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METHYLOTROPHS AS PLANT RESCUERS: MECHANISTIC STRATEGIES FOR COMBATING ABIOTIC STRESS

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ABSTRACT

Climate change and environmental degradation have intensified the occurrence of abiotic stresses such as drought, salinity, extreme temperatures, heavy metal contamination, ultraviolet (UV) radiation, and nutrient deficiencies, posing major threats to global agricultural productivity and food security. Plants exposed to these stresses experience significant physiological, biochemical, and molecular disturbances, including impaired germination, reduced photosynthetic efficiency, oxidative damage, nutrient imbalance, growth inhibition, and yield losses. In recent years, plant-associated methylotrophic bacteria have emerged as promising microbial resources for enhancing plant resilience against diverse abiotic stresses. Methylotrophs, particularly members of the genera *Methylobacterium* and *Methylorubrum*, are ubiquitous colonizers of the phyllosphere, rhizosphere, and endosphere, where they utilize plant-derived methanol and establish beneficial associations with host plants. This review comprehensively summarizes the biodiversity, ecological distribution, and functional characteristics of methylotrophic microbial communities, with special emphasis on their role in plant–microbe interactions and abiotic stress mitigation. The review discusses the detrimental effects of major abiotic stresses on plant growth, development, physiology, and productivity, and critically examines the underlying mechanisms through which methylotrophs confer stress tolerance. These mechanisms include phytohormone production, ACC deaminase activity, biological nitrogen fixation, phosphate solubilization, siderophore production, exopolysaccharide synthesis, osmotic adjustment, antioxidant enhancement, modulation of stress-responsive signaling pathways, and production of protective metabolites such as methylobamine. Overall, this review provides an integrated understanding of the ecological significance and biotechnological potential of methylotrophs in promoting climate-resilient and sustainable agricultural systems under increasingly challenging environmental conditions.

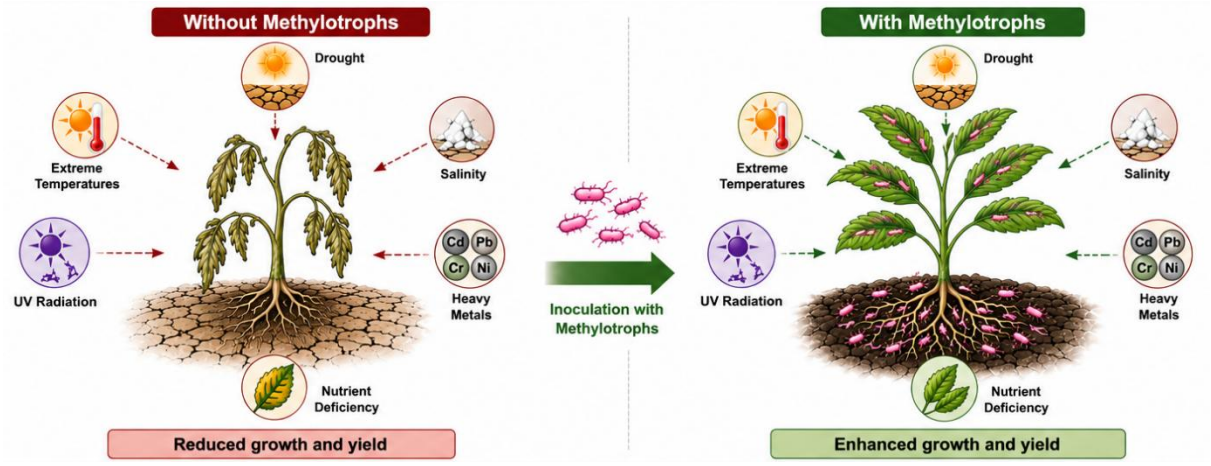

Figure 1. Comparative illustration of plant performance under multiple abiotic stresses in the absence and presence of methylotrophic bacteria

KEYWORDS: Abiotic stress, Plant–microbe interactions, Methylotrophic bacteria, Climate-resilien agriculture, Sustainable crop production, Stress mitigation mechanisms

1. INTRODUCTION

Crops have to deal with drought, salinity, extreme temperature, pest and disease incidence and nutrient deficits which are a few biotic and abiotic stressors that makes the growth and survival of crop difficult. Food security is globally

threatened by population growth and global warming. Global food production has already declined as a result of climate change (Tito et al., 2018). Still, years of usage on chemical fertilizers and pesticides (Insecticide, Herbicide, Fungicide, Nematicide) have seriously harmed the ecosystem, causing water pollution, deteriorating soil health, and changing soil nutrient balance (Aktar et al., 2009). In order to adapt to adverse stress situations, plants have evolved complex mechanisms to lessen the effects. Physiological, biochemical, and molecular alterations are among the methods that assist plants in preserving cellular homeostasis and guaranteeing survival. Utilizing plant growth-promoting bacteria (PGPB) has been a viable strategy in recent years to increase plant resilience and productivity under both normal and stressful circumstances (Vandenkoornhuyse et al., 2015). Through direct activities including nitrogen fixation, nutrient solubilisation, and phytohormone synthesis, PGPB promotes plant development. They also make an indirect contribution like production of siderophores, enzymes, and antibiotics for the inhibition of infections (Kundan et al., 2015). By controlling important physiological processes including ethylene levels, scavenging reactive oxygen species (ROS), and promoting osmoregulation, these bacteria not only improve the health of soil ecosystems but also increase plant resistance against environmental stress conditions (Ehinmitan et al., 2025; Kumar et al., 2024; Singh et al., 2022). A physiologically and ecologically diverse community of microorganisms known as methylotrophic bacteria are able to use reduced one-carbon (C1) molecules, such as methanol, methane, methylamine, and formate, as their sole form of carbon as well as energy. By converting the methane and methanol for generation of carbon dioxide and biomass, these microbes are essential to maintain the global carbon cycle (Iguchi et al., 2015). Since methanol is constantly released during pectin demethylation, which is linked to cell wall expansion and plant growth, plants are one of the main natural sources of methanol in terrestrial ecosystems (Nemecek-Marshall et al., 1995). Thus, vast colonies of methylotrophic bacteria, mostly belonging to the genera *Methylobacterium* and *Methylorubrum*, are supported by plant surfaces, especially the phyllosphere, which offers a nutrient-rich ecological niche (Vorholt, 2012). These plant-associated methylotrophs are important contributors to plant growth promotion, nutrient cycling, stress tolerance, and ecosystem functioning (Grossi et al., 2025). Methanol emitted through stomata and leaf tissues is a major factor in the interaction between plants and methylotrophs. Methylotrophic bacteria can form permanent colonies on leaf surfaces, roots, and interior tissues because methanol released by plants provides them with an exclusive carbon supply. In exchange, these bacteria produce phytohormones, improve nutrient uptake, fix nitrogen biologically, produce siderophores, and induce systemic resistance to environmental stressors, all of which increase plant fitness (Sy et al., 2001; Madhaiyan et al., 2006; Vorholt, 2012). Colonisation of *Methylobacterium extorquens* in plant tissues enhances seed germination, root elongation, chlorophyll production, and biomass accumulation, according to studies, underscoring the mutualistic nature of plant–methylotroph relationships (Omer et al., 2004). Additionally, some plant growth-promoting genes have been found in plant-associated methylotrophs that involved in auxin biosynthesis, cytokinin production, ACC deaminase activity, and stress adaptation pathways (Madhaiyan et al., 2007; Kwak et al., 2014). Exceptional ability of Methylotrophs to adapt themselves to adverse climatic conditions enhances their ability to be utilised in climate-smart agriculture. Methylotrophs are frequently subjected to temperature fluctuations, dryness, oxidative stress, and UV radiation as they are naturally found in the phyllosphere. They have effective antioxidant systems, carotenoid pigments, osmoprotectants, DNA repair mechanisms, and stress-responsive regulatory proteins like PhyR to withstand these circumstances (Gourion et al., 2008). According to recent findings, plant-associated *Methylobacterium* species create novel UV-protective compounds like methylobamine, which may have further ecological roles in shielding host plants and microbial cells from sun radiation injury (Yoshida et al., 2017). These adaptable characteristics offer important chances to use methylotrophs as microbial biostimulants in more demanding agricultural circumstances. The majority of research that is now accessible has concentrated on particular crop-microbe systems or distinct stress conditions, leading to a fragmented understanding of the underlying physiological, biochemical, molecular, and ecological mechanisms. Thus, to properly understand how methylotrophs contribute to stress tolerance across various crop species and environmental situations, a thorough synthesis of recent research is required. In addition to identifying present research gaps and potential future applications for methylotrophic bacteria in sustainable agriculture, this review attempts to critically assess the habitat features, plant–microbe interactions, physiological mechanisms, and stress mitigation strategies of these bacteria.

2. Habitat And Characteristics Of Methylotrophs

In terrestrial, marine, and atmospheric habitats where reduced one-carbon (C1) compounds are naturally formed, methylotrophic bacteria are widely found. Species from the genera *Methylobacterium*, *Methylorubrum*, *Methylophilus*, *Methylobacillus*, *Hyphomicrobium*, *Methylibium*, and many methanotrophic genera make up the majority of plant-associated methylotrophs (Vorholt, 2012; Iguchi et al., 2015).

The continual supply of methanol from plant metabolism, organic matter decomposition, methane oxidation processes, and human activity are all responsible for their extensive diffusion. Plant surfaces are among the best environments for methylotrophic colonisation because they release significant amounts of methanol during cell wall formation and development (Nemecek-Marshall et al., 1995; Galbally and Kirstine, 2002). Methylotrophic bacteria are characterised by their capacity to oxidise methanol and other C1 compounds via specific metabolic pathways. Methanol dehydrogenase enzymes, which are encoded by genes like mxaF and xoxF, catalyse the oxidation of methanol (Chistoserdova and Lidstrom, 2011).

Depending on the metabolic ability of the species, the resultant formaldehyde is then absorbed by the serine cycle, the Calvin–Benson–Bassham cycle, or the ribulose monophosphate pathway (RuMP) (Vorholt, 2012).

Extreme environmental circumstances such as UV radiation, drought, temperature variations, osmotic stress, oxidative stress, and nutrient constraint are frequently encountered by plant-associated methylotrophs. They have extremely

effective stress-adaptation systems that include antioxidant enzymes, DNA repair proteins, carotenoid pigments, osmoprotectants, and global stress regulators like PhyR in order to withstand these difficulties (Gourion et al., 2009).

According to experimental data, PhyR is essential for successful phyllosphere colonisation and controls several stress-response pathways. The ecological significance of PhyR is highlighted by the decreased survival of mutants lacking it under UV radiation, osmotic stress, and oxidative stress (Iguchi et al., 2015). One of the most widely studied environments for methylotrophic bacteria is the phyllosphere, which is defined as the aerial surfaces of plants. Methanol is continuously released through stomata as a result of pectin methylesterase activity, releasing methanol from cell wall pectin during leaf expansion (Nemecek-Marshall et al., 1995).

Methylotrophic development is significantly encouraged by the selective niche created by methanol concentrations close to leaf surfaces. As a result, *Methylobacterium* species can make up as much as 70–80% of culturable bacterial populations on some plant species and often dominate phyllosphere microbial communities (Knief et al., 2012).

Plant genotype, environmental factors, leaf age, geographic location, and seasonal variation all affect the quantity and makeup of methylotrophic communities (Iguchi et al., 2015).

By controlling the release of methanol and other surface chemicals, host plants actively mould these microbial populations, creating species-specific microbiomes. Many investigations have documented the presence of methylotrophs in the rhizosphere and endosphere of a variety of crops, including rice, maize, wheat, soybean, sugarcane, tomato, and Arabidopsis, despite the fact that they are most commonly recognised as phyllosphere dwellers (Madhaiyan et al., 2006; Omer et al., 2004).

Methanol, methylated substances, amino acids, and organic acids that promote methylotrophic development are found in root exudates. Numerous organisms can establish endophytic populations inside plant tissues without producing indications of illness (Sy et al., 2005). Methylotrophs' ability to produce protective secondary metabolites is a key factor in their ecological survival. From *Methylobacterium* sp. strain W-213, Kamo et al. (2018) discovered a novel UVA-absorbing substance known as methylobamine. Methylobamine showed robust UVA absorption and remained stable after extended radiation exposure. These substances probably lessen oxidative stress in the surrounding microenvironment while shielding methylotrophic cells from photodamage. Furthermore, a lot of methylotrophs produce antioxidants, carotenoids, and exopolysaccharides that improve survival in stressful environments (Kamo et al., 2018; Vorholt, 2012).

Table 1. Ecological Distribution, Dominant Taxa and Functional Roles of Plant-Associated Methylotrophs

Habitat/Niche	Dominant Genera	Methyotroph Species	Major Carbon Source	Ecological Role	References
Leaf phyllosphere	*Methylobacterium*, *Methylorubrum*	*M. extorquens*, *M. radiotolerans*, *M. mesophilicum*, *M. phyllosphaerae*, *M. gnaphalii*	Methanol released through stomata	Plant growth promotion, UV protection, hormone production	Iguchi et al. (2015); Knief et al. (2010); Madhaiyan et al. (2009)
Leaf epiphytes of crop plants	*Methylobacterium*	*M. populi*, *M. thiocyanatum*, *M. suomiense*, *M. aminovorans*, *M. fujisawaense*	Methanol and methylamines	Colonization of cotton, maize, soybean, sunflower and mentha leaves	Raja et al. (2008); Balachandar et al. (2008)
Rice stem endosphere	*Methylobacterium*	*M. oryzae*	Internal plant metabolites	Endophytic colonization, cytokinin production, drought mitigation	Madhaiyan et al. (2007)
Rice seed endosphere	*Methylobacterium*	*M. indicum*	Seed-associated metabolites	Seed colonization and vertical transmission	Chaudhry et al. (2016)
Root nodules	*Methylobacterium*	*M. nodulans*	Plant-derived carbon compounds	Symbiotic nitrogen fixation	Jourand et al. (2004)
Rhizosphere	*Methylobacterium*, *Methylorubrum*, *Hyphomicrobium*	*M. populi*, *M. extorquens*	Root exudates and methanol	Nutrient acquisition, phytohormone production	Madhaiyan et al. (2006); Grossi et al. (2020)
Sugarcane microbiome	*Methylobacterium*	*M. radiotolerans*	Methanol from plant tissues	Growth promotion and niche specialization	Andrade et al. (2018)
Aquatic plants	Methanotrophs (*Methylomonas*, *Methylosinus*,	Various methanotrophs	Methane transported through aquatic	Methane oxidation and greenhouse gas	Iguchi et al. (2015)

	Methylocystis)		plants	mitigation	
Airborne environments	*Methylorubrum*	*M. extorquens*	Atmospheric methanol	Atmospheric C1 cycling	Green and Ardley (2018)
Soil	*Methylobacterium*, *Methylorubrum*	*M. populi*, *M. suomiense*	Methanol, methylamine, formate	Carbon cycling and rhizosphere colonization	Van Aken et al. (2004); Doronina et al. (2002)
Lichens	*Methylobacterium*	*M. planium*	C1 compounds from symbiotic metabolism	Adaptation to extreme habitats	Jiang et al. (2020)
Liverwort thalli	*Methylobacterium*	*M. marchantiae*	Plant-derived methanol	Early land-plant association	Schauer et al. (2011)

3. Plant–Microbe Interaction

Methylotrophic bacteria that are connected with plants have dynamic, highly specialised relationships with their host. Methylotrophs are specially designed to utilise the methanol generated from plant tissues during pectin demethylation linked to cell wall expansion and leaf growth, in contrast to many rhizospheric microorganisms that mainly rely on root exudates (Nemecek-Marshall et al., 1995; Vorholt, 2012).

A selective ecological niche is created for methylotrophic bacteria, especially species of *Methylobacterium* and *Methylorubrum*, when methanol is continuously released through stomata and builds up in the phyllosphere (Iguchi et al., 2015). A mutualistic relationship in which plants supply carbon resources and methylotrophs support plant development, nutrient uptake, and stress tolerance is based on this methanol-mediated interaction. These interactions are now understood to be an essential part of the idea of a plant holobiont, in which plants and the microbiota they are connected with work together as a single biological entity (Vandenkoornhuyse et al., 2015). Methylotrophic bacteria start the colonisation process by migrating toward nutrient-rich microhabitats after identifying chemical signals that are released by plant tissues. Bacterial attachment to the leaf surface, microcolony formation, and the development of stable populations inside stomatal chambers, epidermal grooves, trichomes, and internal tissues are all necessary for successful colonization (Knief et al., 2010; Vorholt, 2012). *Methylobacterium extorquens* effectively colonises both epiphytic and endophytic niches, enabling close interactions with host metabolism, according to studies (Sy et al., 2005). Numerous genes linked to adhesion, biofilm formation, exopolysaccharide synthesis, and stress tolerance that promote persistence inside plant tissues have been found through genomic studies (Kwak et al., 2014). Compared to many other bacteria that promote plant growth, methylotrophs have a major advantage in that they can occupy both internal and exterior plant compartments, which guarantees extended contact with host physiological processes. Phytohormone synthesis is one of the most significant features of interactions between plants and methylotrophs. Indole-3-acetic acid (IAA), cytokinins, gibberellins, and other growth regulators that significantly affect plant growth, have been demonstrated to be produced by a number of *Methylobacterium* species (Ivanova et al., 2001; Koenig et al., 2002). IAA improves water and nutrient uptake under stressful circumstances by promoting root elongation, lateral root creation, and root hair growth. During environmental stress, cytokinins control cell division, postpone leaf senescence, and preserve photosynthetic activity. In crops inoculated with plant-associated methylotrophs, experimental inoculation studies have shown notable benefits in seed germination, shoot development, chlorophyll content, and biomass accumulation (Madhaiyan et al., 2006; Omer et al., 2004). These findings suggest that phytohormones produced by methylotrophs are essential for regulating plant development and adaptability. Another crucial aspect of interactions between plants and methylotrophs is nitrogen uptake. Numerous methylotrophic organisms give their host plants biologically fixed nitrogen because their genomes contain nitrogenase genes (Sy et al., 2001). This capacity is especially crucial in situations when crop yield is limited by nitrogen availability. Methylotrophs enhance nutrient intake by phosphate solubilisation, siderophore synthesis, and root growth stimulation in addition to biological nitrogen fixation (Madhaiyan et al., 2007). Increased biomass output and increased resistance to various abiotic stressors, such as salt and drought, where nutrient transport is frequently compromised, are both facilitated by enhanced nutrient uptake. According to recent research, methylotrophs may potentially affect plant immunological and stress-signaling networks. Systemic reactions including salicylic acid, jasmonic acid, ethylene, and abscisic acid signalling pathways are triggered by methylotrophic bacterial colonisation (Grossi et al., 2020). Induced systemic tolerance (IST) is the term used to describe this process, which prepares plants for quicker responses when subjected to environmental stressors. Methylotroph-treated plants show better osmotic adjustment, less membrane damage, and higher antioxidant enzyme activities during drought and salt stress as compared to uninoculated controls (Tani et al., 2015; Egamberdieva et al., 2017). As a result, methylotrophs regulate plant stress physiology in addition to providing nutrients (Figure 2).

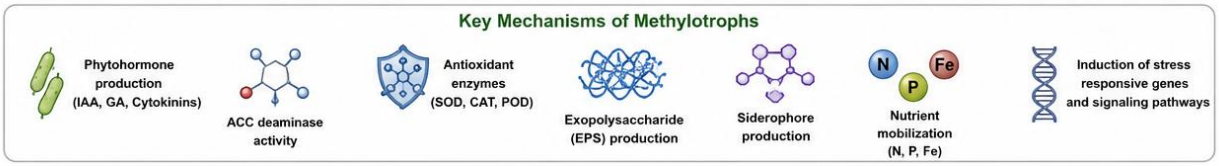

Figure 2. Schematic representation of the principal mechanisms underlying methylotroph-mediated abiotic stress mitigation in plants.

4. Effect Of Abiotic Stress On Plant

Crop growth, development, and yield are significantly reduced by abiotic stressors, which are one of the biggest factors that are limiting agricultural output globally. Environmental stressors that interfere with basic physiological and biochemical processes necessary for plant life include drought, salt, extreme - temperatures, heavy metal pollution, nutritional shortages, UV radiation, and oxidative stress (Zhu, 2016). According to current estimates, abiotic stressors are responsible for over 50% of significant agricultural production decrease that occur worldwide, and climate change is predicted to exacerbate these limitations in the upcoming decades (Sehgal et al., 2018) To fully appreciate the importance of methylotroph-mediated stress reduction techniques, one must comprehend how these pressures impact plants. According to Farooq et al. (2009), drought stress mainly restricts the amount of water available, which lowers photosynthetic activity, stomatal conductance, cell growth, and seed germination. When there is a water shortage, the relative water content of leaves decreases and reactive oxygen species (ROS) build up, that cause potential oxidative damage to membranes, proteins, and nucleic acids. Long-term drought stress often results in poor root development, decreased biomass accumulation, chlorophyll degradation, and a notable decrease in yield (Boyer, 1982; Farooq et al., 2009). About 20% of irrigated agricultural land globally is affected by salinity stress, which is growing as a result of inadequate irrigation techniques and soil degradation brought on by climate change (Munns and Tester, 2008). Osmotic stress, nutrient uptake inhibition, and ionic balance disruption are all brought on by excessive sodium and chloride buildup. High salt concentrations cause ROS buildup while interfering with membrane stability, protein synthesis, and photosynthesis. Across many crop species, salinity frequently causes delayed germination, decreased root and shoot development, decreased chlorophyll content, and significant production losses (Zhu, 2001; Munns and Tester, 2008). Plant production is also impacted by variations in temperature. Protein denaturation, membrane instability, enzyme inactivation, and pollen sterility are all accelerated by high temperatures, which eventually lowers grain production and successful reproduction (Bita and Gerats, 2013). On the other hand, low-temperature stress increases oxidative damage, limits membrane fluidity, and hinders photosynthetic electron transfer (Theocharis et al., 2012). Reduced germination rates, poor seedling establishment, poorer biomass output, and degraded crop quality are all consequences of heat and cold stress. An increasing environmental concern is heavy metal stress brought on by pollution with cadmium, chromium, lead, arsenic, and mercury. According to Shahid et al. (2014), heavy metals cause cellular damage, interfere with enzyme activity, interfere with nutrition intake, and produce ROS. Chlorosis, limited root growth, decreased photosynthetic efficiency, and decreased yields are frequently the results of exposure. Additionally, edible plant tissues may get contaminated with heavy metals, endangering human health and food safety. The overproduction of reactive oxygen species, such as singlet oxygen, hydrogen peroxide, superoxide radicals, and hydroxyl radicals, is a characteristic shared by all abiotic stressors (Mittler, 2002). At low concentrations, ROS serve as signalling molecules, but when they build up too much, they can lead to lipid peroxidation, DNA damage, protein oxidation, and metabolic problems. Thus, a key factor in determining a plant's ability to withstand stress is its antioxidant defence mechanisms.

Table 2. Effect of Abiotic Stress on Plant Growth and Yield

Abiotic Stress	Germination	Growth	Yield	Major Physiological Effect	References
Drought	Reduced	Stunted	Severe reduction	Water deficit, ROS	Boyer (1982); Farooq et al. (2009)
Salinity	Delayed	Reduced	Severe reduction	Ionic toxicity	Munns & Tester (2008); Zhu (2001)
Heat	Poor establishment	Reduced biomass	Reduced fertility	Protein denaturation	Bita & Gerats (2013)
Cold	Delayed germination	Reduced growth	Yield loss	Membrane damage	Theocharis et al. (2012)
Heavy metals	Reduced	Chlorosis	Reduced yield	Oxidative stress	Shahid et al. (2014)
UV stress	Poor seedling vigor	DNA damage	Quality reduction	ROS accumulation	Hideg et al. (2013); Kamo et al. (2018)

5.Mechanisms Of Methylotrophs In Mitigating Abiotic Stress

5.1. Drought Stress Mitigation by Methylotrophs

One of the most severe environmental restrictions impacting agricultural output globally is drought stress. Many physiological and biochemical processes, including as seed germination, cell growth, nutrient transport, photosynthesis, and reproductive development, are disrupted by water shortage, which eventually results in significant production losses (Farooq et al., 2009). Reduced soil moisture during drought conditions reduces plant water potential, which leads to stomatal closure, reduced absorption of CO2, degradation of chlorophyll, and decreased photosynthetic efficiency (Boyer, 1982). Additionally, chronic water deficiency causes an overabundance of reactive oxygen species (ROS), including hydrogen peroxide, superoxide radicals, and hydroxyl radicals, which harm proteins, lipids, nucleic acids, and cellular membranes (Mittler, 2002). Methylotrophic bacteria linked with plants have shown promise as biological agents to increase crop drought resistance. Because they live on aerial plant surfaces where desiccation is frequent, members of the genera *Methylobacterium* and *Methylorubrum* are naturally adapted to varying moisture levels (Vorholt, 2012;

Iguchi et al., 2015). Methylotrophic colonisation is often facilitated by drought stress, which enhances cell wall turnover and methanol emission from plant tissues (Nemecek-Marshall et al., 1995). Once developed, methylotrophs engage in tight interactions with their host plants, triggering a variety of physiological and molecular processes that improve drought resistance. The synthesis of phytohormones, especially indole-3-acetic acid (IAA), is one of the most significant ways that methylotrophs reduce drought stress. IAA may be produced from tryptophan-dependent pathways by a variety of *Methylobacterium* species associated with plants (Ivanova et al., 2001; Omer et al., 2004). IAA increases the absorptive surface area for water absorption by promoting root elongation, lateral root production, and root hair growth. Plants inoculated with IAA-producing methylotrophs frequently have larger, deeper root systems that may draw water from deeper soil levels during dry spells. Following methylotrophic bacterial inoculation, studies on rice, wheat, and tomatoes have consistently demonstrated increased root biomass and greater drought tolerance (Madhaiyan et al., 2006; Grossi et al., 2020). Additionally, methylotrophic bacteria alter cytokinin homeostasis, which is essential for postponing drought-induced senescence. According to Koenig et al. (2002), cytokinins control nutrient mobilisation, cell division, chloroplast development, and photosynthetic apparatus maintenance. Endogenous cytokinin concentrations frequently drop during drought stress, hastening leaf senescence and decreasing photosynthetic activity. According to reports, *Methylobacterium* species generate cytokinin-like substances that counteract this decrease and support leaf function in stressful situations (Koenig et al., 2002; Madhaiyan et al., 2007). As a result, compared to uninoculated controls, inoculated plants often show increased biomass formation, delayed yellowing, enhanced stomatal regulation, and higher chlorophyll content. Since carbon uptake directly affects crop output, maintaining photosynthetic efficiency under drought is very crucial.

The synthesis of exopolysaccharides (EPS) is another important mechanism for mitigating drought. Many bacteria that are linked with plants release high-molecular-weight extracellular polymers, or EPS. According to Sandhya et al. (2009), these substances enhance soil aggregation, boost water-holding capacity, and provide protective microenvironments surrounding microbial cells and roots. EPS-producing methylotrophs improve soil moisture retention and slow soil water loss in the rhizosphere. Additionally, EPS matrices aid in the production of biofilms, which enhance microbial survival under desiccation stress and encourage persistent root colonisation. Numerous studies have shown that by preserving rhizosphere hydration and enhancing root–soil interaction, EPS-producing plant growth-promoting bacteria greatly increase plant drought tolerance (Vurukonda et al., 2016). Another essential element of drought tolerance is osmotic adjustment. A lack of water lowers cellular turgor pressure and interferes with regular metabolic functions. Plants build up suitable solutes such proline, glycine betaine, trehalose, and soluble sugars to offset these effects (Ashraf and Foolad, 2007). By directly generating osmoprotective chemicals or by promoting their production in host plants, methylotrophic bacteria can intensify this reaction. Under drought circumstances, plants inoculated with plant growth-promoting methylotrophs have been shown to accumulate more proline and other osmolytes (Madhaiyan et al., 2006; Tani et al., 2015). During extended periods of water stress, these substances stabilise proteins, shield cellular membranes, sustain enzyme function, and keep cells hydrated. Drought stress is characterised by excessive ROS formation, which is frequently a primary cause of cellular damage. Methylotrophic bacteria help plants withstand drought by strengthening their antioxidant defence mechanisms. Superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX) activities are often elevated in inoculated plants, leading to more effective ROS detoxification (Mittler, 2002; Hasanuzzaman et al., 2020). Improved antioxidant capacity protects photosynthetic components from oxidative damage, maintains membrane integrity, and lowers lipid peroxidation. As a result, as compared to uninoculated plants under drought stress, methylotroph-treated plants frequently show lower quantities of malondialdehyde (MDA) and less oxidative damage. Additionally, recent research indicates that methylotrophic bacteria interact with ethylene, stress-related transcription factors, and abscisic acid (ABA) to take part in drought-responsive signalling networks. ACC deaminase activity in some methylotrophs reduces stress-induced ethylene levels, a hormone that prevents root development under extreme stress situations (Glick, 2014). Methylotrophs support root growth and enhance plant drought adaptability by lowering ethylene buildup. The intricacy of plant–microbe interactions during drought adaptation is highlighted by advances in transcriptomic and metabolomic analyses, which show that methylotroph inoculation can change the expression of genes involved in osmoprotection, antioxidant metabolism, and hormone signalling pathways (Vurukonda et al., 2016).

5.2. Salinity Stress Mitigation by Methylotrophs

Salinity affects around 800 million hectares of land worldwide and is one of the most harmful abiotic pressures limiting agricultural output (Munns and Tester, 2008). High concentrations of soluble salts, especially Na^+ and Cl^- ions, cause osmotic stress and lower soil water potential, which makes it harder for plants to absorb water. Excessive buildup of harmful ions in plant tissues as salinity increases damages cellular membranes, interferes with photosynthesis, upsets nutrient balance, and stunts plant growth and development (Munns and Tester, 2008). Additionally, salt stress increases the production of reactive oxygen species (ROS), such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals, which oxidatively damage proteins, lipids, nucleic acids, and chloroplast structures (Hasanuzzaman et al., 2020). It is becoming more widely acknowledged that plant-associated methylotrophs, especially species of *Methylobacterium* and *Methylorubrum*, are advantageous microbial partners that can enhance plant performance under salt stress (Kumar et al., 2019). The synthesis of phytohormones is one of the main processes. Under osmotically stressed circumstances, a number of methylotrophic species produce cytokinins and indole-3-acetic acid (IAA), which increase root surface area and promote root growth, improving water and nutrient uptake (Madhaiyan et al., 2006; Kumar et al., 2019). The control of stress-induced ethylene synthesis is another significant way that methylotrophs reduce salt stress. Excessive amounts of ethylene, a stress hormone that stunts root growth, speeds up senescence, and slows overall plant development, are

frequently accumulated by plants in saltwater environments (Glick, 2014). The immediate precursor of ethylene, 1-aminocyclopropane-1-carboxylate (ACC), is broken down by ACC deaminase activity, which is present in certain methylotroph. Methylotrophs support root elongation, enhance nutrient uptake, and preserve plant development under salt stress situations by lowering ethylene buildup (Kumar et al., 2019).

Methylotroph-associated plants often show increased activities of antioxidant enzymes such superoxide dismutase (SOD), catalase (CAT), and peroxidases, according to Kumar et al. (2019). By effectively detoxifying ROS and lowering membrane lipid peroxidation, these enzymes protect cellular integrity in saline environments. Increased biomass accumulation, higher chlorophyll retention, and increased photosynthetic efficiency are all important factors that determine stress tolerance and are all influenced by enhanced antioxidant protection (Hasanuzzaman et al., 2020).

Another significant adaptive characteristic of methylotrophs under salinity stress is the production of exopolysaccharides (EPS), which can enhance soil aggregation, increase water-holding capacity, and bind excess sodium ions in the rhizosphere (Kumar et al., 2019). Hormonal regulation, ACC deaminase activity, antioxidant enhancement, osmolyte accumulation, and exopolysaccharide production all work together to produce methylotroph-mediated salinity tolerance (Kumar et al., 2019; Iguchi et al., 2015).

5.3. Mitigation of Extreme Temperature Stress by Methylotrophs

Deviations from the optimum temperature range, whether in the form of excessive heat or chilling/freezing temperatures, severely affect plant physiological processes and frequently result in substantial reductions in crop yield (Bita and Gerats, 2013). Heat stress causes membrane destabilization, protein denaturation, enzyme inactivation, and disruption of photosynthetic machinery, particularly photosystem II, thereby reducing carbon assimilation and biomass production (Bita and Gerats, 2013). In contrast, low-temperature stress decreases membrane fluidity, inhibits nutrient transport, impairs enzymatic reactions, and causes cellular dehydration due to extracellular ice formation (Theocharis et al., 2012). Methylotrophic bacteria have emerged as promising microbial partners capable of enhancing plant resilience under temperature extremes through multiple physiological and biochemical mechanisms. Plant-associated methylotrophs, particularly species belonging to the genera *Methylobacterium* and *Methylorubrum*, are known to produce phytohormones such as cytokinins and indole-3-acetic acid (IAA), which play crucial roles in maintaining plant growth under unfavorable environmental conditions (Madhaiyan et al., 2006; Kumar et al., 2019). Cytokinins synthesized by methylotrophs delay chlorophyll degradation and stress-induced senescence, thereby preserving photosynthetic capacity during heat stress (Kumar et al., 2019). One of the major consequences of temperature stress is oxidative damage resulting from uncontrolled ROS accumulation. Under both high and low temperature conditions, electron transport chains in chloroplasts and mitochondria become disrupted, leading to increased production of superoxide radicals and hydrogen peroxide (Theocharis et al., 2012). Methylotroph-associated plants frequently exhibit elevated activities of antioxidant enzymes, which efficiently detoxify ROS and reduce lipid peroxidation (Kumar et al., 2019). Cold stress additionally causes osmotic imbalance and membrane rigidification, which compromise cellular functionality and increase susceptibility to freezing injury. Methylotrophs contribute to cold tolerance by stimulating the accumulation of compatible solutes, including proline, trehalose, and soluble sugars, which stabilize proteins and cellular membranes during dehydration stress (Kumar et al., 2019). These osmolytes function as cryoprotectants, reducing cellular damage and improving seedling establishment under chilling conditions. Recent molecular studies further suggest that methylotrophs influence the expression of stress-responsive genes associated with heat shock proteins, antioxidant metabolism, and hormonal signaling pathways (Grossi et al., 2020). Such regulation strengthens the plant's intrinsic defense network and enables faster adaptation to fluctuating temperatures.

5.4. Heavy Metal, UV Radiation & Nutrient Deficiency Stress Mitigation by Methylotrophs

Heavy metal contamination has become a major environmental concern due to increasing industrialization, mining activities, excessive fertilizer application, and wastewater irrigation practices. Toxic metals such as cadmium (Cd), lead (Pb), chromium (Cr), mercury (Hg), arsenic (As), and nickel (Ni) accumulate in agricultural soils and adversely affect plant growth and productivity (Shahid et al., 2014). Heavy metal stress disrupts membrane integrity, inhibits enzyme activity, impairs nutrient uptake, damages photosynthetic systems, and induces severe oxidative stress through excessive ROS generation. Methylotrophic bacteria possess several adaptive characteristics that enable them to survive in metal-contaminated environments and simultaneously protect plants from metal toxicity. Many species of *Methylobacterium* exhibit intrinsic tolerance to heavy metals and can colonize contaminated rhizospheres, phyllospheres, and endospheres (Kumar et al., 2019). One of the primary mechanisms involved in heavy metal mitigation is biosorption, whereby metal ions bind to negatively charged functional groups present on bacterial cell surfaces. This process reduces metal bioavailability and limits the quantity of toxic ions entering plant tissues (Shahid et al., 2014). Methylotroph-derived EPS can chelate heavy metal ions and immobilize them within the rhizosphere, thereby reducing their mobility and toxicity (Kumar et al., 2019). Such immobilization creates a protective microenvironment around plant roots and minimizes the adverse effects of metal stress on nutrient uptake and root development. Heavy metal toxicity is strongly associated with oxidative stress. Metal ions stimulate the production of ROS, resulting in lipid peroxidation, protein oxidation, and DNA damage (Shahid et al., 2014). Methylotroph-associated plants frequently exhibit enhanced antioxidant defense systems characterized by increased activities of antioxidant enzymes (Kumar et al., 2019).

Ultraviolet radiation represents an important environmental stress factor affecting plant growth and productivity, particularly under conditions of ozone depletion and increasing solar exposure. UV-B radiation (280–315 nm) is especially harmful because it directly damages DNA, proteins, chloroplast structures, and cellular membranes while simultaneously enhancing ROS generation (Hideg et al., 2013). The phyllosphere, which serves as the primary habitat

for many plant-associated methylotrophs, is continuously exposed to intense solar radiation, desiccation, and fluctuating temperatures (Iguchi et al., 2015). Consequently, methylotrophs have evolved unique adaptive mechanisms that enable survival under these harsh environmental conditions. Among these adaptations, the discovery of methylobamine, a UV-absorbing compound produced by *Methylobacterium* sp. strain W-213, represents a significant breakthrough in understanding microbial contributions to UV stress tolerance (Kamo et al., 2018). Beyond direct UV absorption, methylotrophs also contribute to radiation tolerance through antioxidant-mediated protection. Exposure to UV radiation promotes excessive ROS accumulation, leading to oxidative damage of cellular components (Hideg et al., 2013). Methylotroph-associated plants frequently exhibit enhanced antioxidant enzyme activities, which reduce ROS accumulation and maintain cellular integrity (Kumar et al., 2019).

Deficiencies of essential nutrients such as nitrogen, phosphorus, iron, potassium, and micronutrients disrupt photosynthesis, protein synthesis, enzyme activity, and metabolic regulation, ultimately reducing plant growth and yield. Nutrient-starved plants frequently exhibit chlorosis, reduced root development, impaired biomass accumulation, and poor reproductive performance. Methylotrophic bacteria play a significant role in alleviating nutrient deficiency stress through multiple plant growth-promoting activities. One of the most important mechanisms involves biological nitrogen fixation. Certain methylotrophs, including *Methylobacterium nodulans*, possess nitrogen-fixing capabilities and can supply plants with biologically available nitrogen under nutrient-limited conditions (Jourand et al., 2004). This function is particularly important in low-input agricultural systems where nitrogen availability frequently limits productivity. In addition to nitrogen fixation, many methylotrophs contribute to phosphorus nutrition through phosphate solubilization. Insoluble phosphate compounds present in soil are converted into plant-accessible forms through the release of organic acids and other metabolites. Improved phosphorus availability enhances root growth, energy metabolism, and overall plant development. Similarly, siderophore production by methylotrophs increases iron availability by chelating ferric ions and facilitating their uptake by plant roots (Kumar et al., 2019). Phytohormone production represents another critical mechanism through which methylotrophs alleviate nutrient stress. Indole-3-acetic acid stimulates root proliferation and increases root surface area, enabling plants to explore larger soil volumes and acquire nutrients more efficiently (Madhaiyan et al., 2006). Cytokinin production further supports nutrient utilization by maintaining photosynthetic activity and delaying senescence under nutrient-deficient conditions (Iguchi et al., 2015).

Table 3. Mechanisms of Methylotroph-Mediated Abiotic Stress Mitigation in Plants

Abiotic Stress	Methylotroph Genus / Species	Plant Host	Mechanism of Action	Physiological Response in Plant	References
Drought	*Methylobacterium oryzae*	Rice (Oryza sativa)	IAA and cytokinin production; stimulation of root growth	Increased root length, improved water uptake, delayed senescence	Madhaiyan et al. (2007); Kumar et al. (2019)
Drought	*Methylobacterium extorquens*	Soybean, tobacco	Enhancement of antioxidant enzymes and osmolyte accumulation	Reduced ROS damage and improved osmotic adjustment	Sy et al. (2005); Kumar et al. (2019)
Drought	*Methylobacterium mesophilicum*	Maize	Root stimulation and hormone production	Enhanced nutrient and water acquisition	Omer et al. (2004)
Salinity	*Methylorubrum extorquens*	Soybean	ACC deaminase activity and hormonal modulation	Reduced stress ethylene levels	Glick (2014); Kumar et al. (2019)
Salinity	*Methylobacterium* spp.	Tomato	EPS production and ion buffering	Reduced Na^+ toxicity and improved rhizosphere conditions	Kumar et al. (2019)
Salinity	*Methylobacterium* radiotolerans	Rice	Antioxidant enhancement and chlorophyll protection	Maintenance of photosynthetic activity	Kumar et al. (2019)
Heat Stress	*Methylobacterium* spp.	Multiple crops	Cytokinin production and antioxidant activation	Delayed senescence and reduced oxidative damage	Kumar et al. (2019); Grossi et al. (2020)
Heat Stress	*Methylorubrum* spp.	Crop phyllosphere	Maintenance of photosynthetic machinery	Reduced membrane damage and chlorophyll degradation	Kumar et al. (2019)
Cold Stress	*Methylobacterium* spp.	Cereals and vegetables	Induction of osmolytes (proline, soluble sugars)	Membrane stabilization and cryoprotection	Kumar et al. (2019)
Cold Stress	*Methylobacterium* spp.	Multiple crops	Antioxidant activation and stress-responsive signaling	Reduced lipid peroxidation	Kumar et al. (2019); Grossi et al. (2020)
Heavy	Metal-tolerant	Mangrove	EPS-mediated	Reduced oxidative	Kumar et al.

Metal Stress	*Methylobacterium* isolates	plants	immobilization of heavy metals	stress and membrane injury	(2019)
Heavy Metal Stress	*Methylobacterium* spp.	Mustard (Brassica juncea)	Antioxidant enzyme activation	Protection against ROS-induced cellular damage	Shahid et al. (2014)
UV Radiation	*Methylobacterium* sp. W-213	Phyllosphere-associated plants	Production of methylobamine (UV-absorbing metabolite)	Reduced UV-induced oxidative damage	Kamo et al. (2018)
UV Radiation	*Methylobacterium radiotolerans*	Leaf surfaces	Pigment production and antioxidant activity	Protection from photooxidative stress	Iguchi et al. (2015); Kumar et al. (2019)
Nutrient Deficiency	*Methylobacterium nodulans*	Legumes	Biological nitrogen fixation	Increased N availability	Jourand et al. (2004); Kumar et al. (2019)
Nutrient Deficiency	*Methylobacterium* spp.	Rice, wheat, maize	Phosphate solubilization	Improved phosphorus uptake	Kumar et al. (2019)
Nutrient Deficiency	*Methylobacterium* spp.	Multiple crops	IAA-mediated root proliferation, Siderophore production	Greater soil exploration capacity, Improved iron acquisition	Iguchi et al. (2015); Kumar et al. (2019)

6. CONCLUSION

Methylotrophic bacteria have emerged as a unique and highly promising group of plant-associated microorganisms capable of enhancing crop performance under adverse environmental conditions. Their ecological association with plants is primarily driven by the utilization of methanol released from plant tissues, enabling the establishment of stable populations within the phyllosphere, rhizosphere, and endosphere. Beyond their ecological significance, methylotrophs contribute directly to plant growth and stress adaptation through multiple mechanisms, including phytohormone production, biological nitrogen fixation, phosphate solubilization, siderophore production, antioxidant activation, exopolysaccharide synthesis, osmotic adjustment, and regulation of stress-responsive signaling pathways. Evidence accumulated over the last two decades demonstrates that methylotrophs can mitigate the detrimental effects of drought, salinity, heat, cold, heavy metals, ultraviolet radiation, and nutrient limitations through diverse physiological, biochemical, and molecular mechanisms. By enhancing root development, maintaining photosynthetic efficiency, improving antioxidant defenses, reducing oxidative damage, and promoting nutrient acquisition, these microorganisms significantly improve plant resilience and productivity under stress conditions. The discovery of novel metabolites such as methylobamine further highlights the remarkable adaptive potential of methylotrophs and suggests that additional stress-protective compounds remain to be identified. Despite these advances, significant gaps remain in our understanding of methylotroph-mediated stress tolerance, particularly regarding molecular signaling, plant genotype specificity, microbiome interactions, and long-term field performance. Addressing these challenges through integrated physiological, molecular, and ecological studies will be essential for translating laboratory findings into practical agricultural applications. The integration of omics technologies, synthetic biology, microbiome engineering, and precision agriculture offers exciting opportunities to accelerate the development of next-generation methylotroph-based bioinoculants.

CRediT authorship contribution statement

Dinesh Antony Vedhamuthu: Conceptualization, Writing – original draft. Sivakumar Uthandi: Review & editing. Boominathan Parasuraman: Review & editing. Muthuvel Iyyamperumal: Review & editing. Viveganandan Gopal: Conceptualization, Review & editing. Puhazhselvan Puhazhendi: Writing, Review & editing. Senthilkumar Murugaiyan: Supervision, Conceptualization, Writing – review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

REFERENCES

1. Aktar, W., Sengupta, D., Chowdhury, A., 2009. Impact of pesticides use in agriculture: Their benefits and hazards. Interdiscip. Toxicol. 2 (1), 1–12. https://doi.org/ 10.2478/v10102-009-0001-7.
2. Andrade, P. A. M. D., Dias, A. C. F., Cotta, S. R., Costa, D. P. D., Oliveira, J. T. C., Oliveira, L. F. P. D., ... & Kuklinsky-Sobral, J. (2018). Differential niche occupation and the biotechnological potential of Methylobacterium species associated with sugarcane plants. African Journal of Microbiology Research, 12(25), 595-605.
3. Ashraf, M. F. M. R., & Foolad, M. R. (2007). Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and experimental botany, 59(2), 206-216.
4. Balachandar, D., Raja, P., & Sundaram, S. P. (2008). Genetic and metabolic diversity of pink-pigmented facultative methylotrophs in phyllosphere of tropical plants. Brazilian Journal of Microbiology, 39(1), 68-73.
5. Bita, C. E., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Frontiers in plant science, 4, 273.
6. Boyer, J. S. (1982). Plant productivity and environment. Science, 218(4571), 443-448.
7. Chaudhry, V., Baindara, P., Pal, V.K., Chawla, N., Patil, P.B., and Korpole, S. (2016) Methylobacterium indicum sp. nov., a facultative methylotrophic bacterium isolated from rice seed. Syst Appl Microbiol 39: 25–32
8. Chistoserdova L (2011) Modularity of methylotrophy, revisited. Environ Microbiol 13(10):2603–2622. https:// doi. org/ 10.1111/j. 1462- 2920. 2011. 02464.x
9. Doronina, N. V., Trotsenko, Y. A., Kuznetsov, B. B., Tourova, T. P., & Salkinoja-Salonen, M. S. (2002). Methylobacterium suomiense sp. nov. and Methylobacterium lusitanum sp. nov., aerobic, pink-pigmented, facultatively methylotrophic bacteria. International Journal of Systematic and Evolutionary Microbiology, 52(3), 773-776.
10. Egamberdieva D, Wirth S, Alqarawi AA, Abd_Allah E (2015) Salt tolerant Methylobacterium mesophilicum showed viable colonization abilities in the plant rhizosphere. Saudi J Biol Sci 22(5):585–590. https:// doi. org/ 10. 1016/j. sjbs. 2015. 06. 029
11. Ehinmitan, E., Losenge, T., Mamati, E., Juma, P., Siamalube, B., Ngumi, V., 2025. Characterization of drought-tolerant bacterial strain from semiarid soil of kenya for plant growth promotion and drought stress amelioration. Int. J. Agron. 2025 (1), 3965809.
12. Farooq, M., Wahid, A., Kobayashi, N. S. M. A., Fujita, D. B. S. M. A., & Basra, S. M. (2009). Plant drought stress: effects, mechanisms and management. Agronomy for sustainable development, 29(1), 185-212.
13. Galbally, I.E.; Kirstine, W. The production of methanol by flowering plants and the global cycle of methanol. J. Atmos. Chem. 2002, 43, 195–229.
14. Glick, B.R., 2014. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol. Res. 169 (1), 30–39. https://doi.org/10.1016/j. micres.2013.09.009.
15. Gourion, B.; Francez-Charlot, A.; Vorholt, J.A. PhyR is involved in the general stress response of Methylobacterium extorquens AM1. J. Bacteriol. 2008, 190, 1027–1035.
16. Green P, Bousfield I (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. https:// doi. org/ 10. 1099/00207 713- 33-4- 875
17. Green, P. N., & Ardley, J. K. (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. International journal of systematic and evolutionary microbiology, 68(9), 2727-2748.
18. Grossi CEM, Fantino E, Serral F, Zawoznik MS, Fernandez Do Porto DA, Ulloa RM (2020) Methylobacterium sp. 2A is a plant growth-promoting rhizobacteria that has the potential to improve potato crop yield under adverse conditions. Front Plant Sci 11:71. https:// doi. org/ 10. 3389/ fpls. 2020. 00071
19. Grossi, C.E.M., Ulloa, R.M., Sahin, N., Tani, A., 2025. Methylobacterium as a key symbiont in plant-microbe interactions: its ecological and agricultural significance. Plant Biotechnol. 25–309.
20. Hasanuzzaman, M., Bhuyan, M. B., Parvin, K., Bhuiyan, T. F., Anee, T. I., Nahar, K., ... & Fujita, M. (2020). Regulation of ROS metabolism in plants under environmental stress: A review of recent experimental evidence. International Journal of Molecular Sciences, 21(22), 8695.
21. Hideg, É., Jansen, M. A., & Strid, Å. (2013). UV-B exposure, ROS, and stress: inseparable companions or loosely linked associates? Trends in plant science, 18(2), 107-115.
22. Iguchi, H., Yurimoto, H., & Sakai, Y. (2015). Interactions of methylotrophs with plants and other heterotrophic bacteria. Microorganisms, 3(2), 137–151. https://doi.org/10.3390/microorganisms3020137
23. Ivanova, E.G., Doronina, N.V., Trotsenko, Y.A., 2001. Aerobic methylobacteria are capable of synthesizing auxins. Microbiology 70, 392–397.
24. Jiang, L., An, D., Wang, X., Zhang, K., Li, G., Lang, L., ... & Jiang, Y. (2020). Methylobacterium planium sp. nov., isolated from a lichen sample. Archives of microbiology, 202(7), 1709-1715.
25. Jourand, P., Giraud, E., Béna, G., Sy, A., Willems, A., Gillis, M., ... & de Lajudie, P. (2004). Methylobacterium nodulans sp. nov., for a group of aerobic, facultatively methylotrophic, legume root-nodule-forming and nitrogen-fixing bacteria. International Journal of Systematic and Evolutionary Microbiology, 54(6), 2269-2273.
26. Kamo, T., Hiradate, S., Suzuki, K., Fujita, I., Yamaki, S., Yoneda, T., Koitabashi, M., & Yoshida, S. (2018). Methylobamine, a UVA-absorbing compound from the plant-associated bacteria Methylobacterium sp. Natural Product Communications, 13(2), 141–143.

27. Knief C, Dengler V, Bodelier PL, Vorholt JA (2012) Characterization of Methylobacterium strains isolated from the phyllosphere and description of Methylobacterium longum sp. nov. Antonie Van Leeuwenhoek 101:169–183. https:// doi. org/ 10.1007/ s10482- 011- 9650-6
28. Knief, C., Ramette, A., Frances, L., Alonso-Blanco, C., Vorholt, J.A., 2010. Site and plant species are important determinants of the Methylobacterium community composition in the plant phyllosphere. ISME J. 4 (6), 719–728.
29. Koenig RL, Morris RO, Polacco JC. tRNA is the source of low level trans-zeatin production in Methylobacterium spp. J Bacteriol. 2002;184(7):1832-1842. doi: 10.1128/ JB.184.7.1832-1842.2002
30. Kumar, M., Kour, D., Yadav, A. N., Saxena, R., Rai, P. K., Jyoti, A., & Tomar, R. S. (2019). Biodiversity of methylotrophic microbial communities and their potential role in mitigation of abiotic stresses in plants. Biologia, 74(3), 287-308.
31. Kumar, R., Singh, A., Shukla, E., Singh, P., Khan, A., Singh, N.K., Srivastava, A., 2024. Siderophore of plant growth promoting rhizobacterium origin reduces reactive oxygen species mediated injury in Solanum spp. caused by fungal pathogens. J. Appl. Microbiol. 135 (2), lxae036
32. Kundan, R., Pant, G., Jadon, N., Agrawal, P.K., 2015. Plant Growth Promoting Rhizobacteria: Mechanism and Current Prospective. J. Fertil. Pestic. 06 (02). https:// doi.org/10.4172/2471-2728.1000155.
33. Kwak MJ, Jeong H, Madhaiyan M, Lee Y, Sa TM, Oh TK, Kim JF (2014) Genome information of Methylobacterium oryzae, a plant-probiotic methylotroph in the phyllosphere. PLoS ONE 9(9):e106704. https:// doi. org/ 10. 1371/ journ al. pone. 01067 04
34. Madhaiyan M, Poonguzhali S, Kwon SW, Sa TM (2009) Methylobacterium phyllosphaerae sp. nov., a pink-pigmented, facultative methylotroph from the phyllosphere of rice. Int J Syst Evol Microbiol 59(1):22–27. https:// doi. org/ 10. 1099/ ijs.0. 001693-0
35. Madhaiyan M, Poonguzhali S, Senthilkumar M, Lee JS, Lee KC (2012) Methylobacterium gossipiicola sp. nov., a pink-pigmented, facultatively methylotrophic bacterium isolated from the cotton phyllosphere. Int J Syst Evol Microbiol 62(1):162–167. https:// doi.org/ 10. 1099/ ijs.0. 030148-0
36. 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.https:/ /doi.org/10.1099/ ijs.0.64603-0.
37. 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.https://doi.org/10.1007/s00425-005- 0211-y.
38. Mittler, R. (2002). Oxidative stress, antioxidants and stress tolerance. Trends in plant science, 7(9), 405-410.
39. Munns, R., & Tester, M. (2008). Mechanisms of salinity tolerance. Annu. Rev. Plant Biol., 59, 651-681.
40. Nemecek-marshall M, MacDonald RC, Franzen JJ, Wojciechowski CL, Fall R. Methanol emission from leaves: enzymatic detection of gas-phase methanol and relation of methanol fluxes to stomatal conductance and leaf development. Plant Physiol. 1995;108(4):1359-1368. doi: 10.1104/pp.108.4.1359
41. Omer ZS, Tombolini R, Gerhardson B (2004) Plant colonization by pink-pigmented facultative methylotrophic bacteria (PPFMs). FEMS Microbiol Ecol 47(3):319–326. https:// doi. org/ 10. 1016/S0168- 6496(04) 00003-0
42. Raja, P., Balachandar, D., & Sundaram, S. P. (2008). Genetic diversity and phylogeny of pink-pigmented facultative methylotrophic bacteria isolated from the phyllosphere of tropical crop plants. Biology and fertility of soils, 45(1), 45-53.
43. Sandhya, V. Z. A. S., SK. Z, A., Grover, M., Reddy, G., & Venkateswarlu, B. S. S. S. (2009). Alleviation of drought stress effects in sunflower seedlings by the exopolysaccharides producing Pseudomonas putida strain GAP-P45. Biology and fertility of soils, 46(1), 17-26.
44. Schauer, S., Kämpfer, P., Wellner, S., Spröer, C., & Kutschera, U. (2011). Methylobacterium marchantiae sp. nov., a pink-pigmented, facultatively methylotrophic bacterium isolated from the thallus of a liverwort. International journal of systematic and evolutionary microbiology, 61(4), 870-876.
45. Sehgal, A., Sita, K., Siddique, K.H.M., Kumar, R., Bhogireddy, S., Varshney, R.K., HanumanthaRao, B., Nair, R.M., Prasad, P.V.V., Nayyar, H., 2018. Drought or/and heat-stress effects on seed filling in food crops: impacts on functional biochemistry, seed yields, and nutritional quality. Front. Plant Sci. 9, 1705.
46. Shahid, M., Pourrut, B., Dumat, C., Nadeem, M., Aslam, M., & Pinelli, E. (2014). Heavy-metal-induced reactive oxygen species: phytotoxicity and physicochemical changes in plants. Reviews of Environmental Contamination and Toxicology Volume 232, 1-44.
47. Singh, R.P., Ma, Y., Shadan, A., 2022. Perspective of ACC-deaminase producing bacteria in stress agriculture. J. Biotechnol. 352, 36–46.
48. Sy A, Giraud E, Jourand P, Garcia N, Willems A, De Lajudie P, Prin Y, Neyra M, Gillis M, Boivin-Masson C (2001) Methylotrophic Methylobacterium bacteria nodulate and fix nitrogen in symbiosis with legumes. J Bacteriol 183(1):214–220. https:// doi. org/ 10.1128/ JB. 183.1. 214-220. 2001
49. Sy, A.; Timmers, A.C.; Knief, C.; Vorholt, J.A. Methylotrophic metabolism is advantageous for Methylobacterium extorquens during colonization of Medicago truncatula under competitive conditions. Appl. Environ. Microbiol. 2005, 71, 7245–7252.
50. Tani, A., Sahin, N., Fujitani, Y., Kato, A., Sato, K., Kimbara, K., 2015. Methylobacterium species promoting rice and barley growth and interaction specificity revealed with whole-cell matrix-assisted laser desorption/ionization-time-of-flight mass spectrometry (MALDI-TOF/MS) analysis. PLoS One 10 (6), e0129509.

51. Theocharis, A., Clément, C., & Barka, E. A. (2012). Physiological and molecular changes in plants grown at low temperatures. Planta, 235(6), 1091-1105.
52. 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. https://doi.org/10.1111/gcb.13959.
53. Van Aken, B., Peres, C. M., Doty, S. L., Yoon, J. M., & Schnoor, J. L. (2004). Methylobacterium populi sp. nov., a novel aerobic, pink-pigmented, facultatively methylotrophic, methane-utilizing bacterium isolated from poplar trees (Populus deltoides× nigra DN34). International journal of systematic and evolutionary microbiology, 54(4), 1191-1196.
54. 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.h t t p s : / / d o i . org/10.1111/nph.13312.
55. Vorholt, J.A. Microbial life in the phyllosphere. Nat. Rev. Microbiol. 2012, 10, 828–840.
56. Vurukonda, S. S. K. P., Vardharajula, S., Shrivastava, M., & SkZ, A. (2016). Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiological research, 184, 13-24.
57. Yoshida S, Hiradate S, Koitabashi M, Kamo T, Tsushima S. (2017) Phyllosphere Methylobacterium bacteria contain UVA-absorbing compounds. Journal of Photochemistry and Photobiology B: Biology, 167, 168-175.
58. Zhu, J. K. (2001). Plant salt tolerance. Trends in plant science, 6(2), 66-71.
59. Zhu, W.-L., Cui, J.-Y., Cui, L.-Y., Liang, W.-F., Yang, S., Zhang, C., Xing, X.-H., 2016. Bioconversion of methanol to value-added mevalonate by engineered Methylobacterium extorquens AM1 containing an optimized mevalonate pathway. Appl. Microbiol. Biotechnol. 100, 2171–2182.