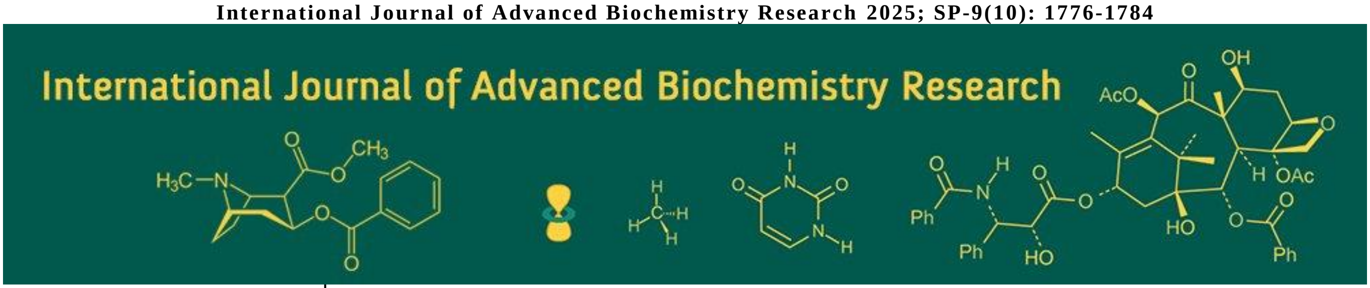

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Phyllosphere methylotrophs and climate resilience: The emerging role of PPFMS in mitigating abiotic stresses

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Abstract
Global agricultural systems are increasingly threatened by abiotic stresses-including drought, salinity, and heavy metal contamination-which are exacerbated by climate change and unsustainable farming practices. This review highlights the emerging and critical role of methylotrophic bacteria, with a focus on Pink Pigmented Facultative Methylotrophs (PPFMs), as a sustainable solution to these challenges. As natural residents of the phyllosphere and rhizosphere, PPFMs enhance plant growth and development directly through nitrogen fixation, phosphate solubilization, and the production of phytohormones. More significantly, they confer systemic resistance to abiotic stresses by modulating plant ethylene levels via ACC deaminase, stimulating the synthesis of osmoprotectants and antioxidants, and in some cases, directly detoxifying heavy metals. By improving nutrient and water use efficiency, PPFMs reduce reliance on synthetic agrochemicals, thereby offering an eco-friendly pathway to bolster crop productivity and resilience. Their integration into agricultural frameworks represents a pivotal strategy for advancing climate-smart, sustainable food production and ensuring long-term soil and ecosystem health.

Keywords: Abiotic stress, drought, methylotrophs, PPFM

Introduction
The expansion of the global human population is a principal factor instigating planetary-scale transformations, including biodiversity decline, ozone layer erosion, and climatic shifts. This demographic trend profoundly influences climate patterns, a situation exacerbated by the widespread application of chemical fertilizers. The primary impacts on flora include alterations to essential physiological processes that are sensitive to climate. Through secondary pathways, a changing climate disrupts the nuanced symbiotic and pathogenic relationships plants maintain with organisms like insects and microbes. Plant development and vitality are highly responsive to environmental conditions, making them vulnerable to both living (biotic) and non-living (abiotic) stressors. The latter category comprises extremes in temperature, inadequate or excessive light and solar radiation, water scarcity or flooding, nutrient imbalances, soil salinity, and atmospheric pollution (Patel *et al*., 2017, 2018; Gopi *et al*., 2020) [45, 44, 15]. Among these, drought stands out as a major peril to agricultural sustainability and plant health on a global scale. Confronting these issues to safeguard worldwide food supplies demands an urgent focus on innovating new cultivation methods and integrating agricultural practices that are resilient to climate variability. This situation calls for a fundamental strategic shift in farming systems to both alleviate and adjust to the detrimental consequences of a warming planet.
Abiotic stresses are a major threat to that depletes plant development, impedes seed germination, and diminishes crop yields. Research indicates that microorganisms which promote plant growth are vital biological tools for climate change mitigation (Kabiraj *et al*., 2020; Krishnamoorthy *et al*., 2021) [23, 26]. The microbial world has diverse roles; for instance, methanogens in environments like wetlands and ruminant digestive systems release methane, whereas methylotrophs consume it as a carbon source, thereby reducing its atmospheric concentration. Beneficial microbes associated with plants have recently gained significant interest for their capacity to boost agricultural output and confer resilience against

environmental stresses (Gopi *et al*., 2020; Rani *et al*., 2021) [15, 51]. Plant Growth-Promoting Bacteria (PGPB), support plants through direct and indirect strategies. These include nitrogen fixation, phytohormone synthesis, improved micronutrient absorption, and the secretion of bioactive compounds such as siderophores, antibiotics, and enzymes that suppress pathogens and enhance soil structure (Pérez-Flores *et al*., 2017; Prittesh *et al*., 2020) [46, 50]. Collectively, these Plant Growth Promotion (PGP) activities are fundamental to advancing ecosystem health and securing agricultural productivity.

Methylotrophs

Methylotrophs are a class of microorganisms characterized by their unique metabolic ability to use single-carbon (C1) molecules for growth and energy. A principal natural environment for these methanol-consuming bacteria is the phyllosphere, or leaf surface, which hosts substantial populations from genera such as *Methylobacterium*, *Methylophilus*, *Methylibium* and *Hyphomicrobium*. The prevalence of methanol, a by-product of plant pectin metabolism, on leaves offers a competitive niche for these specialized bacteria (Sy *et al*., 2005) [64]. The composition of this leaf-dwelling microbial community is influenced by multiple factors, with plant genetics and geographical location being the most significant drivers (Vorholt, 2012) [68]. While chemical fertilizers can boost plant growth and yield, their residual presence disrupts natural ecosystems. As a sustainable alternative, methylotrophs residing in the phyllosphere show great promise as bioinoculants. These bacteria can promote plant development by modifying plant physiology, secreting growth hormones, and alleviating biotic and abiotic stresses. Their application aligns with the principles of organic farming and presents a solution to the rising costs, environmental damage, and food safety concerns linked to synthetic fertilizers. Consequently, microbial biofertilizers are increasingly recognized as a viable strategy for enhancing crop yield and quality within sustainable agricultural frameworks (Ryu *et al*., 2006) [52]. Foliar application of such biofertilizers is particularly effective, as it bypasses the limiting factors often present in the soil environment.

Methylotrophs are ubiquitous, non-pathogenic bacteria that thrive on methanol and other compounds. Their metabolic versatility and rapid growth under varying conditions underscore their significant biotechnological potential. As phytosymbionts, their ability to produce plant-growth regulators like cytokinins, auxins, and vitamins further enhances their agricultural value. Genomic studies reveal that these methylotrophs possess a suite of genes that enable survival on plant surfaces, including defenses against UV radiation, oxidative stress, and desiccation, as well as genes for motility and signaling (Kwak *et al*., 2014) [29]. Inoculation with *Methylobacterium* has been demonstrated to improve plant health by modulating stress responses, such as lowering stress-induced ethylene levels and elevating pathogen-related proteins (Table 1).

Table 1: Plant growth promoting associations of methylotrophs

Host Plant	Associated Methylotroph	Isolation Source/Niche	Primary Documented Function or Effect	References
Rice	*Methylobacterium extorquens*, *Methylobacterium fujisawaense*	Phyllosphere (Leaves)	Synthesis of the phytohormone Indole-3-acetic acid (IAA)	(Madhaiyan *et al*., 2006) [31]
Wheat	*Methylobacterium* sp.	Phyllosphere (Leaves)	Production of Cytokinin class phytohormones	(Meena *et al*., 2012) [39]
Rice	*Methylobacterium* sp.	Rhizosphere (Root zone)	Biological Nitrogen Fixation (N_2 Fixation)	(Madhaiyan *et al*., 2006) [31]
Red Pepper	*Methylobacterium suomiense*	Rhizosphere (Root zone)	Enhanced root colonization and establishment	(Sivakumar *et al*., 2017) [60]
Tomato	*Methylobacterium suomiense*	Rhizosphere (Root zone)	Enhanced root colonization and establishment	(Sivakumar *et al*., 2017) [60]
Sugarcane	*Methylobacterium* sp.	Rhizosphere (Root zone)	Indole-3-acetic acid (IAA) synthesis and other Plant Growth-Promoting (PGP) activities	(Sathyan *et al*., 2018) [55]
Soybean	Pink-Pigmented Facultative Methylotrophs (PPFMs)	Phyllosphere (Leaves)	Synthesis of the phytohormone Indole-3-acetic acid (IAA)	(Sivakumar *et al*., 2017) [60]
Groundnut	Pink-Pigmented Facultative Methylotrophs (PPFMs)	Phyllosphere (Leaves)	Synthesis of the phytohormone Indole-3-acetic acid (IAA)	(Sivakumar *et al*., 2017) [60]
Mung Bean	*Methylobacterium organophilum*	Mud (Soil substrate)	Application as a Bio-fertilizer to enhance plant growth	(Collet *et al*., 2015) [7]
Green Gram	Pink-Pigmented Facultative Methylotrophs (PPFMs)	Phyllosphere (Leaves)	Application as a Bio-fertilizer to enhance plant growth	(Sivakumar *et al*., 2017) [60]
Black pepper	Pink-Pigmented Facultative Methylotrophs (PPFMs)	Phyllosphere and rhizosphere	Application as a plant growth promoter and drought stress mitigator	ManjuBhargavi *et al*., 2024 [35]
Bird's eye chilli	Pink-Pigmented Facultative Methylotrophs (PPFMs)	Phyllosphere	Application as a plant growth promoter and drought stress mitigator	JasnaSherin *et al*., 2025 [19]

Pink pigmented facultative methylotrophs (PPFMs)

Pink pigmented facultative methylotrophs (PPFMs), a distinct subgroup within methylotrophic bacteria, are of significant physiological interest. Bacteria of the genus Methylobacterium demonstrate a notable capacity to withstand extreme environmental challenges, such as desiccation, freezing, exposure to chlorine and various forms of radiation, and high temperatures (Trotsenko *et al*., 2001) [67]. These strictly aerobic, Gram-negative, rod-shaped α-Proteobacteria typically engage in a symbiotic relationship with plants, predominantly colonizing the phyllosphere. Their metabolic versatility allows them to grow on single-carbon substrates like methanol and methylamine, in addition to multi-carbon compounds (Chistoserdova *et al*., 2003) [6]. A defining trait is their pink pigmentation, which stems from carotenoids, mainly xanthophylls, and provides protection against intense light and radiation.

The diversity of PPFMs is reflected in their associations with various plant species. For example, *Methylobacterium populi* inhabits poplar tree tissues, *M. nodulans* forms nodules on the legume *Crotalaria glaucoides*, and *M. goesingense* is linked to the hyperaccumulator *Thlaspi goesingense* (Jourand *et al*., 2004) [22]. Other species, including *M. extorquens* and *M. fujisawaense*, are common inhabitants of the leaf surface on numerous plants. Methylotrophic bacteria, comprising a wide range of genera and species, are commonly associated with diverse plants. These bacteria colonize both leaf surfaces where they can constitute 14-20% of the microbial population in temperate climates and soil or root zones where methanol is present (Delmotte *et al*., 2009) [9]. Their ability to metabolize methanol via specialized oxidative pathways distinguishes them ecologically. Evidence of their broad distribution includes isolates from internal poplar tissues, different anatomical parts of sunflowers (Schauer and Kutschera, 2008), and the phyllosphere of several crops.

The plant growth-promoting capabilities of *Methylobacterium* are multifaceted. They can fix atmospheric nitrogen, solubilize phosphates, and lower plant ethylene levels via the enzyme ACC deaminase, thereby enhancing stress tolerance and growth (Jourand *et al*., 2004; Madhaiyan *et al*., 2006) [22, 31]. They also contribute to induced systemic resistance against pathogens. Manish *et al*. (2016) [34] reported their importance in sustainable agriculture, noting their critical function in soil biogeochemical cycles. They improve air quality by metabolizing volatile organic compounds and are integral to the global cycling of carbon, nitrogen, and phosphorus, potentially helping to mitigate climate change. Consequently, both rhizospheric and phyllospheric methylotrophs are increasingly deployed as eco-friendly and cost-effective bioinoculants, serving as alternatives to synthetic fertilizers. Their application improves plant water status, boosts photosynthetic efficiency, and elevates the concentration of protective osmolytes like proline and antioxidant enzymes such as catalase, thereby strengthening the plant's defense against abiotic stress.

Plant growth promotion by PPFMs

Extreme biotic and abiotic stresses are major constraints to plant growth and productivity. Numerous studies have demonstrated that methylotrophs exhibit plant growth-promoting (PGP) traits under adverse conditions. Research on *Methylobacterium* has revealed multiple PGP mechanisms, including the synthesis of phytohormones such as indole-3-acetic acid (IAA), gibberellins, and cytokinins, which enhance root and shoot development and increase overall plant biomass (Lidstrom and Chistoserdova, 2002; Grossi *et al*., 2020) [30, 16]. PPFMs establish symbiotic associations with plants, particularly in the rhizosphere, and serve as a source of bioactive compounds for plant protection. They also harbor polyketide synthases and demonstrate resistance to harmful UV radiation. Inoculation with PPFMs has been shown to improve the growth and yield of crops such as rice and soybean by promoting nitrogen fixation, solubilizing mineral phosphate, and inducing systemic resistance against pathogens (Fig. 1.).

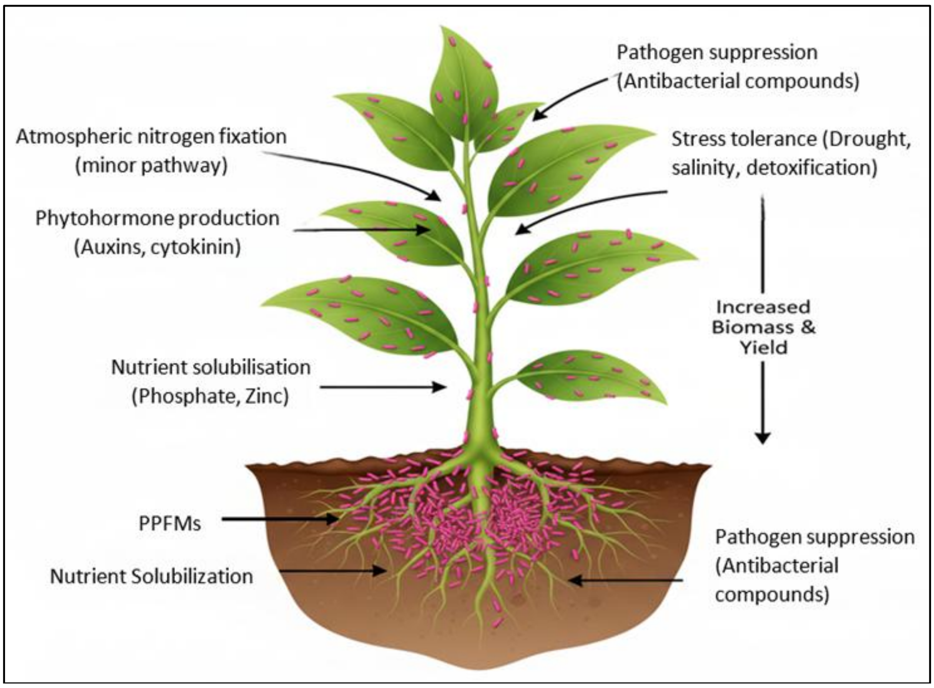

Fig 1: Plant growth promotion mechanisms by PPFMs

Inoculation with *Methylobacterium* strains has been shown to enhance seed germination, seed vigor, dry matter accumulation, and colonization across various plant tissues, along with stimulating quorum-sensing activity (Poonguzhali *et al*., 2007, 2008) [47, 48]. Both epiphytic and endophytic methylotrophs contribute directly to plant growth by producing phytohormones, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, siderophores, secondary metabolites, hydrogen cyanide, and extracellular hydrolytic enzymes. These compounds, together with antagonistic substances, play key roles in safeguarding plants against pathogens and mitigating environmental stress (Subhaswaraj *et al*., 2017; Yadav and Yadav, 2018) [62, 69].

Beneficial effects of *Methylobacterium* application have been demonstrated in several crops including wheat

(Poonguzhali *et al*., 2007) [47], barnyard millet (*Echinochloa frumentacea* Var. COKV 2), biodiesel plant *Crambe abyssinica*, ginger, rice, cotton, and cardamom. These studies collectively highlight the diverse interactions between *Methylobacterium* and host plants. Due to their multiple plant growth-promoting traits, PPFMs are considered promising bioinoculants in sustainable agriculture. Classified as biosafety level one organisms, *Methylobacterium* species are non-pathogenic and safe for agricultural applications. Based on their beneficial features, several *Methylobacterium* based biofertilizers have been commercialized. For example, NewLeaf Symbiotics developed a bioproduct consisting solely of *Methylobacterium* strains to promote the growth of cotton, tomato, peanut, rice, corn, soybean, and wheat. Despite their potential, only a few commercial formulations are available. Recently, innovative technologies such as seed coatings using immobilized cells of *Methylorubrum aminovorans* in chitosan-polyvinyl alcohol nanofiber matrices have been introduced to improve cotton seed quality.

Abiotic stress and plant health

Plant health and agricultural yield are primarily limited by abiotic stress factors on a global scale. These non-living challenges, which include extremes of temperature, drought, flooding, soil salinity, and contamination from heavy metals such as cadmium, copper, and mercury, significantly disrupt fundamental physiological processes (Zhang *et al*., 2009; Hussain *et al*., 2020) [70, 20]. Specifically, heavy metal pollution can impair essential functions like photosynthesis, respiration, and nutrient assimilation. The impact of temperature is particularly deleterious. High temperatures induce photooxidation and a surge in reactive oxygen species (ROS), leading to protein denaturation and aggregation, which culminates in cell death (Fig 2.). On the other hand, low temperatures alter membrane fluidity, slow metabolic rates, and inhibit enzymatic activity, severely compromising plant growth and potentially reducing crop yields by as much as 50% (Theocharis *et al*., 2012) [65].

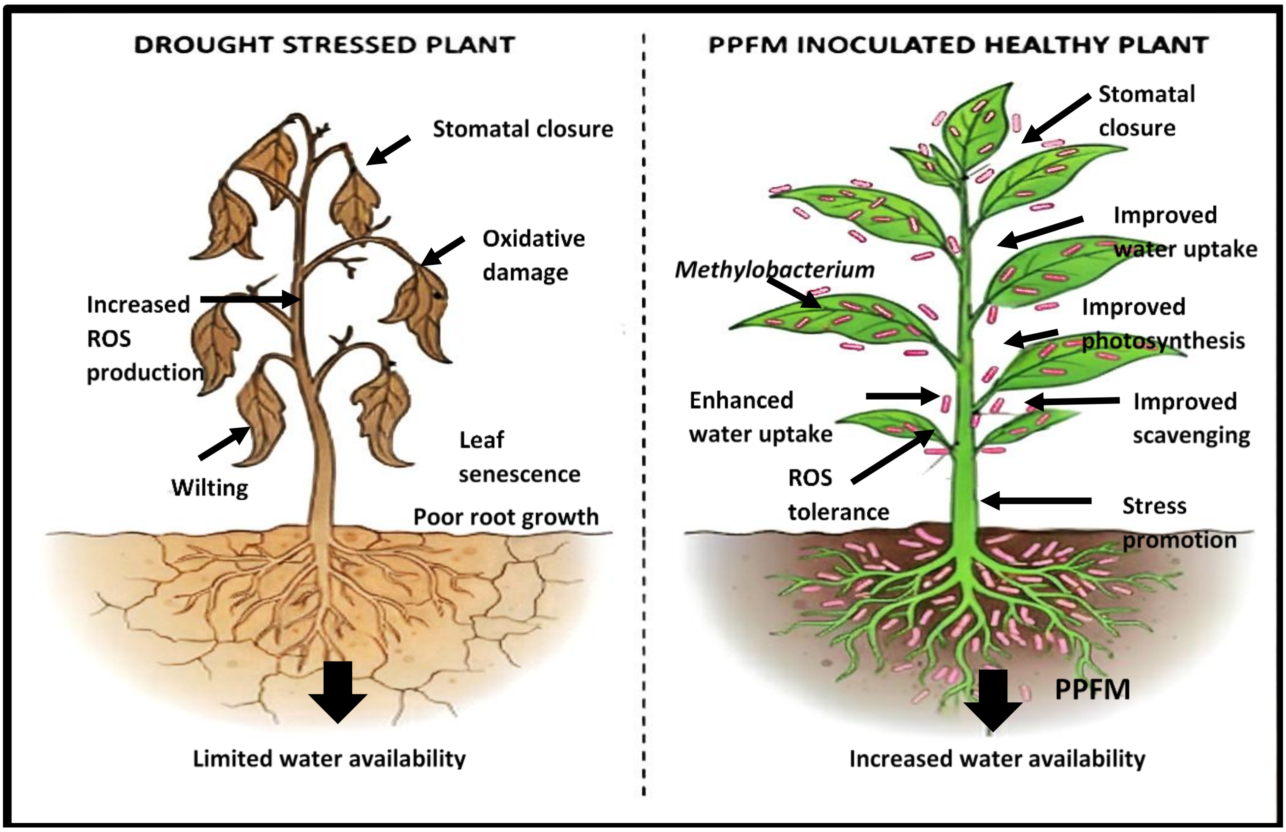

Fig 2: Drought stressed plant and PPFM inoculated plant

Salinity stress is another major factor that depletes plant immunity and hinders development by inducing osmotic stress, nutrient deficiencies, and ion toxicity. The excessive accumulation of sodium and chloride ions can be directly lethal to cells. Supporting this, research on tomato plants has shown a height reduction of approximately 15.8% under saline conditions (Han *et al*., 2016) [18]. Furthermore, solar radiation can cause direct damage to genetic material (DNA), leading to heritable abnormalities and reduced viability in subsequent generations (Cavinato *et al*., 2017) [4]. PPFMs have been demonstrated to enhance plant resilience. *Methylobacterium oryzae* can protect rice from salinity stress, while they aid tomato plants in withstanding drought (Chanratana *et al*., 2017) [5]. Similarly, the successful colonization of rhizospheric *Methylobacterium mesophilicum* has been observed in tomatoes under salinity stress and in cucumbers under drought conditions, underscoring its potential role in stress alleviation (Egamberdieva *et al*., 2015) [10].

Abiotic stress management mediated by methylotrophs

PPFMs play a crucial role in enhancing plant resilience against diverse environmental stresses, including drought, salinity, and heavy metal toxicity. This ability is largely attributed to their production of metabolites that trigger stress-resistance responses. PPFMs possess adaptive mechanisms that allow them to endure challenging conditions in the rhizosphere and soil environments. Under drought stress, they promote plant tolerance through the synthesis of osmoprotectants and antioxidants osmoprotectants maintain cellular water balance, while antioxidants mitigate reactive oxygen species (ROS) damage. In saline conditions, PPFMs contribute to plant adaptation by producing compounds such as proline and glycine betaine, which stabilize osmotic balance and prevent ionic toxicity. Moreover, certain PPFM strains can tolerate and detoxify heavy metals by sequestering and immobilizing them within their cells, thereby reducing their harmful effects on plants and soil ecosystems. These bacteria also thrive across broad temperature and pH ranges, enabling survival and function in diverse and fluctuating environments.

Drought stress

Drought stress severely impacts global crop production, forcing plants to rely on their internal metabolic mechanisms for adaptation. Water deficit reduces turgor pressure, limits cell division and expansion, and disrupts photosynthesis by lowering pigment content and altering hormonal balance and osmotic regulation (Silva *et al*., 2020) [58]. Studies indicate that plant growth-promoting regulators can partly alleviate such abiotic stress effects (Saikia *et al*., 2018; Yadav and Yadav, 2018; Filgueiras *et al*., 2020) [54, 69, 13].

Drought stress causes substantial yield losses in crops such as rice, pea, and alfalfa by reducing germination, shoot-root growth, and overall vigor (Manickavelu *et al*., 2006) [31]. Limited water availability disturbs osmotic balance, elevating reactive oxygen species and ethylene levels, which damage cellular components and impair energy metabolism (Priestley, 1986; Farooq *et al*., 2009) [49, 12]. PPFMs counteract these effects by boosting catalase activity and improving stress tolerance indices. PPFMs have been shown to enhance seed germination and mitigate drought effects through foliar applications (Sivakumar *et al*., 2017) [60]. Similarly, several methylotrophs isolated from long-stored paddy soils exhibit drought resilience (Collet *et al*., 2015) [7]. Foliar or root application of PPFMs enhances the growth of tomato and wheat under drought conditions through modulation of phytohormone synthesis. *Methylobacterium oryzae* and related species *M. mesophilicum*, *M. fujisawaense* and *M. radiotolerans* have also been documented to colonize plant tissues and enhance cytokinin levels, thereby improving plant survival under drought stress (Egamberdieva *et al*., 2015; Sathyan *et al*., 2018) [10, 55].

Salinity stress

Soil salinity is a major global constraint on agricultural productivity, affecting about one billion hectares across nearly 100 countries. In India, around 20% of irrigated land is becoming saline due to continuous irrigation with salt-rich water (Mann *et al*., 2020; Sahab *et al*., 2021) [36, 53]. Excessive soil salts induce stress in plants, suppress growth, and may lead to crop failure, making salinity a critical abiotic stress in arid and semi-arid regions (Mishra *et al*., 2016) [41]. High salinity at any growth stage especially early development impairs nutrient absorption, hinders root growth, and lowers germination (Sorty *et al*., 2016) [61].

Accumulated sodium ions in chloroplasts disrupt photosystem II and electron transport, reducing photosynthetic efficiency and causing oxidative stress through excess ROS, which triggers membrane damage and early leaf senescence (Hameed *et al*., 2021) [17]. While plants have inherent stress resistance systems, beneficial microbes enhance tolerance by inducing stress-responsive genes, antioxidants, and osmolyte accumulation (Meena *et al*., 2017; Kumar and Verma, 2018) [40, 27]. A methylotrophic actinobacterium, *Nocardioides*, isolated from fresh soybean leaves, has been shown to enhance wheat growth under saline stress (Meena *et al*., 2020) [38]. *Methlylophaga lonarensis* from Lonar Lake sediments (Antony *et al*., 2012) [2], *Methlylophaga muralis* from soda lake brine (Shmareva *et al*., 2018) [57], and *Methyloligella halotolerans* gen. nov., sp. nov. from saline habitats of the Ural region demonstrated tolerance ranges between 0.5%-2.0% and up to 16.0% NaCl (w/v). *Methylobacterium mesophilicum* isolated from wheat roots tolerated up to 6.0% NaCl and continued producing indole-3-acetic acid (IAA) under 4.0% NaCl conditions (Egamberdieva *et al*., 2015) [10].

Heavy metals stress

Heavy metals released from industrial activities represent a major threat to agriculture and human health (Glick, 2010). Common contaminants like zinc (Zn), cadmium (Cd), copper (Cu), chromium (Cr), arsenic (As), nickel (Ni), and lead (Pb) frequently accumulate in soils (Khan *et al*., 2008) [24]. Their bioaccumulation disrupts food chains and reduces crop yield. Although some plants can extract metals from polluted soils, excess concentrations impair metabolism, causing oxidative stress, DNA and cellular damage, osmotic imbalance, and declines in photosynthesis, respiration, and protein synthesis all of which hinder growth and reproduction (Fatima *et al*., 2021) [11]. Plant-microbe interactions offer a sustainable strategy for remediating metal-contaminated soils. These interactions detoxify hazardous ions through uptake, immobilization, mobilization, and biotransformation, where metals undergo chemical alteration via microbial metabolic activity (Tiwari *et al*., 2017; Afsal *et al*., 2020) [66, 11]. Among plant growth-promoting bacteria, methylotrophs show remarkable potential in mitigating heavy metal toxicity. *Methylobacterium oryzae* CBM20, isolated from rice, reduced Ni and Cd stress while promoting tomato growth (Madhaiyan *et al*., 2007) [32]. Similarly, *Methylobacterium* sp. AF-M from *Acacia farnesiana* enhanced arsenate tolerance (Alcántara-Martínez *et al*., 2018) [3], and *M. hispanicum* EM2 from mine tailing soil exhibited lead resistance up to 800 mg L^{-1} (Jeong *et al*., 2019) [21]. *M. fujisawanense* CT4 and *M. goesingense* from *Thlaspi goesingense* demonstrated tolerance to Zn, Ni, and Cd (Kunito *et al*., 1997) [28].

Importance of PPFMs in sustainable agriculture

Sustainable agriculture aims to balance food security with the responsible management of natural resources, and PPFM play a vital role in achieving this goal. By solubilizing nutrients such as phosphorus and iron, PPFM improve soil fertility and reduce reliance on synthetic fertilizers, minimizing both costs and environmental pollution. Their ability to enhance nutrient uptake and promote plant hormone production supports healthier, disease-resistant crops and decreases pesticide use. PPFM also regulate stomatal conductance, improving water-use efficiency and drought resilience key aspects of climate-adaptive farming. Additionally, they enrich rhizospheric microbial diversity, strengthen soil structure, and enhance nutrient cycling, contributing to long-term soil health. Integrating PPFM into sustainable practices not only promotes ecosystem conservation but also offers economic gains through reduced inputs and improved yields. PPFMs play a vital ecological role across diverse habitats due to their unique metabolic abilities and interactions with the environment. As active participants in the global methane cycle, they oxidize methane a potent greenhouse gas—into carbon dioxide, thereby mitigating methane emissions and contributing to climate regulation and the carbon cycle. Several PPFM strains also possess the capacity to biodegrade aromatic and methylated pollutants, transforming them into less toxic or harmless compounds. This biodegradation potential is essential for bioremediation efforts aimed at restoring contaminated environments. Additionally, certain PPFMs exhibit antagonistic effects against plant pathogens, supporting plant health and reducing the need for chemical pesticides, thus promoting eco-friendly pest management. Overall, PPFMs contribute significantly to nutrient cycling, greenhouse gas regulation, and environmental restoration, reinforcing their importance for ecosystem sustainability, agricultural productivity, and global environmental preservation.

Conclusion

Confronting the immense pressure of climate change and population growth necessitates a strategic shift away from input-intensive agriculture. This review underscores that abiotic stresses including drought, salinity, and heavy metal contamination are primary constraints on global food security. In this context, Pink Pigmented Facultative Methylotrophs (PPFMs) emerge as a powerful, sustainable bio-solution. These bacteria, native to plant surfaces, directly promote growth by producing phytohormones, fixing nitrogen, and solubilizing nutrients. Crucially, they are instrumental in building plant resilience. They alleviate abiotic stress by modulating stress ethylene, enhancing antioxidant defense, and accumulating protective osmolytes, thereby mitigating the damaging effects of drought, salinity, and toxic metals. Integrating PPFMs into agricultural practice aligns with the core goals of sustainable farming: reducing synthetic fertilizer and pesticide use, improving soil health, and enhancing water-use efficiency. Their proven role in promoting crop yield and stress tolerance, coupled with their safety and environmental benefits, positions PPFM bioinoculants as a cornerstone for developing climate-resilient and productive agricultural systems for the future.

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