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REVIEW

Prospecting the significance of methane-utilizing bacteria in agriculture

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Abstract

Microorganisms act as both the source and sink of methane, a potent greenhouse gas, thus making a significant contribution to the environment as an important driver of climate change. The rhizosphere and phyllosphere of plants growing in natural (mangroves) and artificial wetlands (flooded agricultural ecosystems) harbor methane-utilizing bacteria that oxidize methane at the source and reduce its net flux. For several decades, microorganisms have been used as biofertilizers to promote plant growth. However, now their role in reducing net methane flux, especially from flooded agricultural ecosystems is gaining momentum globally. Research in this context has mainly focused on taxonomic aspects related to methanotrophy among diverse bacterial genera, and environmental factors that govern methane utilization in natural and artificial wetland ecosystems. In the last few decades, concerted efforts have been made to develop multifunctional microbial inoculants that can oxidize methane and alleviate greenhouse gas emissions, as well as promote plant growth. In this context, combinations of taxonomic groups commonly found in rice paddies and those used as biofertilizers are being explored. This review deals with methanotrophy among diverse bacterial domains, factors influencing methane-utilizing ability, and explores the potential of novel methane-utilizing microbial consortia with plant growth-promoting traits in flooded ecosystems.

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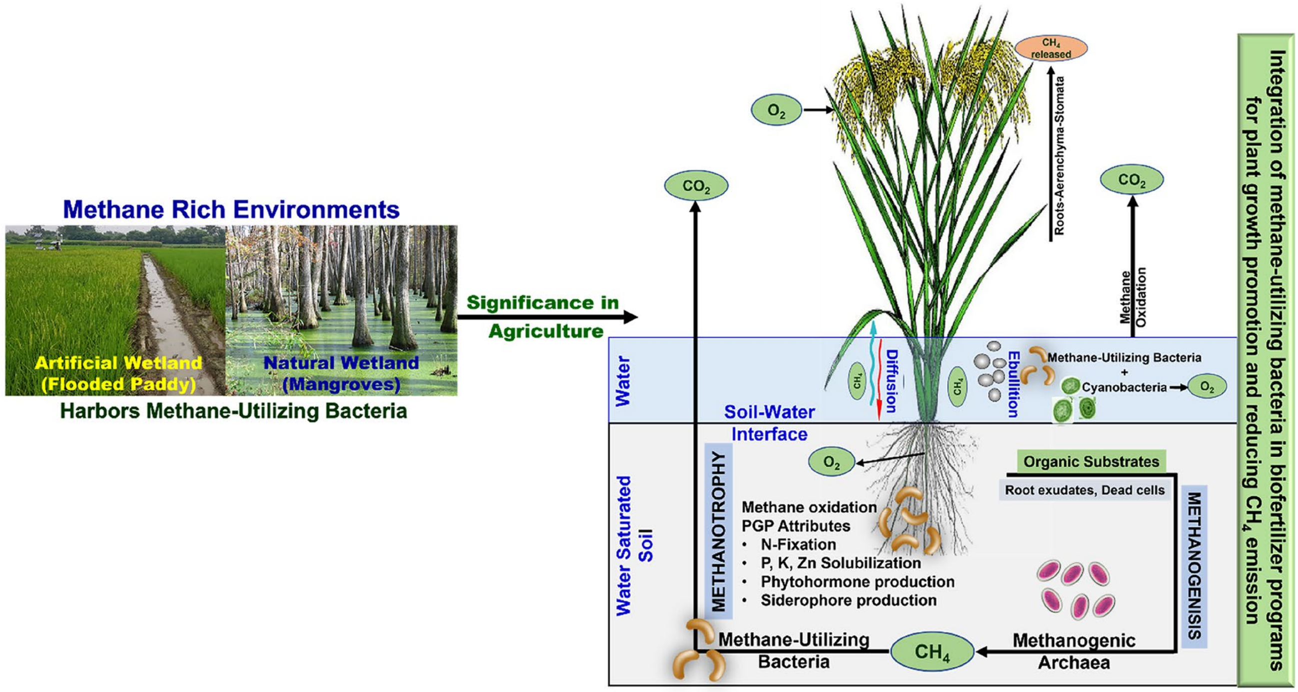
Graphical abstract



Keywords Biofertilizers · Methane oxidation · Methane-utilizing Bacteria · Methanotrophy · Plant growth promotion

Introduction

Microorganisms belonging to diverse taxa have evolved the ability to utilize single-carbon compounds (such as methane, methanol, and other methylated compounds) as the sole source of carbon for meeting their energy demands and are termed methylotrophs. However, some of the methylotrophs can utilize only methane as the sole C source for their energy metabolism and are referred to as methanotrophs. The phenomenon of methylotrophy was recognized after the isolation of the first methane-oxidizing bacteria, *Bacillus methanicus*, in the year 1906 (Sohngen 1906). However, research in the field of bacterial methane utilization gained impetus only after 1970, when Whittenbury and co-workers isolated over 100 strains of methane-utilizing bacteria and described their properties, isolation technique, and introduced the Type I, Type II, and Type X classification system (Whittenbury et al. 1970; Whittenbury and Dalton 1981). Methane-utilizing bacteria play an important role in the global carbon cycle, regulating natural and anthropogenic methane emissions. The biochemical conversion of methane to methanol is the first step in methane utilization by methane-utilizing bacteria. The catabolic process is well studied in traditionally known obligate (belonging to the genera *Methylomonas*, *Methylosinus*, and *Methylococcus*) and facultative methanotrophic bacteria (e.g., *Methylobacterium*, *Methylocella*, *Paracoccus denitrificans*). The first step of the reaction in these bacterial genera is either carried out by membrane-bound copper-containing particulate methane monooxygenase (pMMO) or a di-iron center containing soluble methane monooxygenase (sMMO) (Ross and Rosenzweig 2017). The pMMO is ubiquitous among all known obligate methanotrophs, whereas sMMO appears in some obligate and facultative methanotrophs (Nielsen et al. 1997). The sMMO can oxidize wide varieties of alkanes and has structural specificity with other alkane monooxygenases (Ji et al. 2013). This non-specific degradation chemical property of sMMO makes the facultative methanotrophic microorganisms an important candidate for their exploitation in agriculture, bioremediation, and commercial applications (Theisen et al. 2005). The enzyme pMMO exhibits broad substrate specificity and shares functional similarities and evolutionary linkages with ammonia monoxygenases (key enzymes in ammonia oxidizers) (Zheng et al. 2014). In an environment, where methane-utilizing bacteria are abundant, the assimilation of N by these microbes is likely to bring about significant effects on nitrification (Kowalchuk and Stephan 2001). A few pure culture studies have reported that ammonia-oxidizing bacteria also play a role in methane oxidation however, removal of methane in a significant amount from the agricultural fields is yet to be verified (Kowalchuk and Stephen 2001; Zheng et al. 2014). The role of ammonia-oxidizing bacteria in the association with nitrate oxidizing bacteria is more evident in wastewater and activated sludge treatment (Sepehri et al. 2019). For many years, the model microorganisms that shaped our concepts of methanotrophy belonged to the bacterial families- *Methylococcaceae, Methylocystaceae, Beijerinckiaceae, Methylobacteriaceae*, and *Rhodobacteraceae* of the phyla Proteobacteria and Verrucomicrobia (Dedysh 2009; Ghashghavi et al. 2017; Kravchenko and Sukhacheva 2017). However, in the last decade, with advances in microbial diversity using next-generation sequencing tools and intensive sampling across distinct ecological niches, various workers have reported the concept of methylotrophy in diverse bacterial and yeast genera such as *Methylobacterium, Burkholderia*, *Hyphomicrobium, Paenibacillus, Rahnella*, *Meyerozyma* and *Pseudomonas* (Van Aken 2004; Kumar et al. 2012; Jhala et al. 2014; Yang et al. 2019; Rani et al. 2020, 2021c). However, the biochemical and genetic basis of methane utilization in selected species of these genera is not yet elucidated.

Most of the methane-utilizing bacteria have been isolated from a large diversity of plants. Methane-utilizing bacteria have been found to inhabit the rhizosphere and phyllosphere of flooded ecosystems in large numbers where methane is produced, such as natural (mangroves) or man-made (flooded paddy fields) wetland ecosystems (Iguchi et al. 2012). The leaf surfaces of most of the plant species across different agroecological zones are occupied by active methane or methanol utilizing microbes and constitute about 14–20% of the total microbial community of the phyllosphere (Fedorov et al. 2011; Wellner et al. 2011). The high population of different methane-utilizing microbial communities occupying roots, leaves, stems, and internal tissues of plants, with no prevalence of any disease, highlights their important role in sustaining plant growth promotion, mediated through integrated nutrient and abiotic stress management (Wagner et al. 1999; Rani et al. 2021c). Many methane-utilizing and plant growth-promoting bacteria were isolated, belonging to genera *Methylobacterium*, *Burkholderia*, *Hyphomicrobium*, *Paenibacillus*, *Pseudomonas*, and *Rahnella* from the flooded paddy ecosystem of India. Besides, plant growth-promoting attributes, such isolates exhibited a reduction in cumulative methane emissions by 7 to 12% from flooded paddy fields, when used as root and spray inoculants (Rani et al. 2021c).

Methane emission from natural or man-made wetlands is the net balance of methane production by methanogenic archaea and its oxidation by methane-utilizing bacteria (Malyan et al. 2016). Along with suitable agronomic management practices, prospecting methane-utilizing bacteria residing in various plant parts as a significant sink of methane can help and play an important role in managing the threat of methane emissions from the agricultural domain, particularly from flooded paddy ecosystems. This review provides an overview of the diversity of methane-utilizing bacteria, explores their multifaceted roles in agriculture, and proposes future projections leading to the development of next-generation microbial inoculants with the dual ability of crop growth promotion and reduction in methane emission.

Diversity of methane-oxidizing bacteria

The unique property of aerobic oxidation of methane into methanol and its further assimilation in cells/tissues is widespread among several genera of bacteria, archaea, and yeasts (Dedysh and Knief 2018; Rani et al. 2021b). The reaction step is catalyzed by particulate (pMMO) and soluble methane monooxygenases (sMMO). The methanol formed as a byproduct is further oxidized to formaldehyde by the action of methanol dehydrogenases (MDHs) (Keltjens et al. 2014). The diversity and phylogeny of aerobic methanotrophs have been reviewed extensively earlier by Dedysh and Knief (2018). Whittenbury et al. (1970) categorized methanotrophs into Type I (produce pMMO), Type II (produce both pMMO and sMMO), and Type X (have some features of Types I and II). Later, based on the 16S rRNA gene sequence analysis the methane-utilizing bacteria were taxonomically placed in the phylum Proteobacteria and grouped into Type I (including Type X) and Type II (Chistoserdova et al. 2009). Type I (including Type X) and Type II were further sub-classified into class gamma- and alpha-proteobacteria, respectively (Fei et al. 2014). Some of the traditionally known Type I methane-utilizing bacteria belonging to the gamma-proteobacteria are *Methylomicrobium, Methylosphaera, Methylosarcina, Methylothermus, Methylomonas, Methylohalobius, Methylobacter, Methylosoma, Clonothrix, Crenothrix, Methylococcus* (Type X) *Methylocaldum* (Type X). Similarly, some Type II methane-utilizing bacteria belonging to the class alpha-proteobacteria are *Methylocystis, Methylocella*, *Methylosinus*, and *Methylocapsa* (Chistoserdova et al. 2009). Besides alpha- and gamma-proteobacteria, some of the bacteria belonging to beta-proteobacteria have also been identified as methane utilizers viz., *Methylophilus* (Madhaiyan et al. 2009), *Methylovorus* (Govorukhina and Trotsenko 1991), *Methylibium* (Nakatsu et al. 2006), *Burkholderia* and *Methylobacterium* (Rani et al. 2021c). Over the last two decades, sulfate-, nitrate- and nitrite-dependent anaerobic methane oxidation has been reported (Guerrero-Cruz et al. 2019). Sulfate-oxidizing anaerobic archaea belonging to the order Methanosarcinales, and Methanomicrobiales have been isolated from anoxic zones of marine sediments, soda lakes, continental margins, methane seeps, and vents (Valentine and Reeburg

2000). The nitrate-dependent anaerobic oxidation of methane is catalyzed by archaea belonging to the ANME-2d clade (*Candidatus Methanoperedens nitroreducens*) (Ettwig et al. 2016). The archaea carrying out sulfate- and nitrate-dependent anaerobic methane oxidation play an important role in limiting methane emissions from marine sediments. Various mechanisms viz. reverse methanogenesis, acetogenesis, and methylogenesis have been proposed to explain this unique function of anaerobic archaea (Caldwell et al. 2008; Ettwig et al. 2016). The nitrite-dependent anaerobic oxidation of methane was reported in the bacteria belonging to the NC10 phylum (*Candidatus Methylomirabilis oxyfera*, *Candidatus Methylomirabilis lanthanidiphila*, and *Candidatus Methylomirabilis sinica*) (Versantvoort et al. 2018). Despite their anaerobic metabolism, these bacteria oxidize methane using an intra-aerobic pathway and activate methane using oxygen through a pMMO, while reducing nitrite to N_2 (Ettwig et al. 2010). Apart from phylum proteobacteria, methane-utilization ability has also been reported in the family Methylacidiphilaceae of the phylum Verrucomicrobia and in the intra-aerobic bacteria of the phylum NC10 candidate (Dunfield et al. 2007; Ettwig et al. 2010). For the utilization of methane and other C1 compounds such as formaldehyde, gamma-proteobacteria (Type I and X), and alpha-proteobacteria (Type II) utilize the ribulose monophosphate cycle and serine cycle, respectively. However, some of the bacteria belonging to the species of Type X, Verrumicrobia, and NC10 (*Methylomirabilis spp*) phyla can also grow as autotrophs through the Calvin-Benson-Bassham cycle, thus contributing significantly to the global carbon cycle (Sahoo et al. 2021). They possess the advantage of sequestering CO_2 and its subsequent enzymatic hydrogenation into methanol (Sahoo et al. 2021). The conversion is carried out in a two-stage process, where the first stage comprises the utilization of CH_4 as a carbon substrate to produce biomass and the second stage involves the reduction of CO_2 to produce methanol (Sahoo et al. 2021). The role of these CH_4 oxidizing autotrophic bacteria in the agricultural ecosystem is still not clear as these microbes are mainly reported from extreme environments such as geothermal vents, volcanoes, low pH levels, and hot springs (van Teeseling et al. 2014; Kim et al. 2021).

Methane-utilizing bacteria belonging to the phylum Proteobacteria are found in a vast variety of natural and extreme ecological niches, including agricultural fields (especially flooded paddy fields), wetlands, thermal springs, volcanic soils, and peatlands (Kolb and Horn 2012; Islam et al. 2020; Hogendoorn et al. 2021; Rani et al. 2021c) (Table 1). Among peatlands, α-proteobacteria dominate oligotrophic and acidic bogs, while γ-proteobacteria dominate nutrient-rich, methanotrophic, and mildly acidic fens (Verbeke et al. 2019). It has been found that among α-proteobacteria prevalent in bogs, *Methylocystis* are most active, while *Methylocella* and *Methylocapsa* species are also common (Verbeke et al. 2019). They even found that *Methylobacter*, *Methylomonas*, and *Methylomicrobium* are the most abundant γ-proteobacteria. In the past few years, various workers have reported the significant presence of methane-utilizing bacteria in agricultural soils, rhizosphere, and phyllosphere of crop plants. Diverse genera of methane-utilizing bacteria and yeast have been isolated from natural wetlands and flooded agroecosystems (paddy fields), where a large quantity of methane is released because of methanogenesis in submerged soil. Metagenomic analysis (V3 region of 16 S rRNA gene) of selected arable and no-tillage soils in the Lublin region of Poland revealed the presence of a 0.1% population of methanotrophs, dominated by the genus *Methylocystis* (Szafranek-Nakonieczna et al. 2019). The *pmo*A sequence analysis of forest and agricultural soil revealed the dominance of type I (*Methylobacter, Methylocaldum*) and type II (*Methylocystis, Methylosinus*) methanotrophs (Kravchenko and Sukhacheva 2017). They further reported that the differential CH_4 oxidation rates between forest and agricultural soils were primarily resulting due to the variation in the composition of the methane-oxidizing communities. Looking at their environmental significance, several researchers focused their attention on demonstrating the presence of methane-utilizing bacteria and the role they play in different wetland, agricultural, and forest ecosystems (Kravchenko and Sukhacheva 2017; Rani et al. 2021c). Further, it is important to recognize that the methanotrophic activity in a flooded agricultural ecosystem such as rice paddies is important in managing net CH_4 emissions and promoting plant growth.

Methane-utilizing bacteria: role in agriculture

From an agricultural perspective, flooded agricultural ecosystems (especially rice paddies) and soils rich in organic matter are hotspots of methane emissions and harbor high concentrations of methane in their anoxic, carbon-rich environment. They are the largest source of global atmospheric methane, emitting 142–284 Tg CH_4 per year (Kirschke et al. 2013). The methane in such an environment is generated as the end-product of the anaerobic degradation of organic matter under flooded anoxic conditions. The well-known ‘low-affinity’ methanotrophs, which contain the type I (γ-proteobacteria) and type II (α-proteobacteria) subgroups, catalyze methane oxidation at the aerobic–anaerobic interfaces. These interfaces include the oxygenated surface soil layers and the area around the oxygen-releasing roots of wetland plants. It is crucial to recognize the importance of methanotrophic activity in agricultural soils, not just from

Table 1 Diversity of methane utilizing bacteria in a methane-rich environment

S. No.	Genera	Habitat	Salient finding	Reference
[A] Artificial wetlands				
1	Type Ia—*Methylomonas, Methylomicrobium*, and *Methylocucumis* Type Ib—*Methylocaldum* and *Methylomagnum* Type II—*Methylocystis* and *Methylosinus*	Rice field, India	Used enrichment culture technique.	Rahalkar et al. (2021)
2	Type I—Closely related to *Methylomonas* spp. and *Methyloccocus Methylocaldum-Methylogaea* clade Type II—Related to *Methylocystis* methanotrophs	Rice fields, Japan	The diversity of methane-utilizing bacteria was deciphered using a combination of culture-dependent and fluorescence in situ hybridization techniques.	Dianou et al. (2012)
3	*Methylobacterium, Paenibacillus, Hyphomicrobium, Burkholderia, Pseudomonas, Rahnella*, and *Meyerozyma.*	Rice field, India	*Methylobacterium oryzae* MNL7 is reported to be a good CH_4 oxidizer and plant growth promoter	Rani et al. (2021c)
[B] Natural wetlands				
4	Type I—*Methylomonas*, and *Methylovulum* Type II—*Methylocystis*	Peat Bog Average pH- 3.5 to 4.0	Metagenomes and next-generation sequencing of *pmo*A cDNA amplicons revealed the predominance of *Methylocystis* at the surface	Esson et al. (2016)
5	Type I—*Methylobacter, Methylobacter*, and *Methylomicrobium* Type II—*Methylocystis*	Mangrove forest soils, Taiwan	*Methylobacter* and *Methylomicrobium*-like Type I methanotrophs dominated methane-oxidizing communities in the field conditions. *Methylobacter* were well adapted to high salinity and low temperature	Shiau et al. (2020)
6	*Candidatus 'Methanoperedens nitroreducens'*	Freshwater sediment and anaerobic wastewater sludge in Brisbane, Australia	Catalyzes independent anaerobic oxidation of CH_4 (AOM) through reverse methanogenesis using nitrate as the terminal electron acceptor Play an important role in linking the global carbon and nitrogen cycles in anoxic environments	Haroon et al. (2013)
7	Archaea of ANME-2d clade (*Ca*. Methanoperedenaccae)	Freshwater lake sediment in Lake Orn, Denmark	Potential electron acceptors for anaerobic oxidation of methane include Fe (III) and sulfate Sulfate dependent AOM signifies the importance of sulfur and iron cycling in the regulation of methane emission	Mostovaya et al. (2022)
[C] Extreme environment				
8	*Methylococcus*-like Type Ib methanotroph	Thermal spring, Alkaline- saline Lake Shalla, Ethiopia	First isolated obligate moderately thermophilic methanotroph from an alkaline thermal spring of the family *Methylococcaceae.*	Islam et al. (2020)
9	*Methylobacter*	Volcanic soils of Pantelleria Island, Italy	Reported the presence of *Methylobacter* in thermoacidophilic niche Confirmed presence of particulate methane monooxygenase and methanol dehydrogenase involved in CH_4 oxidation and assimilation	Hogendoorn et al. (2021)

Table 1 (continued)

S. No.	Genera	Habitat	Salient finding	Reference
[D] Livestock				
10	*Methylobacterium*, *Methylomonas*, and *Methylomicrobium*	*Bos Taurus* cattle	The diversity of methanotrophic organisms was greater in high CH_4 emitters as compared to low emitters	Auffret et al. (2018)

the perspective of managing the net CH_4 emissions, but also other possible benefits to the soil or crop.

Role in reducing methane emission from agricultural ecosystem

Various researchers have reported the findings of the diversity of methane-utilizing bacteria in a methane-rich environment like a natural wetland, rice field, livestock rumen, peats, and bogs (Dianou et al. 2012; Esson et al. 2016; Auffret et al. 2018; Rani et al. 2021c) (Table 1). However, exploring their potential as inoculants in agriculture for reducing overall methane flux is still in its infancy. In the last few years, various workers have reported a reduction in methane flux using methane-utilizing bacteria in flooded paddies. Inoculation of methanotrophic *Ochrobactrum anthropi* in combination with nitrogen-fixing *Azotobacter* and *Azospirillum* at 25% recommended fertilizer dose decreased the CH_4 flux from less than 18.31 mmol m^{-2} h^{-1} in control to – 19.57 mmol m^{-2} h^{-1} during vegetative phase (Pingak et al. 2014; Sutanto et al. 2014) reported 12.29% lower CH_4 emissions from flooded paddy fields (cultivated by applying 2/3rd recommended dose of fertilizer) by inoculating a consortium of methanotrophic bacteria comprising *Methylocystis rosea* BGM 1, *M. rosea* BGM 5, *Methylococcus capculatus* BGM 9, and *Methylobacte*r sp. SKM. Sukmawati et al. (2016) reported a significant decrease in CH_4 flux (on the 21st day after transplanting) from less than 74346.45 moles d^{-1} ha^{-1} in control to – 24018.80 moles d^{-1} ha^{-1} in plots inoculated with *Methylocystis rosea* BGM 5 and N_2O reducing bacteria *Ochrobactrum anthropi* BL2. Similar findings were reported by Taopan et al. (2018) who reported a decline in CH_4 flux from less than 10 mg/m^2/d in un-inoculated control to – 23.87 mg/m^2/d in rice inoculated with a bacterial consortium, comprising different strains of *Methylocystis*¸ *Methylobacter*, and *Methylococcus* at 60th d after transplanting. Nontji and co-workers (2016) reported a decrease in methane emission by 51–88% in rice fields depending on the type of methane-utilizing bacteria. They observed a significant decline in methane flux till the 5th day of inoculation followed by a gradual decrease in % methane reduction. A similar finding was recorded by Davamani and co-workers (2020) who claimed a 57–68% reduction in CH_4 emission during active tillering, flowering, and maturity stage of rice, by the application of methanotrophic bacterial consortium over un-inoculated control. Rani et al. (2021a) investigated the effect of different N fertilizer regimes on cumulative methane emission from paddy fields by performing dual inoculation of paddy by methane-utilizing *Methylobacterium oryzae* MNL7 (at different growth stages) and plant growth-promoting *Paenibacillus polymyxa* MaAL70 (seed treatment during nursery sowing). They reported a significant decrease in the cumulative methane flux by 12.03, 11.47, and 6.92% in Urea, DAP + Urea, and FYM fertilized plots, over their respective uninoculated treatments.

In rice paddies, studies have found that methane oxidation activity of methane-utilizing bacteria is affected by oxygen availability under anoxic flood conditions (De Bont et al. 1978). Cyanobacteria are routinely used as biofertilizers in paddy cultivation, and their ability to liberate oxygen due to photosynthetic activity in the flooded ecosystem is known to be beneficial, but their role in complementing or supplementing methane-utilizing bacteria inhabiting rice rhizosphere and soil water-air continuum (Mancinelli 1995; Prasanna et al. 2002) is less investigated. Cyanobacteria and Azolla (an aquatic fern harboring cyanobacterium, *Anabaena azollae*, often found floating in flooded paddy fields) are among the various biological inputs routinely used in rice fields for providing nitrogen to the plants (Prasanna et al. 2002). However, their role in methane production and oxidation is less documented. Therefore, a study was undertaken using laboratory simulation experiments with rice field soil samples and combinations of cyanobacteria and *Azolla* (Prasanna et al. 2002). Interesting results in terms of rapid decrease in the headspace concentration of methane were obtained with moist soil cores, taken from treatments involving the application of urea in combination with *Azolla microphylla*, a cyanobacterial mixture, and cyanobacterial mixture + *A. microphylla*. These values were distinct, as compared to those from soil cores from plots treated with urea alone (30, 60, 90, and 120 kg N ha^{-1}), illustrating that the application of biofertilizers such as cyanobacteria and *Azolla* can help in the mitigation of methane emissions, mainly facilitated through the photosynthetic evolution of oxygen in the wetland rice environment. Malyan et al. (2021) studied the effect of 9 different combinations of methane-utilizing bacteria, cyanobacteria biofertilizer, and Azolla on reduction in methane and nitrous oxide flux for the 2 consecutive years in flooded paddy. They observed a maximum significant decrease in cumulative CH_4 emission by the application of *Methylobacteruim oryzae* MNL7 alone (19.9%) followed by treatment of *Azolla* + cyanobacteria combination (13.2%) as compared to un-inoculated control. Application of *Azolla* in flooded paddy assists in reducing cumulative CH_4 emission due to liberation of oxygen in standing water and an increase in soil Eh (Bharati et al. 2000; Xu et al. 2017). From the limited number of reports in the literature, the idea of managing methane emissions using microorganisms has generated significant interest among the scientific community across the world. However, there are certainly important issues (discussed later in this review) that need to be addressed before developing biofertilizers capable of not only promoting plant growth but also mitigating GHG emissions from agriculture-based ecosystems, especially methane.

Role in plant growth promotion

The plant growth-promoting (PGP) traits exhibited by microorganisms have been reported in several genera of bacteria (Glick 2012), cyanobacteria (Manjunath et al. 2011), archaea (Naitam and Kaushik 2021), and fungi (Hossain et al. 2017). The PGP traits include fixation of atmospheric N, solubilization of P, K, and Zn from complex mineral sources present in the soil, production of phytohormones (auxin, gibberellic acid, abscisic acid, cytokinin, and salicylic acid), induction of systemic resistance to abiotic stress (salinity, moisture, temperature, pH), and biocontrol of pests and diseases (Grover et al. 2011; Glick 2012; Divekar et al. 2022). Among different bacterial genera, the ability to promote plant growth by methane-utilizing bacteria has also been reported by a few researchers. However, obligate methanotrophs have not yet been investigated for the PGP traits. Methane-oxidizing bacteria belonging to the genus *Methylophilus, Methylobacillus, Methylovorus, Methylopila, Methylobacterium, Delftia*, and *Ancyclobacter* can solubilize tri-calcium phosphate (Agafonova et al. 2013). These bacteria secrete formic acid and lower the pH of the culture medium converting insoluble tri-calcium phosphate into a soluble form. However, none of them was found to possess the ability to solubilize K and Zn in the growth medium or soil. In another study, Rani et al. (2021c) reported P, K, and Zn solubilization activity in non-traditional methane-utilizing bacteria belonging to genera *Methylobacterium*, *Hyphomicrobium*, *Paenibacillus*,*Pseudomonas*, and *Burkholderia*. The P solubilization among different methane-utilizing bacteria ranged from 9.44 to 115.67 mg L^{-1} (using tri-calcium phosphate as P source), whereas the K solubilization index on potassium aluminum silicate as K source and the Zn solubilization index on ZnO, $ZnCO_3$ and $ZnPO_4$ varied between 1.70 and 2.90, 3.34–6.45, 3.59–6.29, and 3.34–5.73, respectively (Rani et al. 2021c).

Earlier, N_2-fixation ability was thought to be limited to type II methanotrophs except for the type I genus *Methylococcus* (Murrell and Dalton 1983). However, results from DNA hybridization studies and acetylene reduction assays suggest that some members of the type I genus *Methylomonas* and the type I strain *Methylobacter marinus* A45 may fix nitrogen (Oakley and Murrell 1988). *Methylomonas*-like *nif*H fragments have been amplified from rice roots and freshwater lakes (Zani et al. 2000). Reports are available on the role and localization of type II methanotrophic bacteria of the family *Methylocystaceae* in rice crops. They are known to fix N_2 and oxidize CH_4 in the rice plant as they inhabit the vascular bundles and epidermal cells of the roots and thus play a major role in reducing methane emissions besides providing fixed nitrogen (Bao et al. 2014). Among non-traditional methane-utilizing bacteria *viz. Burkholderia, Hyphomicrobium, Paenibacillus, Methylobacterium*, and

Rahnella were isolated from the flooded paddy ecosystem, and the nitrogen fixation in terms of acetylene reduction assay ranged from 122.72 ± 21.91 to 768.86 ± 25.89 nmoles of C_2H_2 mg protein^{-1} h^{-1} (Rani et al. 2021c). It has been hypothesized that nitrogen fixation may reduce the activity of methane oxidation due to competition in terms of energy consumption, therefore it is essential to investigate the role of N_2-fixing and methane-utilizing bacteria in detail before using them for the dual purpose of N_2 fixation and methane oxidation in the natural environment (Kruistum et al. 2018).

Indole-3-acetic acid (IAA) is one of the most widespread auxins and plays a major role in determining root growth. IAA production in a few genera capable of oxidizing methane such as *Methylobacillus, Methylomonas*, and *Methylobacter* in the range of 6–8 µg mL^{-1} has been reported (Doronina et al. 2002). Similarly, methanotrophs isolated from the rhizosphere region of the paddy could produce IAA (28.15 µg mL^{-1} of culture filtrate) and gibberellic acid (70.84 µg mL^{-1} of culture filtrate) (Davamani et al. 2020). They found that using a consortium of these methanotrophic bacteria increased paddy grain and straw yields by 34.61 and 11.46%, respectively, over the un-inoculated control. Similarly, inoculation of a methanotrophic bacterial consortium comprising *Methylocystis rosea* BGM 1, *Methylobacter* sp. SKM 14, *Methylocystis palvus* BGM 3, and *Methylococcus capsulatus* BGM 9) significantly increased the paddy yield by 4.9 t ha^{-1} (without fertilizer) to 6.6 t ha^{-1} (Taopan et al. 2018).

Among different genera of methane-utilizing bacteria, the most widely studied genus is *Methylobacterium*. Different species of *Methylobacterium* are known for their ability to promote the growth of various crops by the production of different phytohormones such as IAA, gibberellic acid, and cytokinins (Ivanova et al. 2001; Lidstrom and Chistoserdova 2002; Siddikee et al. 2010), and by alleviating abiotic stress of heat, drought, and salinity (Egamberdieva et al. 2015; Jorge et al. 2019; Grossi et al. 2020; Rani et al. 2021c) reported IAA production by methane-utilizing isolates belonging to 7 bacteria and 1 yeast genera obtained from a flooded paddy ecosystem. Among these 7 bacterial (*Hyphomicrobium*, *Burkholderia*, *Methylobacterium*, *Pseudomonas*, *Paenibacillus*, *Curtobacterium*, and *Rahnella*) and 1 yeast (*Meyerozyma guilliermondii*) genera, the IAA production ranged from 13.37 to 82.02 µg mL^{-1} and 26.94 to 132.99 µg mL^{-1} in the absence and presence of tryptophan, respectively (Rani et al. 2021c). Field evaluation of methane-utilizing and plant growth-promoting bacterial consortium, comprising *Methylobacterium oryzae* MNL7 and *Paenibacillus polymyxa* MaAL70 in different fertilizer treatments showed a significant increase in the crop yield by 11.08–14.04% over un-inoculated control and reduced cumulative net methane flux by 6.92 to 12.03% (Rani et al. 2021a). *Methylobacterium* species also hold great potential as a biocontrol agent for plant disease management and are effective against fungal (*Phytophthora infestans, Botrytis cinerea*, and *Fusarium graminearum*) and bacterial (*Pectobacterium atrosepticum* and *Pseudomonas syringae*) pathogens (Ardanov et al. 2012; Grossi et al. 2020). They are effective against *Ralstonia solanacearum* causing bacterial wilt in tomatoes by synthesizing ACC (aminocyclopropane-1-carboxylic acid) deaminase enzyme and pathogenesis-related proteins (β-1,3-glucanase, phenylalanine ammonia-lyase, polyphenol oxidase, peroxidase) leading to low ethylene levels in plants (Yim et al. 2013). Research exploring the biocontrol potential of methanotrophic isolates against *Xanthomonas oryzae* pv. *oryzae* causing bacterial leaf blight in rice has shown positive results (Nontji and Amra 2019).

The above studies show that methane-utilizing bacteria at the aerobic–anaerobic niche in a flooded agricultural ecosystem play a crucial role in reducing the net methane flux and stimulating plant growth by producing plant growth-promoting substances. However, various factors influencing the growth and proliferation of methane-utilizing bacteria in the agricultural ecosystem are poorly understood. These factors play a major role in determining the net methane flux of any ecosystem, essential to be considered while cultivating crops to combat climate change.

Factors affecting microbial utilization of methane in the agricultural ecosystem

The net CH_4 emission from the paddy field is governed by the abundance of methane-utilizing bacteria and three major processes viz. CH_4 production, CH_4 oxidation, and its transport through diffusion, ebullition, and aerenchymal routes (Cai et al. 2007). The abundance of methane-utilizing bacteria and their methane oxidation ability in paddy fields is influenced by a variety of soil physicochemical factors such as temperature, pH, nitrogenous fertilizer application, and rice varieties. Among these factors, no detailed reports are available about the effect of temperature and soil pH on the methane oxidation ability of methane-utilizing bacteria in agricultural soils. The pH requirement for the growth and oxidation of methane by these bacteria is influenced by their habitat. In agricultural soils, these bacteria are generally mesophilic and grow at an optimum temperature of 25–35 °C (Sadasivam and Reddy 2014). Methane-utilizing bacteria are adapted to a wider range of pH (Reddy et al. 2020). The alkalophilic methane-utilizing bacteria *Methylomicrobium alcaliphilum* was isolated from saline Tuva soda lakes with an optimum pH requirement of 9.0-9.5 (Khmelenina et al. 1997). The acidophilic or acid-tolerant methane utilizing bacteria has been reported in the families Methylocystaceae, Beijerinckiaceae, and Methylococcaceae (Nguyen et al. 2018). The effect of nitrogenous fertilizer and different rice varieties is discussed below (Fig. 1).

(a) Effect of different nitrogenous fertilizers on the activity of methane-utilizing bacteria

The application of N fertilizers affects CH_4 transport as plant biomass responds positively to the dose of fertilizer and provides a channel for the release of CH_4 into the atmosphere (Le Mer and Roger 2001). Researchers suggest that the application of N-fertilizer will increase plant biomass and root exudate formation, thus providing more substrate for the growth of methanogenic archaea and a channel for the release of CH_4 causing increased emission (Xu et al. 2004; Jia et al. 2006). Simultaneously, at the microbial level, the application of N-fertilizer will augment the activities of both methanogens and methanotrophs depending on the soil moisture content and existing CH_4 and O_2 concentration in the paddy field (Bodelier et al. 2000a, b). Studies showing both stimulation and repression of CH_4 flux on the use of N- fertilizer are documented, which highlights that nitrogenous fertilizer may show a varying effect on CH_4 emission based on several factors (Liu and Greaver 2009; Bin-feng et al. 2016).

Dose and time of fertilizer application

The effect of nitrogenous fertilizer on CH_4 emissions is said to be dose-dependent with higher emissions on the application of a small dose of fertilizer and vice-versa (Banger et al. 2012; Linquist et al. 2012). However, the opposite trend was observed by Aronson and Helliker (2010). Linquist and coworkers (2012) reported that application of N-fertilizer at low rates (≈ 79 kg N ha^{-1}) increased the CH_4 emission by 18%, whereas emissions were reduced by 15% at high N application rate (≈ 249 kg N ha^{-1}). Their findings suggest that excess NH_4^+-N formed in soil due to the application of higher doses of N fertilizer increases the CH_4 oxidation activity, which decreases CH_4 emissions. N fertilization at the tillering stage, when anaerobic conditions are prevalent in flooded paddy fields with ample CH_4 supply, increases the activity of methanotrophs, which results in lower net methane flux (Cai et al. 2007). However, N fertilizer application during panicle initiation and grain filling stages increases the root exudation and methanogenesis, resulting in higher CH_4 emissions (Cai et al. 2007). The findings suggest that the effect of the application of N-fertilizer on net CH_4 emission is governed by the prevailing CH_4 concentration in the rice ecosystem, as well as the growth stage of plants, which regulate stimulation in the activity of methanogens or methanotrophs (Bin-feng et al. 2016).

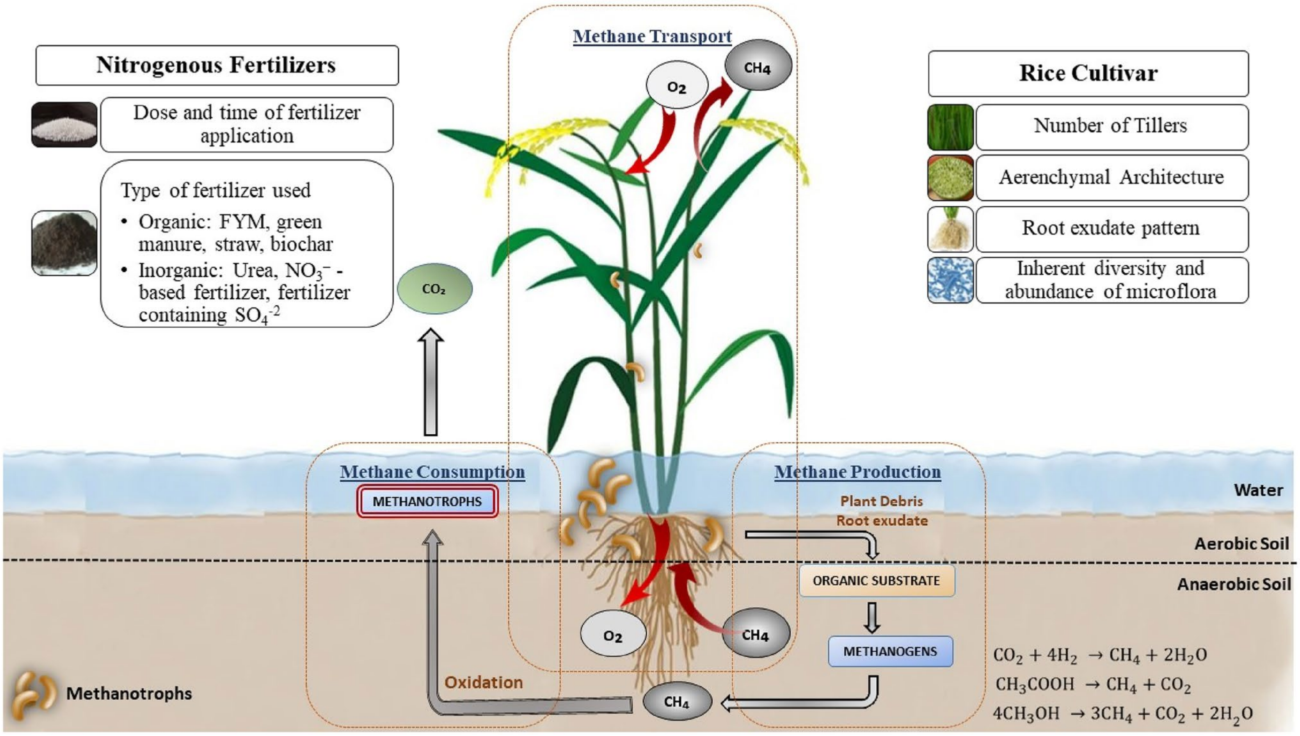


Fig. 1 Factors affecting net CH_4 production from the rice ecosystem

Type of fertilizer used in rice crops

Nitrate and ammonium-based fertilizer differ in terms of their effect on net CH_4 emission. Nitrate-based fertilizers are usually not recommended for paddy crops due to their high mobility, low use efficiency, and stimulatory effect on N_2O emissions which is another potent GHG (Gaihre et al. 2020). But the application of nitrate-based fertilizer show lower CH_4 emission as denitrification of nitrate consumes electrons and H_2 required by CH_4 producers (Kluber and Conrad 1998). Nitrate and its denitrified product are toxic to acetate-utilizing methanogens resulting in lower CH_4 emissions (Lindau et al. 1990). However, this effect is reported to be short-lived as an increase in CH_4 production is observed after the denitrification process is over (Lu et al. 2000). Moreover, nitrate has been found inhibitory to the activity of methane-utilizing bacteria at very high concentrations mainly because of the osmotic effect (Bodelier and Laanbroek 2004). Therefore, the use of nitrate-based fertilizer cannot be recommended as a remedy to mitigate CH_4 emission due to its short-term effect, low fertilizer use efficiency, and enhanced N_2O emission.

The effect of ammonium fertilizers on CH_4 emission is determined by their impact on the activity of methanogens and methanotrophs. Enhanced activity of methanogens is observed with the addition of NH_4^+ fertilizers due to the increased plant growth and availability of substrate (Bodelier et al. 2000a). It has been reported that the application of ammoniacal fertilizers inhibits the methane oxidation ability of methane-utilizing bacteria in soil (Le Mer and Roger 2001; Bodelier and Laanbroek 2004). Short-term inhibition in CH_4 oxidation on the addition of NH_4^+ fertilizer is observed which may be due to competitive inhibition of MMO by ammonia (Dunfield and Knowles 1995; Hooper et al. 1997). Moreover, the intermediates and end products of ammonia oxidation i.e., hydroxylamine and nitrite, can be toxic to the methanotrophic bacterial community and thus inhibits CH_4 consumption (Schnell and King 1994). A higher dose of NH_4^+ fertilizer may cause osmotic stress and inhibit the activity of the methane-utilizing bacteria (Whalen 2000). The diverse varying effect of NH_4^+ fertilizer on CH_4 emission may be due to change in the community composition, either by a shift between ammonium tolerant and ammonium-intolerant CH_4-oxidizing species or by a relative increase of ammonia oxidizers consuming CH_4 (Bodelier and Laanbroek 2004).

One of the earliest reports on the positive impact of urea-based fertilizers on methane oxidation was given by Bodelier et al. (2000a) who observed stimulation of methane oxidation in a microcosm planted with rice along with the application of 200 or 400 kg N ha^{-1} urea or $(NH_4)_2SO_4$. Using molecular tools and radioactive fingerprinting, this was attributed to the proliferation and activity of type I methanotrophs. Fertilizer containing sulfate may affect net CH_4 emission either by suppressing methanogenesis or by promoting anaerobic CH_4 oxidation (Segers 1998; Pennock et al. 2010). The use of ammonium sulfate in the paddy field is found to reduce CH_4 emissions by up to 40% as compared to plots treated with urea (Linquist et al. 2012; Malyan et al. 2016). An in-depth analysis shows that the effect of sulfate on CH_4 emission is influenced by the dose of sulfate fertilizer used. A higher dose of sulfate fertilizers @ 208 and 992 kg S ha^{-1} can reduce CH_4 emission by 28% and 53%, respectively (Linquist et al. 2012; Traore et al. 2017) compared the effect of different ammonium nitrate-based fertilizers on CH_4 emission. They reported higher emission of CH_4 in urea treated pots followed by ammonium sulfate, ammonium chloride, and sodium nitrate, which was 2, 1.5, 1.3, and 0.2 times, respectively greater than that of control (pots without N-fertilizer). Their findings indicate that urea can also be substituted by other NH_4^+ based fertilizers like ammonium sulfate in flooded ecosystems.

Organic amendments such as FYM, straw, and green manure are said to increase CH_4 emissions due to the increase in the activity of methanogenic archaea (Cai et al. 2007; Kim et al. 2014; Ho et al. 2015). High organic matter content in the soil activates microbial activities, consumes O_2, lowers soil redox potential, and creates an environment conducive to the growth and proliferation of methanogens (Yang et al. 2010; Zhang et al. 2018). About 46% higher CH_4 emissions were reported on the application of organic amendments as compared to control with a balanced fertilizer dose of NPK (Yang et al. 2010). Statistical analysis shows that the organic amendment and water regime play a major role in determining CH_4 flux as compared to climate and soil properties (Yan et al. 2005). Therefore, the choice of organic substrate for amendment in the rice field will play a major role in determining CH_4 flux. The use of slow-release fertilizer along with safe organic amendments such as biochar has been recommended to increase crop yield, maintain soil health, and reduce CH_4 emission (Miao et al. 2016; Ly et al. 2015). Being recalcitrant, biochar does not provide an ideal organic substrate for the growth of methanogens (Kuzyakov et al. 2009). In addition, it increases soil aeration, thereby reducing methanogenesis (Karhu et al. 2011). This slow-release fertilizer reduces the plant biomass, and thus decreases the amount of methane transported by the plants and the amount of carbon substrate in the plant debris and root exudates (Kim et al. 2017). In a study, a significant reduction in the cumulative methane emission from paddy fields was reported due to the application of biochar and slow-release fertilizer. The cumulative methane emissions were significantly reduced by the combined application of biochar and slow-release fertilizers (8916 mg CH_4 m^{-2} growing $season^{-1}$), as compared to using only slow-release fertilizers (13,858 mg CH_4 m^{-2} growing season^{-1}) and urea (15,864 mg CH_4 m^{-2} growing season^{-1}) (Kim et al. 2017).

Another alternative is to use controlled-release nitrogen fertilizer such as neem oil-coated urea and, polymer-coated urea in rice fields as their application results in lower emission of CH_4 giving additional benefits of enhanced yield and lower disease incidence (Ankita and Bindu 2016; Wang et al. 2016).

The above findings suggest that N-fertilizer influences the CH_4 production, oxidation, and transport process in the paddy field, resulting in variable effects on CH_4 flux. The application of slow-release fertilizers with recalcitrant organic material (biochar) can cause a significant reduction in the net CH_4 emission. The use of sulfate-containing fertilizers like ammonium sulfate along with in-depth placement can be another strategy to reduce net CH_4 emissions. These studies indicate the strong impact of nitrogenous fertilizer on CH_4 emission, and therefore, should be an important consideration, while preparing the fertilization schedule for paddy cultivation.

(b) Effect of different rice cultivars on the activity of methane-utilizing bacteria

The rice plant harbors a diverse group of methane producers and consumers that play a vital role in determining CH_4 flux in a particular area. About 90% of CH_4 generated in a paddy field by the methanogens gets consumed by aerobic methanotrophs even before it is released into the atmosphere (Holzapfel-Pschorn et al. 1986; Hanson and Hanson 1996). A comprehensive study determining the role of rice cultivar in influencing root exudation, aerenchymatous space, the population of methanogenic archaea and methanotrophic bacteria, and its impact on CH_4 oxidation has been carried out by a few workers (Wang and Adachi 2000; Liechty et al. 2020). They observed significant differences in the population of methanogenic archaea at booting and ripening stages with different rice cultivars. Similarly, the population of methane-utilizing bacteria also varied significantly in the root samples collected from different rice cultivars. The population and diversity of both methane-producing and methane-utilizing microbes residing in the rice phyllosphere and rhizosphere in a particular variety can play a major role in determining the net CH_4 flux in that area. CH_4 emission is reported to be positively correlated to tiller number, culm biomass, soil organic matter, dissolved soil organic carbon, and total carbon content in the rice field (Qin et al. 2015). Varieties with high yield and low CH_4 emission have been identified by researchers (Gogoi et al. 2008; Qin et al. 2015; Islam et al. 2019). A significant difference in the microbial community of both methanogens and methanotrophs in low and high-emitting rice cultivars has been demonstrated by Liechty and coworkers (2020). It is reported that hybrid rice as compared to *Indica* and *Japonica* cultivars stimulates the growth of methane-utilizing bacteria in the rice rhizosphere, and hence enhances CH_4 oxidation which limits CH_4 emissions from the paddy soil (Ma et al. 2009). Besides affecting the population of methanogenic archaea and methane-utilizing bacteria, high CH_4 emitting rice cultivars are also associated with a higher population of sulfate-reducing and iron-reducing taxa responsible for lowering soil oxidation-reduction potential to a point where methanogenesis can occur (Liechty et al. 2020). The greater abundance of fermentative taxa which produces methanogenesis precursors (acetate, CO_2, and H_2) along with microorganisms associated with acetogenesis which compete with methanogens for CO_2 and H_2 is reported in high CH_4 emitting cultivars (Liechty et al. 2020). Thus, it is quite evident that CH_4 emission from rice fields is not only influenced by the population of methanogens and methanotrophs, but also by other microbial taxa involved in upstream and downstream processes of CH_4 production.

Rice cultivars differ widely in terms of growth-related parameters like the number of tillers and plant biomass (Wang et al. 1997). A higher number of tillers and plant biomass are found to be positively correlated to the CH_4 exchange rate during the vegetative phase of the rice plant (Aulakh et al. 2001). Root exudates along with plant debris act as an important source of nutrients for the growth and proliferation of diverse groups of microorganisms residing in the soil. They play an important role in determining the complex microbial dynamics in environmental samples (Bakker et al. 2018; Olanrewaju et al. 2019). By way of its exudate pattern, they alter the diversity of both methanogens and methanotrophs residing in the soil. Studies conducted show that the community distribution and abundance of both methanogens and methanotrophs vary with the oxic condition of the soil along with total organic carbon content mainly contributed by the root exudate and decomposition of plant debris (Lee et al. 2015). Transgenic high starch and low CH_4 rice developed by introducing a single transcription factor gene *SUSIBA2* from barley favors allocation of photosynthates to aboveground biomass over-allocation to roots (Su et al. 2015). Transfer of this gene resulted in reduced CH_4 emission by altering root exudate composition and increased plant biomass and starch content in the seeds and stems.

The aerenchymal architecture of the rice plant determines the passage for the emission of CH_4 into the atmosphere. Moreover, they act as a conducting duct for the transport of oxygen from the atmosphere into the plant root zone determining the redox level of the paddy soil. The architecture of aerenchymatous tissue is governed by several genes and the positive impact of ethylene levels and hydrogen peroxide on the development of aerenchyma tissue has been reported (Fukao et al. 2006; Hattori et al. 2009; Steffens et al. 2010).

Research shows that treatment with ethephon, an ethylene releasing compound promotes aerenchyma development across all rice varieties. It promotes the formation of O_2^- radicals, and H_2O_2 which directly promotes aerenchyma formation. The finding was confirmed by the downregulation of the *MT2b* gene involved in scavenging H_2O_2 which directly affects aerenchyma formation (Steffens et al. 2010). Genes like *SNORKEL1, SNORKEL2*, and ethylene response factor (*ERF*) influence ethylene levels in plant and thus indirectly determines the air space in aerenchymatous tissue (Fukao et al. 2006; Hattori et al. 2009). Therefore, genes involved in the upregulation and downregulation of ethylene levels can play an important role in determining the air space in aerenchymatous tissue directly influencing gaseous exchange including CH_4 and O_2. The CH_4 transport capacity of rice plants can be an important factor when choosing a rice variety for cultivation. Its impact on the net CH_4 emission should not be undermined. The use of high-yielding cultivars with low CH_4 transport capacity could be an economically feasible, environmentally sound, and promising approach to mitigate CH_4 emissions from rice fields.

Interaction of other microbial forms with methane-utilizing bacteria that aid in methane mitigation

Methanotrophic bacteria can grow with other organisms and aid in the removal of other greenhouse gases (Singh et al. 2019). Co-culture of a methanotrophic bacterial consortium with cyanobacteria or microalga can lead to complete CH_4 and CO_2 uptake (Hill et al. 2017; Ruiz-Ruiz et al. 2020) and thus, is a promising strategy for greenhouse gases mitigation in a single step (Fig. 2). Earlier research suggested that inoculation of *Synechocystis* sp. (cyanobacteria) in a laboratory simulation experiment using soil samples from rice fields can cause a significant reduction in the headspace concentration of methane. Moreover, co-inoculation of cyanobacteria with *Azolla microphylla* could further enhance the methane removal rate (Prasanna et al. 2002). The cyanobacteria can consume CO_2 creating an oxygen-rich environment via oxygenic photosynthetic in the root zone thereby promoting the growth and activity of methane-utilizing bacteria. Oxygen released by photosynthesis can provide dual benefits as it enhances the growth and activity of methane-oxidizing bacteria as well as limit the growth of anaerobic methanogenic archaea culminating in reduced methane emission. Formulating the ratios of the partners, stage of growth, the C–N dynamics, and media constituents would be interesting as such consortia would be a fructuous model to decipher the feedback and cross-feeding mechanisms.

Synergistic interaction occurs between methanotrophs and non-methane utilizing methylotrophs (NUM) where the intermediates produced by the methanotrophs (methanol, formaldehyde, and formate) can be used as a C-source by the NUM and supports its existence. On the other hand, NUM consumes these toxic intermediates of the methanotrophs by cross-feeding and aid in the methane removal process (Rani et al. 2021d). Besides algae, growth stimulation of methane utilizing *Methylovulum miyakonense* in presence of cobalamin secreting *Rhizobium* has been documented (Iguchi et al. 2011). Removal of toxic intermediates like organic acids can also support the growth and proliferation of methanotrophic partners (Singh et al. 2019). Synergistic interactions occur between the methanotrophs and heterotrophs where one provides the other with a carbon source and the other produces a

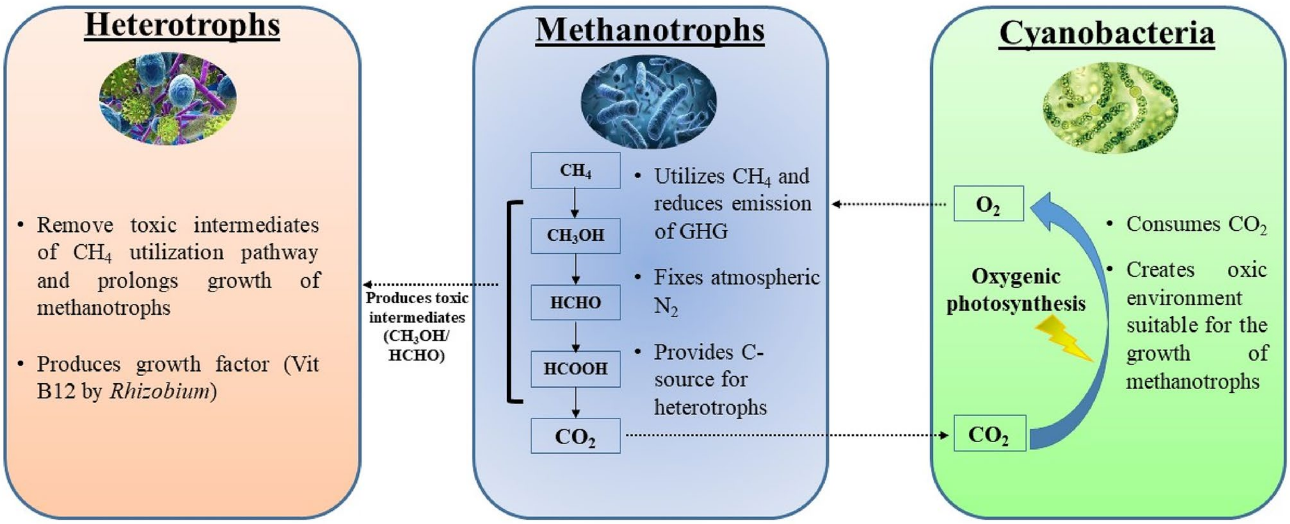


Fig. 2 Effect of co-inoculating methane-utilizing bacteria with cyanobacteria or microalga

growth factor or removes toxic intermediates from the environment and allows them to thrive in natural environments (Stock et al. 2013; Ho et al. 2014; Veraart et al. 2018; Singh et al. 2019).

Limitations and possible solutions of using methane-utilizing bacteria in agriculture

The potential of methane-utilizing bacteria in reducing the overall CH_4 emission by the process of oxidizing the CH_4 released from the paddy ecosystem has not been explored and needs to be integrated into the biofertilizer demonstration, popularization, and commercialization programs at the policy level. Blue-green algae, *Azotobacter*, and *Azospirillum* are still the popular bioinoculants recommended for rice cultivation (Ojha et al. 2018). The effect of other microorganisms like *Burkholderia, Gluconacetobacter, Azoarcus, Herbaspirillum, Alcaligenes, Pantoea, Bacillus*, and *Stenotrophomonas* are known for their promise in growth promotion and yield of the crop, under field condition (Egener et al. 1999; Duangpaeng et al. 2012; Adnan et al. 2016; Gholamalizadeh et al. 2017). But the use of methane-utilizing bacteria for CH_4 mitigation and plant growth promotion in the flooded ecosystem of paddy is still in its infancy. One of the major limitations of using methane-utilizing bacteria is the fluctuating CH_4 concentration which acts as a C source for the growth and proliferation of these microorganisms (Jain et al. 2004). CH_4 concentration in the paddy field varies with the growth stage as well as the water level (Tyagi et al. 2009; Khosa et al. 2011). Higher emission of CH_4 at the tillering to the flowering stage followed by a gradual decrease till maturity has been observed (Islam et al. 2019; Rani et al. 2021a). Some researchers report maximum emission at the tillering stage (Oda and Nguyen 2019), whereas others observed an increase in CH_4 emission till the flowering stage (Gaihre et al. 2011). Slight variation may be observed due to the standing water regime in the rice field determining the redox potential of the soil and the growth and activity of methanogenic archaea responsible for biogenic CH_4 production (Epule et al. 2011). The changing CH_4 concentration in the rice field leads to a fluctuating population of methane-utilizing bacteria in the field (Macalady 2002; Ma et al. 2013). Methane-utilizing bacteria-based bioinoculant when used will face a constant problem of maintaining the microbial load under in vivo conditions for optimum performance. A higher reduction in CH_4 emission was observed till the 5th day of inoculation with methane-utilizing bacteria in a field experiment followed by a gradual decrease signifying the inability of the isolate to sustain their population under natural conditions (Nontji et al. 2016). A possible solution to this problem is the recurrent use of bioinoculant at regular time intervals viz. at the time of sowing, transplanting, tillering, and followed by flowering if required (Rani et al. 2021a). Another alternative is to use methane-utilizing bacteria which can form some resting structures like cysts and spores and can maintain their population under field conditions (Thirumurugan and Asha 2010). Members of type I methanotrophs (*Methylobacter*) along with type II methanotrophs of genera *Methylosinus* and *Methylocystis* can form resting structures (Bowman 2006) and thus can be preferred while choosing methane-utilizing bacteria for field application. The strain selected for field application should also have a good competitive ability and outgrow the natural microflora already present in the soil (Thomas and Singh 2019). Facultative CH_4 oxidizers (*Methylocystis, Methylocapsa*, and *Methylacidiphilum)* that can utilize only one or two alternative substrates viz. acetate, ethanol, or H_2, depending on the strain with high affinity for CH_4 can be selected under field condition so that in the absence of CH_4 they can sustain on other available carbon sources (Dedysh and Dunfield 2010). However, their preference for CH_4 over other carbon sources should be ascertained as *Methylocella* can grow on a range of alternative substrates like acetate, pyruvate, succinate, malate, ethanol, propane, ethane, propanol, propanediol, acetone, methyl acetate, acetol, glycerol, propionate, tetrahydrofuran, and gluconate and thus, cannot be considered for mitigation of CH_4 emission under natural environment (Dedysh and Dunfield 2010). Based on these limitations and precautions, research findings of field experiments on the large-scale application of methane-utilizing bacteria in paddy are limited.

With global warming and climate change being recognized as major challenges, it is time to rethink our approaches to agricultural cultivation and livestock production. Experts recommend that staple crops such as rice, alternate wetting, and drying or direct seeding approaches be popularized that could halve emissions and require one-third less water, making it more economical. They also advocate that paddy be irrigated and drained two to three times throughout the growing season, rather than continuous flooding limiting methane production without impacting yield. Alternatively, the use of methane-utilizing bacteria in agriculture for mitigating CH_4 emissions and promoting crop productivity is an environment-friendly option, which can benefit crop and soil productivity. This requires directed and concentrated focused efforts supported by biologists, farmers, policy makers, and administrators at the village/farm level.

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Declarations

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