.2008.07.008)

Holland, M. A. and J. C. Polacco. 1992. Urease-null and hydrogenase-null phenotypes of a phylloplane bacterium reveal altered nickel metabolism in two soybean mutants. *Plant Physiol.,* **98(3):** 942-948.[10.1104/pp.98.3.942.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1104%5Cpp.98.3.942)

Ivanova, E. G., Doronina, N.V. and Y. A. Trotsenko. 2001. Aerobic methylobacteria are capable of synthesizing auxins. *Microbiology*, **70:** 392-397.[10.1023/A:1010469708107.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1023%5CA%3A1010469708107)

Jinal, H. N., Gopi, K., Prittesh, P., Kartik, V. P. and N. Amaresan. 2019. Phytoextraction of iron from contaminated soils by inoculation of iron-tolerant plant growth-promoting bacteria in Brassica juncea L. Czern. *Environ. Sci. Pollut. Res.,* **26:** 32815-32823. [10.1007/s11356-019-06394-2.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5Cs11356-019-06394-2)

Kazan, K., 2015. Diverse roles of jasmonates and ethylene in abiotic stress tolerance. *Trends Plant Sci.,* **20(4):** 219-229.[10.1016/j.tplants.2015.02.001.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.tplants.2015.02.001)

Kelley, S. T., Theisen, U., Angenent, L. T., St. Amand, A. and N. R. Pace. 2004. Molecular analysis of shower curtain biofilm microbes. Appl. Environ. Microbiol., **70(7):** 4187-4192.[10.1128/AEM.70.7.4187-4192.2004.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1128%5CAEM.70.7.4187-4192.200410.1128%5CAEM.70.7.4187-4192.2004)

Kosobryukhov, A., Khudyakova, A. and V. Kreslavski. 2020. Impact of UV radiation on photosynthetic apparatus: adaptive and damaging mechanisms. *Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives I: General Consequences and Plant Responses*, 555-576.[10.1007/978-981-15-2156-0\_18.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5C978-981-15-2156-0_18)

Krishnamoorthy, R., 2020. Phyllosphere Methylotrophic Bacteria on Plant Growth and Stress Mitigation. *AGRICULTURE & FOOD: e-NEWSLETTER*.

Krishnamoorthy, R., Anandham, R., Senthilkumar, M. and V. Venkatramanan. 2021. Adaptation mechanism of methylotrophic bacteria to drought condition and its strategies in mitigating plant stress caused by climate change. *Exploring synergies and trade-offs between climate change and the sustainable development goals*, 145-158.[10.1007/978-981-15-7301-9\_7.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5C978-981-15-7301-9_7)

Kumar, V., Singh, A., Mithra, S.A., Krishnamurthy, S. L., Parida, S. K., Jain, S., Tiwari, K. K., Kumar, P., Rao, A. R., Sharma, S. K. and J. P. Khurana. 2015. Genome-wide association mapping of salinity tolerance in rice (Oryza sativa). *DNA Res.,* **22(2):** 133-145.[10.1093/dnares/dsu046.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1093%5Cdnares%5Cdsu046)

Kwak, M. J., Jeong, H., Madhaiyan, M., Lee, Y., Sa, T. M., Oh, T. K. and J. F. Kim. 2014. Genome information of Methylobacterium oryzae, a plant-probiotic methylotroph in the phyllosphere. *PloS one*, **9(9):** 106704.[10.1371/journal.pone.0106704](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1371%5Cjournal.pone.0106704).

Madhaiyan, M., Poonguzhali, S. and T. Sa. 2007. Metal tolerating methylotrophic bacteria reduces nickel and cadmium toxicity and promotes plant growth of tomato (Lycopersicon esculentum L.). *Chemosphere*, **69(2):** 220-228.[10.1016/j.chemosphere.2007.04.017.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.chemosphere.2007.04.017)

Madhaiyan, M., Kim, B. Y., Poonguzhali, S., Kwon, S. W., Song, M. H., Ryu, J. H., Go, S. J., Koo, B. S. and T. M. Sa. 2007. *Methylobacterium oryzae* sp. nov., an aerobic, pink-pigmented, facultatively methylotrophic, 1-aminocyclopropane-1-carboxylate deaminase-producing bacterium isolated from rice. *Int. J. Syst. Evol. Microbiol.,* **57(2):** 326-331.[10.1099/ijs.0.64603-0.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5Cijs.0.64603-0)

Madhaiyan, M. and S. Poonguzhali. 2014. Methylobacterium pseudosasicola sp. nov. and Methylobacterium phyllostachyos sp. nov., isolated from bamboo leaf surfaces. *International J. Syst. Evol. Microbiol.,* **64(7):** 2376-2384.[10.1099/ijs.0.057232-0.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5Cijs.0.057232-0)

Madhaiyan, M., Poonguzhali, S., Ryu, J. and T. Sa. 2006. Regulation of ethylene levels in canola (Brassica campestris) by 1-aminocyclopropane-1-carboxylate deaminase-containing Methylobacterium fujisawaense. *Planta*, **224:** 268-278.[10.1007/s00425-005-0211-y.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5Cs00425-005-0211-y)

Mano, Y. and K. Nemoto. 2012. The pathway= of auxin biosynthesis in plants. J*. Exp. Bot.* **63(8):** 2853-2872. [10.1093/jxb/ers091.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1093%5Cjxb%5Cers091)

Mishra, B. K., Meena, K. K., Dubey, P. N., Aishwath, O. P., Kant, K., Sorty, A. M. and U. Bitla. 2016. Influence on yield and quality of fennel (Foeniculum vulgare Mill.) grown under semi-arid saline soil, due to application of native phosphate solubilizing rhizobacterial isolates. *Ecol. Eng.,* **97:** 327-333.[10.1016/j.ecoleng.2016.10.034.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.ecoleng.2016.10.034)

Novikova, N., De Boever, P., Poddubko, S., Deshevaya, E., Polikarpov, N., Rakova, N., Coninx, I. and M. Mergeay. 2006. Survey of environmental biocontamination on board the International Space Station. *Res. Microbiol.,* **157(1):** 5-12. [10.1016/j.resmic.2005.07.010.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C12.10.1016%5Cj.resmic.2005.07.010)

Prittesh, P., Avnika, P., Kinjal, P., Jinal, H. N., Sakthivel, K. and N. Amaresan. 2020. Amelioration effect of salt-tolerant plant growth-promoting bacteria on growth and physiological properties of rice (Oryza sativa) under salt-stressed conditions. *Arch. Microbiol.,* **202(9):** 2419-2428. [10.1007/s00203-020-01962-4.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5Cs00203-020-01962-4)

Raja, P., Uma, S. and S. Sundaram. 2006. Non-nodulating pink-pigmented facultative Methylobacterium sp. with a functional nifH gene. *World Journal of Microbiology and Biotechnology*, **22:** 1381-1384[.https://doi.org/10.1007/s11274-006-9199-0](file:///C%3A%5CUsers%5Chp%5CDownloads%5C.%20https%3A%5Cdoi.org%5C10.1007%5Cs11274-006-9199-0)

Rajagopalan, K., 1956. Variability in size and frequency of stomata in leaves of rice varieties and its correlation in drought resistance. <https://doi.org/10.29321/MAJ.10.A04239.>

Rani, V., Bhatia, A. and R. Kaushik. 2021. Inoculation of plant growth promoting-methane utilizing bacteria in different N-fertilizer regime influences methane emission and crop growth of flooded paddy. *Sci. Total Environ.,* **775:** 145826.[10.1016/j.scitotenv.2021.145826.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5Cj.scitotenv.2021.145826)

Sage, E., Girard, P. M. and S. Francesconi. 2012. Unravelling UVA-induced mutagenesis. *Photochem. Photobiol. Sci.,* **11(1):** 74-80. [10.1039/c1pp05219e.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1039%5Cc1pp05219e)

Schauer, S., Kämpfer, P., Wellner, S., Spröer, C. and U. Kutschera. 2011. *Methylobacterium marchantiae* sp. nov., a pink-pigmented, facultatively methylotrophic bacterium isolated from the thallus of a liverwort. *Int. J. Syst. Evol. Microbiol.,* **61(4):** 870-876.[10.1099/ijs.0.021915-0.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1099%5Cijs.0.021915-0)

Sharma, A., Shahzad, B., Kumar, V., Kohli, S. K., Sidhu, G. P. S., Bali, A. S., Handa, N., Kapoor, D., Bhardwaj, R. and B. Zheng. 2019. Phytohormones regulate accumulation of osmolytes under abiotic stress. *Biomolecules*, **9(7):** 285. <https://doi.org/10.3390/biom9070285>

Shi, R. L., Hao, H. M., Fan, X. Y., Karim, M. R., Zhang, F. S. and C. Q. Zou. 2012. Responses of aerobic rice (Oryza sativa L.) to iron deficiency. *J. Integr. Agric.,* **11(6):** 938-945.[10.1016/S2095-3119(12)60084-7.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1016%5CS2095-3119%2812%2960084-7)

Silva, R., Filgueiras, L., Santos, B., Coelho, M., Silva, M., Estrada-Bonilla, G., Vidal, M., Baldani, J. I. and C. Meneses. 2020. Gluconacetobacter diazotrophicus changes the molecular mechanisms of root development in Oryza sativa L. growing under water stress. *International Journal of Molecular Sciences*, **21(1):** 333. <https://doi.org/10.3390/ijms21010333>

Singh, D. V., Chauhan, R. P. S., Singh, K. and B. Pal. 1981. Nitrogen and phosphorus needs of gram (Cicer arietinum L.) along with bacterial fertilization. <https://doi.org/10.29321/MAJ.10.A03087.>

Sivakumar, R., Nandhitha, G. K., Chandrasekaran, P., Boominathan, P. and M. Senthilkumar. 2017. Impact of pink pigmented facultative methylotroph and PGRs on water status, photosynthesis, proline and NR activity in tomato under drought. *Int J Curr Microbiol App Sci.*, **6(6):** 1640-1651.[10.20546/ijcmas.2017.606.192.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.20546%5Cijcmas.2017.606.192)

Sorty, A. M., Meena, K. K., Choudhary, K., Bitla, U.M., Minhas, P. S. and Krishnani, K. K., 2016. Effect of plant growth promoting bacteria associated with halophytic weed (Psoralea corylifolia L) on germination and seedling growth of wheat under saline conditions. *Appl. Biochem. Biotechnol.,* **180:** 872-882.[10.1007/s12010-016-2139-z.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5Cs12010-016-2139-z)

Sy, A., Giraud, E., Jourand, P., Garcia, N., Willems, A., De Lajudie, P., Prin, Y., Neyra, M., Gillis, M., Boivin-Masson, C. and B. Dreyfus. 2001. Methylotrophic Methylobacterium bacteria nodulate and fix nitrogen in symbiosis with legumes. *J. Bacteriol.,***183(1):** 214-220.[10.1128/JB.183.1.214-220.2001.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1128%5CJB.183.1.214-220.2001)

Szwetkowski, K. J. and J. O. Falkinham. 2020. Methylobacterium spp. as emerging opportunistic premise plumbing pathogens. *Pathogens*, **9(2):** 149.[10.3390/pathogens9020149.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.3390%5Cpathogens9020149)

Tang, X., Liu, H., Qin, H., Zhao, J., Wang, H., Li, B. and Y. Lu. 2023. Organic/inorganic phosphorus partition and transformation in long-term paddy cultivation in the Pearl River Delta, China. *Sci. Rep.,* **13(1):** 11122.[10.1038/s41598-023-38369-2.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1038%5Cs41598-023-38369-2)

Tito, R., Vasconcelos, H. L. and K. J. Feeley. 2018. Global climate change increases risk of crop yield losses and food insecurity in the tropical Andes. *Glob. Change Biol.,* **24(2):** e592-e602.[10.1111/gcb.13959.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1111%5Cgcb.13959)

Van Aken, B., Yoon, J. M. and J. L. Schnoor. 2004. Biodegradation of nitro-substituted explosives 2, 4, 6-trinitrotoluene, hexahydro-1, 3, 5-trinitro-1, 3, 5-triazine, and octahydro-1, 3, 5, 7-tetranitro-1, 3, 5-tetrazocine by a phytosymbiotic Methylobacterium sp. associated with poplar tissues (Populus deltoides× nigra DN34). *Appl. Environ. Microbiol.,* **70(1):** 508-517.[10.1128/AEM.70.1.508-517.2004.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1128%5CAEM.70.1.508-517.2004)

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A. and A. Dufresne. 2015. The importance of the microbiome of the plant holobiont. *New Phytol*., **206(4):** 1196-1206.[10.1111/nph.13312.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1111%5Cnph.13312)

Ventorino, V., Sannino, F., Piccolo, A., Cafaro, V., Carotenuto, R. and O. Pepe. 2014. Methylobacterium populi VP2: plant growth‐promoting bacterium isolated from a highly polluted environment for polycyclic aromatic hydrocarbon (PAH) biodegradation. *Sci. World J.,* **2014(1):** 931793. [10.1155/2014/931793.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1155%5C2014%5C931793)

Verma, P., Yadav, A. N., Kumar, V., Singh, D. P. and A. K. Saxena. 2017. Beneficial plant-microbes interactions: biodiversity of microbes from diverse extreme environments and its impact for crop improvement. *Plant-microbe interactions in agro-ecological perspectives: volume 2: microbial interactions and agro-ecological impacts*, 543-580.[10.1007/978-981-10-6593-4\_22.](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5C978-981-10-6593-4_22)

Wood, A. P., Kelly, D. P., McDonald, I. R., Jordan, S. L., Morgan, T. D., Khan, S., Murrell, J. C. and E. Borodina. 1998. A novel pink-pigmented facultative methylotroph, *Methylobacterium thiocyanatum* sp. nov., capable of growth on thiocyanate or cyanate as sole nitrogen sources. *Arch. microbiol.*, **169:** 148-158.[10.1007/s002030050554](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1007%5Cs002030050554).

Zhang, W., Zhang, T., Wu, S., Wu, M., Xin, F., Dong, W., Ma, J., Zhang, M. and M. Jiang. 2017. Guidance for engineering of synthetic methylotrophy based on methanol metabolism in methylotrophy. *RSC advances.*, **7(7):** 4083-4091.[10.1039/C6RA27038G](file:///C%3A%5CUsers%5Chp%5CDownloads%5C10.1039%5CC6RA27038G)