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REVIEW ARTICLE

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

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ABSTRACT

Many microorganisms inhabit and interact with plants and play a significant role in improving overall productivity and sustainability. Among the microorganisms, bacteria contribute more to fostering plant growth and development. They are collectively known as Plant Growth Promoting bacteria (PGPRs). *Methylorubrum* is one such group of bacterial genera that has both plant growth-promoting ability and abiotic stress mitigation. *Methylorubrum,* a member of alpha-proteobacteria, is ubiquitous and can colonize the entire plant system, gaining significant importance in crop production due to its multifaceted abilities. Due to their pink pigmentation, members of the *Methylorubrum* genus are 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 bio stimulant, 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.*

INTRODUCTION

Crops face many 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 and an increase in population pose a global threat to 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 CO_2 levels significantly reduces crop growth and alter their physiology (Madhaiyan *et al.,* 2007a; Jinal *et al.,* 2019; Gopi *et al.,* 2020). Due to the intricate nature of stress tolerance, employing conventional breeding techniques to develop crops with strong stress resistance is impossible. Plants developed sophisticated mechanisms to reduce the impacts to adapt to unfavourable stress conditions. The mechanisms include physiological, biochemical, and molecular changes that help plants maintain cellular homeostasis and ensure survival. In recent years, the usage of plant growth-promoting microorganisms has emerged as a sustainable approach to improve plant

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productivity and resilience under both normal and stress conditions (Vandenkoornhuyse *et al.,* 2015).

Plants are not a single entity, but a host of diverse groups of microorganisms that provide both beneficial and detrimental effects through a diverse relationship, including commensal, symbiotic, parasitic, and mutualistic relationships that shape the productivity of crops (Krishnamoorthy *et al.,* 2021; Rani *et al.,* 2021). The microorganisms that can promote plant growth is known as Plant Growth Promoting bacteria (PGPBs). Among these PGPBs, *Methylorubrum,* a genus of pink-pigmented, facultative methylotrophic bacteria, able to colonise the phyllosphere, are commonly known as pink pigmented facultative methylotrophs (PPFMs) (Fig.1). *Methylorubrum* has gained major attention due to its significant potential in mitigating abiotic stress and improving plant growth. These plant-associated microbes help 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, the role of *Methylorubrum* is crucial in improving plant growth and stress mitigation for sustainable agriculture practices. Due to their versatile capabilities, inoculating *Methylorubrum* alone or in combination, is a valuable 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).

Taxonomy

In 2018, Green and Ardley divided *Methylobacterium* into two genera, *Methylobacterium* and *Methylorubrum*. Based on phenotypic traits, 16s rRNA, multilocus sequence analysis (MLSA), 11 species were included 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).

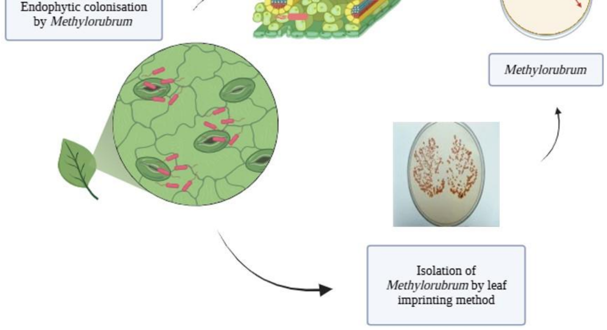

Figure 1. Phyllospheric Colonisation by *Methylorubrum*

Ecology

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

Metabolism of single-carbon compounds

Methylotrophs are a group of microorganisms that can utilize single–carbon compounds such as methanol, methylamine, or formate as a primary carbon source. Methanol dehydrogenase (MDHs) is the key enzyme that catalyses methanol oxidation to generate formaldehyde with hydrogen ions and electrons (Zhang *et al.,* 2017). This produced formaldehyde enters the cell and it is 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 cases, *Methylorubrum* employs the serine cycle for the assimilation of formaldehyde through a series of complex biochemical reactions that convert formaldehyde into building blocks of the cell and energy production. This pathway also helps *Methylorubrum* to produce vital nucleic acids, lipids, and amino acids from the single–carbon compound methanol. Through these metabolic capabilities, *Methylorubrum* thrives in diverse environments and

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)
Contaminated soils	*Methylobacterium suomiense*	(Doronina *et al.,* 2002)
	Methylobacterium thiocyanatum	(Wood *et al.,* 1998)
Manufactured 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)

establishes beneficial interactions with plants, which fosters plant growth and enhances 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 plant nutrient uptake. Another essential micronutrient of plants that plays a crucial role in the physiological processes of plants is iron. Plant Growth Promoting microorganisms produce siderophores, a specific type of molecules that enhance iron bioavailability for uptake (Verma *et al.,* 2017).

Plant Growth-Promoting Mechanisms

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

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

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

Phytohormone Production and Regulation

- ***Auxins***: *Methylorubrum* can synthesize auxins, such as indole-3-acetic acid, which plays a vital 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 cytokinin, which promote cell division, rejuvenate cells, and enhance plant nutrient mobilization (Holland and Polacco, 1992). Cytokinin interacts with auxins to regulate various developmental processes.
- ***Ethylene** Regulation*: *Methylorubrum* can modulate ethylene levels in plants by producing ACC deaminase. ACC deaminase breaks the 1-Aminocyclopropane-1-carboxylic acid (ACC), the precursor to ethylene, into ammonia and alpha-ketoglutaric acid, thereby reducing ethylene levels and mitigating its inhibitory effects under stress conditions (Madhaiyan *et al.,* 2006).

Nutrient Acquisition

- ***Nitrogen Fixation:***

Nitrogen-fixing microorganism can convert atmospheric nitrogen into ammonia (Singh *et al.,* 1981). Using these 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, a crucial nutrient for plant growth (Sy *et al.,* 2001).

- ***Phosphate Solubilization***

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

- ***Siderophore Production:***

Iron is a vital micronutrient mainly available in two oxidation forms, Fe^{3+} (soluble) and Fe^{2+} (insoluble) in soil (Shi *et al.,* 2012). The 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 iron uptake. Several strains that can produce siderophores are presented in the table 3.

Abiotic stresses

The *Methylorubrum* genus has a remarkable ability to mitigate 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, which can cause major yield loss and productivity. Plants associated with a beneficial microbiome are the basic line of defence against any abiotic stresses, especially *Methylorubrum* association, which mitigates the unfavourable effects of all abiotic stress through several mechanisms. These mechanisms include increased accumulation of osmolytes and antioxidant enzymes, promote nutrient uptake, protection against phytopathogens, and alter the ethylene level through ACC-D production. Figure 2 depicts the potential of *Methylorubrum* in abiotic stress mitigation.

Drought stress

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

Salinity stress

Regular irrigation of the field with salt water and sea

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)

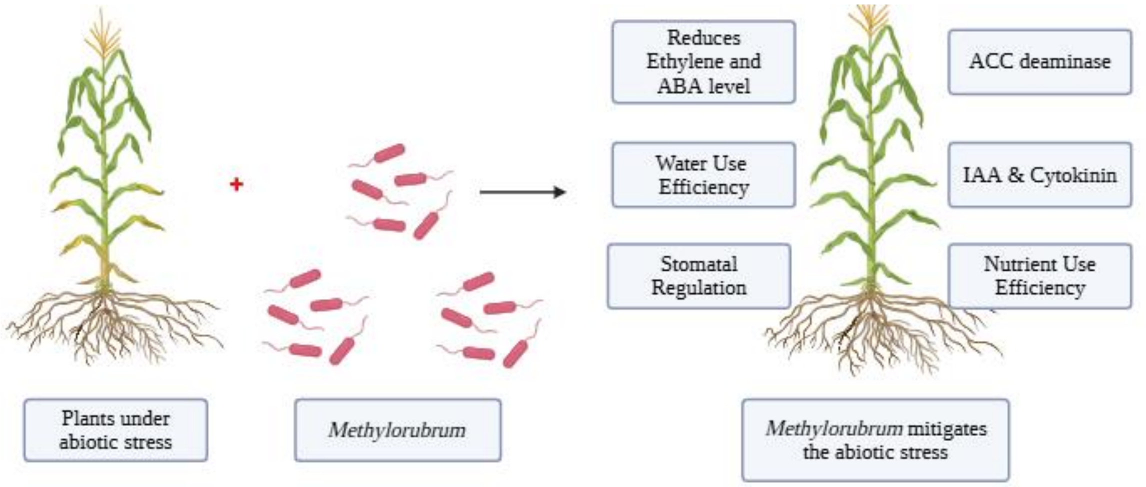

Figure 2. Role of *Methylorubrum* in abiotic stress mitigation

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 exchangeable sodium accumulation, affecting water and air movement. All the critical growth stages of a plant are highly susceptible to salt stress (Kumar *et al.,* 2015; Sorty *et al.,* 2016; Mishra *et al.,* 2016). Salinity stress significantly threatens 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 the soil and causes water to move out of the plant cell to the soil (Egamberdieva *et al.,* 2015).

UV stress

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

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, the endogenous level of ethylene increases significantly. Ethylene, as a stress hormone, can intensify the adverse effects of drought (Glick, 1995). *Methylorubrum* helps plants reduce ethylene levels and 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 osmolytes that can reduce the osmotic pressure induced by abiotic stress conditions. Plants treated with *Methylorubrum* spp. have increased accumulation of osmolytes like glycine betaine, proline and sugars, which help plants 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 on 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 direct and indirect strategies to maintain water balance and gas exchange. Production of ACC deaminase reduces ethylene levels and enhances photosynthesis and water retention (Sivakumar *et al.,* 2017). Accumulation of proline and glycine betaine maintains turgor pressure and osmotic stability. In the direct mechanism, *Methylorubrum* releases volatile organic compounds that activate defense phytohormones like salicylic acid and jasmonic acid, in turn triggering the opening of stomata through the 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 reducing the adverse effects 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, these molecules levels increase and result in oxidative damage. Accumulation of ROS leads to oxidative damage, causes protein degradation, lipid peroxidation, and membrane disruption. Antioxidant enzymes such as peroxidase, superoxide dismutase, catalase and ascorbate peroxidase neutralize the ROS. Application of *Methylorubrum* enhances plant defence by upregulating the antioxidant-related genes and increasing the antioxidant enzyme activity, thereby facilitating ROS detoxification (Chandrasekaran *et al.,* 2017).

Synergistic Effects and Multi-Stress Tolerance

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

- ***Reduced reliance on synthetic chemical fertilizers:*** Enhance nutrient availability and promote plant growth, Methylorubrum reduces the application of synthetic fertilizers, minimizes environmental pollution, and promotes soil health.
- ***Improved crop yields:*** *Methylorubrum* can enhance crop yields under normal and stressful conditions, contributing 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).

CONCLUSION

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

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No human or animal subjects were involved in this review

Originality and plagiarism

The authors ensure that all references, quotations, and paraphrased materials are correctly cited, and we have adhered to ethical standards in avoiding plagiarism.

Data availability

Not applicable

Consent for publication

All the authors agreed to publish the content

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There were no conflicts of interest in the publication of this content

Author contributions

Idea conceptualization- ARUP, KP, MS
Writing original draft – ARUP, KP, MS
reviewing &editing – ARUP, MS, DS, MSK

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