



Review article

Soil methane dynamics: Microbial mechanisms and agricultural management strategies

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Abstract

Importance of the work: Soil methane (CH₄) dynamics remain poorly addressed in terms of microbial interactions and integrated mitigation strategies under agricultural management.

Objectives: To review soil microbial mechanisms of CH₄ production/consumption and to evaluate how management strategies influence CH₄ emissions.

Materials and Methods: A narrative literature review was conducted using scientific databases (Web of Science, Scopus, Google Scholar) and tools such as Connected Papers. Studies were synthesized on methanogenic/methanotrophic microorganisms, biofertilizer applications and management interventions (such as water and fertilizer regimes) across agroecosystems.

Results: CH₄ production in soil is driven by anaerobic methanogenic archaea, while aerobic methanotrophic bacteria consume CH₄. This balance is strongly regulated by environmental factors, such as soil moisture, redox potential and substrate availability. Alternate wetting and drying practices have reduced CH₄ emissions by 30–70%, while ammonium-based fertilizers may suppress methanotrophy. Inoculation with methanotrophs and co-inoculation with plant growth-promoting rhizobacterial strains have produced emission reductions up to 68%. In addition, *Azolla*-cyanobacteria systems decrease emissions by increasing soil redox potential and O₂ availability. However, interactions among practices (such as fertilization × water regime) are complex and many single-factor interventions fail under field conditions. It is essential for consistent mitigation outcomes to maintain microbial diversity and to understand these synergistic/antagonistic effects.

Main finding: Integrated, site-specific strategies, combining microbial agents with optimized water and fertilizer management, enhance CH₄ oxidation and suppress production. Holistic, microbiome-informed interventions are critical for effective and sustainable greenhouse gas mitigation in agriculture.

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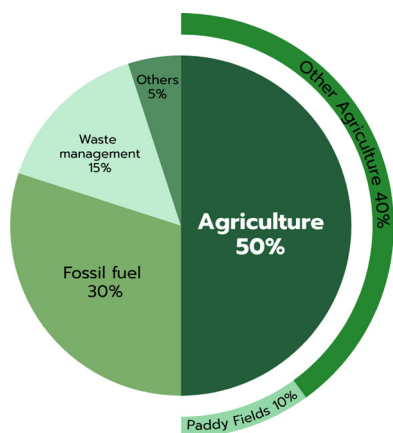
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Introduction

Methane (CH_4) is a potent greenhouse gas that plays a importantrole in the atmospheric greenhouse gas balance. Its global warming potential is approximately 28 times greater than that of carbon dioxide (CO_2) over a 100 year time horizon (Intergovernmental Panel on Climate Change, 2021); however, this value can vary in the literature depending on different time horizons and calculation methods (Malyan et al., 2019). Global CH_4 concentrations have increased by more than 150% compared to the pre-industrial era (~715 parts per billion), reaching levels exceeding 1.9 parts per million today (Saunois et al., 2025). Although CH_4 's atmospheric lifetime approximately 12 yr is shorter than that of CO_2 , its contribution to the acceleration of climate change, especially in the short term, is undeniable (Solomon et al., 2007).

More than 60% of global CH_4 emissions are anthropogenic (human-caused), with a substantialportion originating from sectors such as agriculture (Wanapat et al., 2024), fossil fuel production and use, and waste management (Jackson et al., 2020; Saunois et al., 2025) (Fig. 1). Within the agricultural sector, rice cultivation, particularly under flooded conditions, is a substantialsource of CH_4 emissions, responsible for approximately 10–12% of global anthropogenic CH_4 emissions, by promoting anaerobic microbial processes (Neue, 1993; Van Groenigen et al., 2011; Ciais et al., 2013). The flooded anaerobic soil conditions of rice paddies provide an ideal environment for CH_4 -producing microorganisms (Sass, 1994).



“Paddy fields (10%)” and “Other Agriculture (excluding rice paddies) (40%)” represent direct contributions to the global total, together comprising the overall agricultural share (~50%).

Fig. 1 Distribution of global anthropogenic CH_4 emission sources by sector (Intergovernmental Panel on Climate Change, 2021; Saunois et al., 2025). Percentages for

The net CH_4 flux in soil ecosystems depends on the dynamic balance of two fundamental microbial processes: 1) methanogenesis—the production of CH_4 through the decomposition of organic matter by methanogenic archaea under anaerobic conditions; and 2) methanotrophy—the consumption of CH_4 by oxidation to CO_2 by methanotrophic bacteria (methanotrophs) under aerobic conditions (Conrad, 2007). Typically, methanogenesis intensifies when the soil redox potential (Eh) drops below approximately -150 to -200 mV, utilizing simple substrates such as hydrogen (H_2), CO_2 and acetate (Smith et al., 1993; Ferry, 1999). In contrast, methanotrophy occurs in oxygenated soil layers, particularly at the soil–atmosphere interface and in the plant root zone (rhizosphere), where O_2 diffusion and root-mediated oxygen release create oxic microsites (Bodelier et al., 2000). In these zones, aerobic methanotrophs oxidize CH_4 to CO_2 , with O_2 serving both as a substrate for methane monooxygenase and as the terminal electron acceptor for respiration. Consequently, a substantial fraction of CH_4 produced in deeper anoxic layers can be consumed before reaching the atmosphere, allowing soils to function as a major CH_4 sink (Semrau et al., 2010; Smith et al., 2018). This balance is strongly influenced by environmental factors, including soil moisture (and thus O_2 availability), temperature, pH, Eh and the substrate of organic matter availability (Born et al., 1990; Le Mer and Roger, 2001) (Fig. 2).

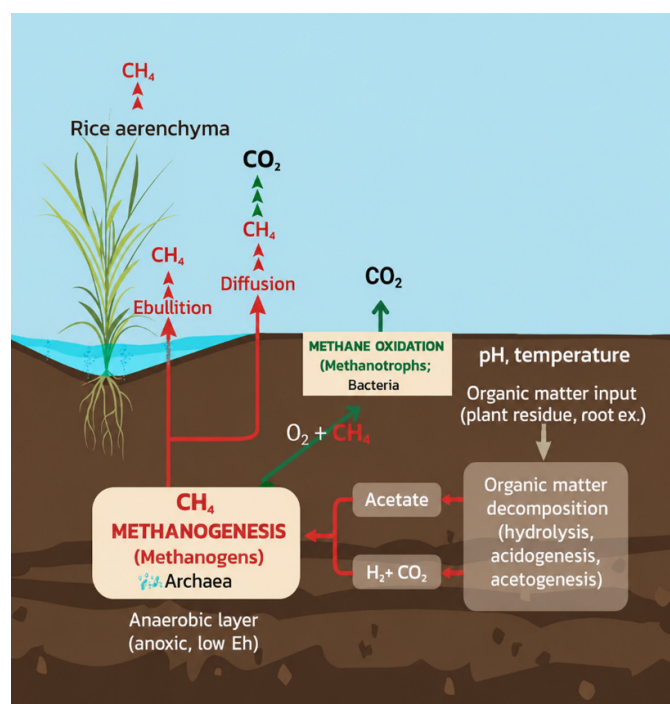


Fig. 2 Mechanisms of methane production and oxidation in soil.

Agricultural practices can greatly alter this delicate balance and consequently net CH₄ emissions. For example, water management strategies, such as alternate wetting and drying (AWD), can reduce CH₄ emissions by 30–70% by periodically aerating the soil (Linguist et al., 2012), while ammonium (NH₄⁺)-based fertilizers can inhibit methanotrophic activity, thereby limiting CH₄ consumption (Bender and Conrad, 1994; Hütsch, 2001). Similarly, biological interventions, such as methanotroph bacterial inoculation or the use of photosynthetic organisms like *Azolla*, offer potential for reducing emissions by increasing soil oxygenation or modifying microbial communities (Bharati et al., 2000; Xu et al., 2017).

However, many studies have examined these management strategies (water, fertilizer, tillage, biological agents) and environmental factors separately rather than in an integrated framework (Le Mer and Roger, 2001; Atav et al., 2025). A comprehensive and integrated understanding of the combined and interactive (synergistic or antagonistic) effects of different management practices on the methanogenic and methanotrophic communities, as well as the underlying microbial mechanisms of these interactions, remains lacking. For example, how does the effectiveness of the AWD application change under different fertilization regimes? To what extent does the success of biological inoculants vary under different soil types and water management conditions? Neglecting such interactions hinders the development of optimized and sustainable strategies for mitigating CH₄ emissions from agricultural systems.

This review study aimed to address the current knowledge gaps surrounding the interactions between agricultural management practices and the microbial mechanisms governing CH₄ dynamics in soil. While many studies have focused on individual factors, such as water management or fertilizer use, there have been limited integrated insights into their combined effects on methanogenic and methanotrophic communities. By synthesizing recent findings, the current review aimed to highlight potential synergies and antagonisms among various strategies, including fertilization, irrigation, tillage organic matter management and biological interventions, as well as the environmental and microbial factors that limit their effectiveness. In addition, the current review emphasized the need for future interdisciplinary research that bridges microbial ecology and agronomy to develop more sustainable and efficient approaches for mitigating CH₄ in agriculture.

A structured narrative survey of the literature was conducted. Relevant peer-reviewed articles were selected primarily through major academic databases, such as Web of

Science, Scopus and Google Scholar, as well as the literature discovery tool Connected Papers, using keywords such as “soil CH₄ emissions”, “methanotrophs”, “rice paddy CH₄ flux” and “biofertilizer CH₄ reduction”. The selection focused on studies investigating microbial CH₄ processes in agricultural soils, particularly in relation to management-based interventions.

Basic mechanisms of soil CH₄ cycle

The net flux of CH₄ in soil ecosystems is controlled by the dynamic balance between CH₄-producing (methanogenesis) and CH₄-consuming (methanotrophy) microbial processes (Conrad, 2007). The relative proportions of these two opposing processes determine whether the soil is a net source or sink of CH₄ and this balance is substantially influenced by environmental conditions and soil properties (Dutaur and Verchot, 2007). Ecosystems, such as rice fields and natural wetlands, especially those dominated by water-saturated conditions, are of global importance for the CH₄ cycle.

CH₄ production (methanogenesis)

Methanogenesis is a biological process carried out exclusively by methanogenic microorganisms, which operate under oxygen-free (anaerobic) conditions (Ferry, 1999; Conrad, 2007). This process is the final step in the anaerobic decomposition of complex organic matter. Typically, it involves several intermediate stages: hydrolysis (the breakdown of polymers to monomers); acidogenesis/fermentation (the conversion of monomers to simpler compounds, such as volatile fatty acids, alcohols, H₂ and CO₂, by fermentative bacteria); and acetogenesis (the production of acetate from fermentation products by acetogenic bacteria). Methanogens utilize these precursors, primarily acetate, H₂ and CO₂, to produce CH₄ (Malyan et al., 2019). Two main methanogenic pathways are recognized: acetoclastic methanogenesis (splitting acetate into CH₄ and CO₂) and hydrogenotrophic methanogenesis (reduction of CO₂ with H₂ to form CH₄) (Deppenmeier, 2002). In addition, some methanogens can utilize methyl-group-containing compounds such as methanol (methylotrophic pathway).

Methanogenesis requires strictly anaerobic conditions and typically commences and intensifies when the soil's Eh drops below approximately -150 to -200 mV (Mah et al., 1977; Le Mer and Roger, 2001). In environments with low Eh, methanogenic activity is strongly enhanced. Factors, such as soil temperature (optimum generally between 25°C and

40°C), pH (usually near neutral, approximately 6.5–7.5) and the amount of available organic carbon also substantially influence the rate of methanogenic activity (Gu et al., 2013). Furthermore, soil texture is important, as high-clay soils can retain water and prolong anaerobic microsites, which may increase the potential for CH₄ production (methanogenesis). However, clay-rich soils can also reduce gas diffusivity and constrain CH₄ transport, which may lower net CH₄ emissions (surface flux) by limiting escape or increasing the opportunity for oxidation during transport or both. In contrast, sandy soils drain more rapidly and typically sustain less methanogenic activity (Dutaur and Verchot, 2007).

CH₄ oxidation (methanotrophy)

Methanotrophy is the biological oxidation of CH₄ by methanotrophs. This process enables soil to act as a major sink for atmospheric CH₄ and can remove a considerable portion (up to 60–80%) of soil-produced CH₄ before it reaches the atmosphere (Singh et al., 2010). Methanotrophs utilize CH₄ as both a carbon and energy source.

The most common form is aerobic methanotrophy, which occurs in the presence of oxygen within the upper, oxic soil layers, where methanotrophs convert CH₄ to CO₂ (Fig. 2). Aerobic methanotrophs phylogenetically belong mainly to two groups within the phylum Proteobacteria: Type I methanotrophs (Gammaproteobacteria, such as *Methylobacter*) assimilating carbon via the ribulose monophosphate (RuMP) pathway and Type II methanotrophs (Alphaproteobacteria, such as *Methylocystis*, *Methylosinus*) assimilating carbon via the serine pathway (Op den Camp et al., 2009). These groups have different adaptations to environmental conditions, particularly in terms of pH and CH₄ concentrations (Kolb, 2009).

The first and key step in CH₄ oxidation is catalyzed by the enzyme methane monooxygenase (MMO), which converts CH₄ to methanol. There are two primary forms: particulate methane monooxygenase (pMMO), found in most methanotrophs and soluble methane monooxygenase (sMMO), produced by some species under copper limitation. Subsequently, methanol is oxidized to formaldehyde, formate and finally CO₂.

Methanotrophic activity is sensitive to environmental factors, primarily O₂. O₂ is required as both a substrate for the MMO enzyme and as the terminal electron acceptor for respiration. Aerobic methanotrophy cannot occur under limited O₂ (microaerophilic) or absent O₂ (anaerobic) conditions. Often, optimal CH₄ consumption rates are observed when the water-filled pore space (WFPS) is between 50% and 70%,

allowing for optimal diffusion of both CH₄ and O₂ (Bowden et al., 1993). Additionally, soil temperature (optimum 20–30°C) and pH (typically in the range 5.5–7.5) are crucial factors directly affecting the growth and activity of methanotroph communities (Castro et al., 1995; Kolb, 2009).

Anaerobic oxidation of CH₄ (AOM) is also an important process, particularly in anoxic marine and freshwater sediments, carried out by archaea or bacteria or both, using alternative electron acceptors such as sulfate (SO₄²⁻), nitrate (NO₃⁻), nitrite (NO) or metal oxides (Ettwig et al., 2010; Nazaries et al., 2013). However, in typical agricultural soils, especially in the upper layers where O₂ is usually present, the role of AOM is considered limited compared to aerobic methanotrophy, although it might play a role in micro-anoxic niches.

Soil moisture and the consequent O₂ availability are the most critical factors controlling the balance between methanogenesis and methanotrophy. Water saturation promotes anaerobic conditions, leading to the production of CH₄, whereas soil aeration facilitates aerobic conditions, resulting in CH₄ consumption. This balance can be continuously altered by agricultural water management practices, climate change (including changes in precipitation regimes) and land-use changes, thereby modifying the role of soils in the CH₄ cycle. Understanding these mechanisms and influencing factors is an effective strategy to mitigate CH₄ emissions.

Key microbial groups involved in CH₄ cycle and importance of diversity

Primarily, the activities of specialized groups of microorganisms drive the CH₄ cycle in soil ecosystems. Key players in this process are the CH₄-producing methanogenic archaea and the CH₄-consuming methanotrophs (Le Mer and Roger, 2001). The diversity within and between these functional groups is critically important in determining the response to environmental changes and the overall CH₄ budget of the soil (Tveit et al., 2019).

Methanogenic archaea (methanogens)

Methanogens, responsible for methanogenesis, are strictly anaerobic microorganisms belonging to the Archaea domain (Conrad, 2007). The structure and diversity of methanogen communities are greatly influenced by environmental factors, including substrate type and availability (especially acetate and H₂/CO₂), pH, temperature and Eh (Ferry, 1999). The diversity of methanogens in the soil is a factor influencing the ecosystem's potential for CH₄ production and its resilience to environmental

changes, with communities showing characteristic structures in ecosystems such as wetlands, rice paddies, peat soils and upland agricultural systems. For example, *Methylocystis* and *Methylocapsa* tend to dominate in acidic soils such as peatlands, whereas *Methylomonas* and other Gammaproteobacteria are more abundant in neutral soils (Nazaries et al., 2013).

Methanotrophs

Methanotrophs are microorganisms capable of oxidizing CH₄, using it as both an energy and a carbon source and they play a central role in making soils a net sink for atmospheric CH₄ (Hanson and Hanson, 1996). Diversity within this group is extensive, encompassing species adapted to different ecological niches. Aerobic methanotrophs are traditionally divided into two main groups based on phylogenetic and metabolic characteristics. Type I methanotrophs belong to the Gammaproteobacteria and include genera such as *Methylomonas*, *Methylobacter* and *Methylococcus*. Bacteria in this group assimilate carbon derived from CH₄ via the RuMP pathway and tend to prefer environments with near-neutral pH and relatively high CH₄ concentrations (Hanson and Hanson, 1996). Type II methanotrophs, classified within the Alphaproteobacteria, include typical examples like *Methylocystis* and *Methylosinus*. This group, which metabolizes carbon via the serine cycle, is generally better

adapted to lower CH₄ concentrations and a broader pH range, including mildly acidic conditions, compared to Type I (Kolb, 2009). Additionally, some Type II methanotrophs are known to form cyst structures that provide resistance to adverse conditions.

Beyond these two main groups, Type X species (such as *Methylococcus capsulatus*), have been identified, which partially share characteristics of both pathways and methanotrophs belonging to the Phylum Verrucomicrobia, particularly adapted to acidic environments (Pol et al., 2007; Dunfield et al., 2007). A summary comparing the key characteristics of these major aerobic methanotroph groups is presented in Table 1. Recent studies have indicated that methanotrophic diversity extends beyond these groups, highlighting a broader microbial repertoire involved in CH₄ oxidation than previously thought (Ahmadi and Lackner, 2024; Bicaldo et al., 2024).

Community structure is shaped strongly by the soil environment; methanotrophs are often concentrated in the rhizosphere, acidic soils commonly harbor *Methylocapsa* and *Methylocystis*, while neutral agricultural soils are dominated by *Methylomonas*. High-affinity taxa, such as *Methylocapsa gorgona*, can oxidize CH₄ even at near-atmospheric concentrations, making them critical for the soil CH₄ sink function.

Table 1 Key characteristics and classification of major aerobic methanotroph groups

Characteristic	Type I methanotrophs	Type II methanotrophs	Verrucomicrobia methanotrophs
Phylogenetic class/phylum	Gammaproteobacteria (e.g., <i>Methylococcaceae</i>) (Nazaries et al., 2013; Rani et al., 2021)	Alphaproteobacteria (e.g., <i>Methylocystaceae</i> , <i>Beijerinckiaceae</i>) (Nazaries et al., 2013; Op den Camp et al., 2009)	Phylum Verrucomicrobia (Dunfield et al., 2007; Nazaries et al., 2013)
Carbon assimilation pathway	RuMP (Hanson and Hanson, 1996; Kolb, 2009)	Serine Cycle (Op den Camp et al., 2009; Kolb, 2009)	Calvin-Benson-Bassham cycle or others (Op den Camp et al., 2009)
Dominant MMO type	pMMO (sMMO in some species) (Semrau et al., 2010)	pMMO (sMMO in some species) (Semrau et al., 2010)	pMMO (Op den Camp et al., 2009; Pol et al., 2007)
Typical genera	<i>Methylomonas</i> , <i>Methylobacter</i> , <i>Methylococcus</i> (Hanson and Hanson, 1996; Rani et al., 2021)	<i>Methylocystis</i> , <i>Methylosinus</i> , <i>Methylocella</i> , <i>Methylocapsa</i> (Op den Camp et al., 2009; Tveit et al., 2019)	<i>Methylacidiphilum</i> , <i>Methylacidimicrobium</i> (Pol et al., 2007; Op den Camp et al., 2009)
Preferred conditions	Near-neutral pH, high CH ₄ concentration (Kolb, 2009; Nazaries et al., 2013)	Mildly acidic/neutral pH, Low CH ₄ concentration (Kolb, 2009; Tveit et al., 2019)	Very Acidic pH (<1-5), Wide CH ₄ range (Pol et al., 2007; Dunfield et al., 2007)
Other characteristics	Generally faster growth, Complex internal membranes (Hanson and Hanson, 1996)	Cyst/Exopolymer formation, generally slower growth (Hanson and Hanson, 1996)	Acidophilic, some can be thermophilic (Pol et al., 2007; Op den Camp et al., 2009)

MMO = methane monooxygenase.

The community structure of methanotrophs and the dominance of specific species vary greatly depending on environmental factors such as soil type, moisture content, O₂ status, pH and temperature (Dedysh et al., 2002). Methane-oxidizing bacteria (MOB) populations are often concentrated near plant roots, with much higher densities in the rhizosphere than in the bulk soil or within the root tissue itself (Bosse and Frenzel, 1997) (Fig. 3). For example, often, *Methylocapsa* and *Methylocystis* species (Type II and Verrucomicrobia) are prevalent in acidic soils and peat. In contrast, *Methylomonas* species (Type I) may be more abundant in neutral pH agricultural soils. "High-affinity" methanotrophs, capable of oxidizing CH₄, even at low atmospheric concentrations approximately 1.8 parts per million by volume, such as some *Methylocystis* species and newly discovered species like *Methylocapsa gorgona*, are critically important for the soil's net CH₄ sink function (Holmes et al., 1999; Tveit et al., 2019). These high-affinity methanotrophs play a major ecological role by remaining active even at low CH₄ levels and may apply oligotrophic strategies, utilizing other atmospheric trace gases, such as H₂ or CO₂. Furthermore, some methanotrophs have been shown to provide additional benefits such as fixing atmospheric nitrogen (N), solubilizing insoluble phosphates and producing plant growth-promoting phytohormones (Doronina et al., 2004; Taopan et al., 2018).

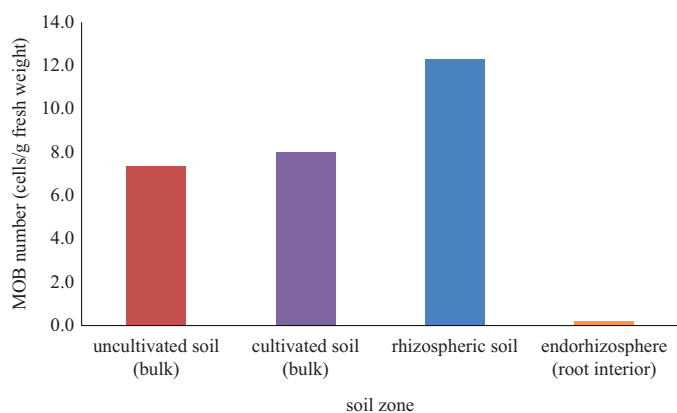


Fig. 3 Density of methane-oxidizing bacteria (MOB) in bulk soil, rhizospheric soil (0.1–0.2 mm layer around roots) and endorhizosphere (root interior) associated with rice plants, redrawn from Bosse and Frenzel (1997).

Importance of microbial diversity in CH₄ cycle and management impacts

The overall diversity of soil microbial communities is vital for regulating the CH₄ cycle and for the ecosystem's resilience to environmental stress. In particular, the diversity and functional integrity of the methanotroph community directly determine the soil's capacity to consume atmospheric CH₄. However, agricultural activities, land-use changes and practices such as intensive fertilization can negatively impact soil microbial diversity (Levine et al., 2011; Nazaries et al., 2013). There is considerable evidence that the long-term application of high doses of NH₄⁺-based fertilizers can alter the methanotroph community structure or inhibit activity, or both, thereby decreasing the CH₄ oxidation capacity (sink function) of soils (Jacinthe and Lal, 2006; Kong et al., 2019).

In this context, conserving soil microbial diversity and supporting the functional groups involved in the CH₄ cycle are strategic goals for both mitigating greenhouse gas emissions and maintaining overall ecosystem health. Agricultural practices that promote microbial diversity, such as appropriate organic matter management, crop rotation, reduced tillage and balanced fertilization, hold considerable potential for the soil CH₄ sink function and reducing CH₄ emissions (Levine et al., 2011).

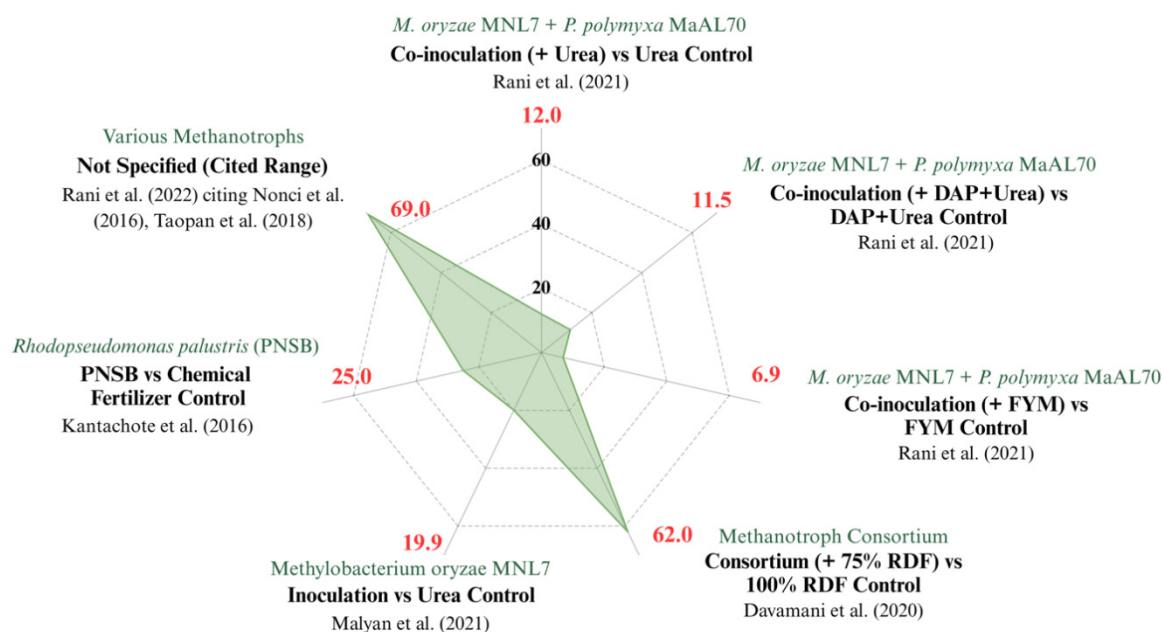
Bacterial intervention approaches in agricultural ecosystems

In line with goals to enhance sustainability and reduce the environmental impact of agricultural production, there is growing interest in strategies that harness the potential of soil microbial communities. Specifically, the application (inoculation) or stimulation of specific bacterial groups to mitigate CH₄ emissions and improve soil fertility stands out as a potential biological intervention approach (Davamani et al., 2020; Malyan et al., 2021). These approaches focus primarily on the use of CH₄-consuming (methanotroph) bacteria or other beneficial bacteria that promote plant growth such as biofertilizers and plant growth-promoting rhizobacteria (PGPR). Theoretically the direct inoculation of methanotrophs into the soil or the plant root zone (rhizosphere) holds the potential to reduce net CH₄ emissions by increasing the soil's CH₄ oxidation capacity (Tveit et al., 2019). Laboratory and greenhouse studies have shown that the application of various methanotroph species, such as *Methylocystis*, *Methylocapsa* and *Methylobacterium*, or consortia thereof, can enhance CH₄ consumption (Horz et al., 2002; Taopan et al., 2018;

Davamani et al., 2020). For example, Davamani et al. (2020) reported that inoculations with a methanotroph consortium substantially reduced CH₄ emissions (by 57–68%) under field conditions.

Besides methanotrophs, other groups of bacteria recognized as PGPR or biofertilizers (such as *Azotobacter*, *Rhizobium*, *Paenibacillus*) may indirectly influence the CH₄ cycle. These bacteria can perform biological N fixation, enhance phosphorus solubility or produce phytohormones (Doronina et al., 2004). Healthier plant growth could potentially support methanotrophic activity indirectly by enhancing rhizosphere oxygenation. Furthermore, it has been suggested that these bacteria might suppress methanogenic activity by competing with native microbial communities or altering substrate utilization (Kantachote et al., 2016). Co-inoculation of bacteria from different functional groups, such as *Paenibacillus polymyxa* and *Methylobacterium oryzae*, has been shown in some studies to both reduce CH₄ emissions and increase rice yield (Rani et al., 2021). Indeed, various studies using different bacterial agents and approaches, such as methanotroph consortia, single strains, co-inoculations with PGPR or even purple non-sulfur bacteria (PNSB), have reported a wide range of CH₄ emission reductions in rice systems (Fig. 4). However, the success and efficacy of bacterial intervention

approaches under field conditions face several challenges and results are not always consistent. One of the biggest hurdles to success is the ability of inoculated bacteria to survive, establish and compete with native microbial communities in the soil environment. Factors (soil type, pH, moisture, temperature organic matter content, the existing microbial community composition) can substantially affect the performance of inoculants (Tveit et al., 2019). Furthermore, in cases where N-fixing bacteria are used, an excessive increase in soil N levels could potentially inhibit the activity of methanotrophs, leading to an undesirable side effect (Bayer et al., 2012). This poses a risk, particularly under conditions where N is not limiting for methanotrophs or where NH₄⁺ concentrations are high. Therefore, the effectiveness of bacterial intervention strategies requires careful planning, appropriate strain selection, correct timing and dosage of application and consideration of local environmental conditions. A major challenge in this field is that many approaches showing promising results under laboratory and greenhouse conditions fail to demonstrate the same success at the field scale. More research is needed on the long-term effects, ecological risks and economic viability of these interventions. Microbial inoculations hold greater potential for success when integrated with other sustainable agricultural practices such as appropriate water and fertilizer management.



The “Not Specified (Cited Range)” value reflects the upper end (approximately 69%) of the range (51–88%) cited by Rani et al. (2022), referring to results from Nonci et al. (2016) and Taopan et al. (2018).

Fig. 4 Comparison of reported CH₄ emission reduction percentages from selected studies using different bacterial inoculation approaches (co-inoculation, consortium, single strain, PNSB in rice paddies) relative to respective control used in each cited study, where baseline conditions differ among studies.

Management of CH₄ emissions with cyanobacteria and *Azolla* applications

Noteworthy among the biological strategies aimed at reducing CH₄ emissions in agricultural wetland ecosystems (particularly rice paddies) is the use of cyanobacteria and aquatic ferns, such as *Azolla*, that live symbiotically with them. These approaches influence the CH₄ cycle through indirect mechanisms, rather than directly consuming CH₄. The primary mechanism of action is the production of O₂ via their photosynthetic activity at the water surface or the soil-water interface, or both (Prasanna et al., 2002; Xu et al., 2017). This produces O₂, which increases the Eh in the upper soil layers, suppressing the activity of methanogenic archaea that require strictly anaerobic conditions. Specifically, this effect is pronounced in the system involving *Azolla*, which forms a cover on the water surface and its symbiotic N-fixing cyanobacterium (*Anabaena azollae*). The *Azolla* cover can enhance O₂ availability at the soil-floodwater interface via increased dissolved oxygen and higher redox potential, thereby suppressing methanogenesis and reducing CH₄ emissions (Bharati et al., 2000). Kimani et al. (2018) showed that integrating *Azolla* into a rice paddy increased the soil Eh and substantially reduced CH₄ emissions (by rates reaching 30–50%) compared to the control. However, the effect of *Azolla* can vary depending on management practices. While incorporating *Azolla* as green manure into the soil might increase CH₄ production by providing additional substrate for methanogens from the decomposing biomass (as reported by Ying et al., 2000), growing it concurrently with rice (dual cropping) has generally been more effective in reducing

emissions (Bharati et al., 2000; Nungkat et al., 2015). This highlights the importance of the management method in determining the net effect.

Another critical, characteristic of cyanobacteria—whether free-living or symbiotic with *Azolla*—is their ability to fix atmospheric N (Singh et al., 2011). This offers the potential to reduce the need for chemical N fertilizers by providing a major N source for plants. Reduced use of NH₄⁺-based chemical N fertilizers may alleviate inhibition of methanotrophs because NH₄⁺ can interfere competitively with methane monooxygenase and may also alter soil oxygen demand and the microbial community structure, thereby reducing CH₄ oxidation capacity. Accordingly, studies comparing *Azolla* application combined with reduced N inputs versus full chemical fertilization have reported substantial reductions in CH₄ emissions; however, yield responses have been variable, ranging from negligible effects to slight decreases (Fig. 5). Nevertheless, consideration should be given to the risk that excessive N input into the soil through biological fixation might, in some cases, suppress methanotroph activity and negatively affect CH₄ oxidation (Bayer et al., 2012).

The use of cyanobacteria and particularly *Azolla*-cyanobacteria systems, offers an environment-friendly approach for managing CH₄ emissions in agricultural wetlands, potentially providing additional benefits (N input) to farmers. At the microbial level, CH₄ production in flooded rice soils is driven primarily by methanogenic archaea such as *Methanosaeta* (*Methanothrix*) *concilii* and *Methanosarcina barkeri* (acetoclastic methanogenesis) as well as *Methanobacterium formicicum* and *Methanocella arvoryzae* (hydrogenotrophic methanogenesis) (Lyu et al., 2018).

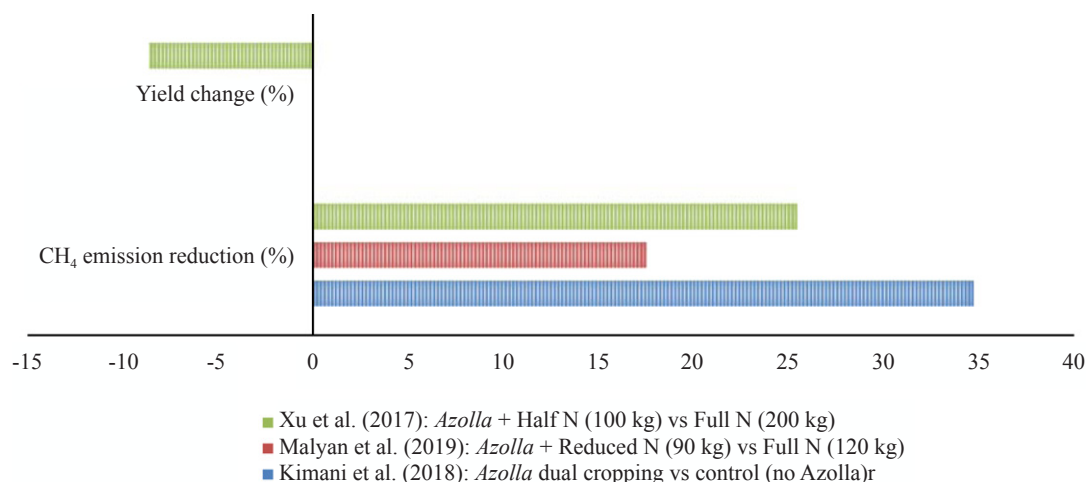


Fig. 5 Percentage change in CH₄ emission reduction and rice grain yield due to *Azolla* application relative to respective control treatments reported in selected studies

In contrast, CH₄ oxidation in oxic microsites at the soil-floodwater interface and rhizosphere is associated commonly with aerobic methanotrophs including *Methylococcus capsulatus*, *Methylomonas methanica*, *Methylobacter luteus*, *Methylosinus trichosporium* and *Methylocystis parvus* (Semrau et al., 2010). Therefore, management practices that increase O₂ availability and redox potential (such as *Azolla* cover and optimized N inputs) are expected to suppress methanogen activity, while supporting methanotroph-mediated CH₄ oxidation. However, the effectiveness of these applications can vary greatly depending on the species used, application method (incorporation versus dual cropping), density, water regime and soil conditions. Further field studies are needed to optimize these biological approaches and provide a better understanding of their long-term effects and performance under different environmental conditions.

Key environmental factors affecting CH₄ cycle

Microbial activity is influenced by the physical and chemical conditions of the soil environment. Key environmental factors that determine the activity of microbial communities and therefore the net CH₄ flux of soils include soil moisture, O₂ status, temperature, pH, Eh and substrate availability (Le Mer and Roger, 2001).

Soil moisture and O₂ availability are perhaps the most critical regulators of the CH₄ cycle and are closely interrelated. The saturation of soil pores with water (high WFPS) substantially limits gas diffusion, especially the entry of O₂ into the soil profile (Gao et al., 2014). This leads to the formation of oxygen-free (anaerobic) conditions and an increase in the activity of CH₄-producing methanogenic archaea (Dilustro et al., 2005; Dutaur and Verchot, 2007). Conversely, drying or well-drained soil allows atmospheric O₂ to enter the pores. Increased O₂ availability creates favorable conditions for the growth and activity of CH₄-consuming aerobic methanotrophs (Conrad and Klose, 1999; Smith et al., 2000). Therefore, changes in soil moisture content directly affect the balance between methanogenesis and methanotrophy, determining whether a soil functions as a source or sink of CH₄. Often, methanotrophic activity has been reported to be maximal at WFPS values in the range 50–70%, indicating a balance point where both CH₄ and O₂ are available optimally (Bowden et al., 1993). Soil temperature is another critical factor affecting the rates of all microbial reactions. Both methanogenesis and methanotrophy exhibit optimal activity within specific temperature ranges. Generally, the optimum temperature range for methanotrophic activity has been reported as 20°–30°C

under temperate conditions, although this range can vary among different methanotroph groups and climate zones (Castro et al., 1995; Kolb, 2009). Extremely low or high temperatures can greatly slow down the rates of both processes. Soil pH regulates the CH₄ cycle by affecting the structure of microbial communities and enzyme activity. Generally, methanogens prefer near-neutral pH conditions, while methanotrophs can be active over a broader pH range. As previously mentioned, Type I methanotrophs tend to dominate under neutral pH conditions, whereas Type II methanotrophs are often more prevalent in mildly acidic environments (Kolb, 2009). Soil pH can also have indirect effects on microbial activity by influencing nutrient solubility and the form of potential inhibitors (such as certain metals). Eh is a critical parameter reflecting the oxidation-reduction status of the soil. Methanogenesis can only occur under strongly reducing conditions where the Eh value drops below a certain threshold (around -150 to -200 mV) (Mah et al., 1977; Le Mer and Roger, 2001). Soil saturation with water leads to O₂ depletion and the reduction of other electron acceptors (including NO₃⁻, Fe, SO₄²⁻), lowering the Eh value and creating a suitable environment for methanogenesis. Conversely, methanotrophy requires oxic conditions with high Eh values. Soil type is another key determinant of CH₄ dynamics and strongly modulates the effects of other environmental factors. Generally, clay-rich soils retain water and create prolonged anaerobic microsites, which enhance methanogenesis, whereas sandy soils allow greater aeration and diffusion, favoring methanotrophy (Dutaur and Verchot, 2007). Peat and organic soils, due to their high carbon content, often sustain large CH₄ fluxes but may also support unique high-affinity methanotrophs that mitigate emissions (Tveit et al., 2019). Consequently, the effectiveness of management practices, such as AWD, biochar application or microbial inoculation, can vary widely across soil types, underscoring the importance of site-specific strategies for CH₄ mitigation. Substrate availability, particularly the amount of decomposable organic matter, determines the potential for methanogenic activity. The end products of anaerobic organic matter decomposition, such as acetate and H₂, are the primary substrates for methanogens (Malyan et al., 2019; Ridla et al., 2025). Therefore, adding very large amounts of fresh organic matter (such as plant residues, manures) to the soil can greatly increase CH₄ production, especially under anaerobic conditions. In addition, vegetation can influence the cycle by providing substrates through root exudates, stimulating methanogenesis and by transporting O₂ via roots, supporting methanotrophy in the rhizosphere (Megonigal et al., 2004; Dalal and Allen, 2008).

Changes in the complex interactions among these environmental factors and agricultural management practices (such as irrigation, tillage, fertilization, crop selection) can have a major impact on soil CH₄ fluxes by altering these factors. Understanding these interactions is essential for developing effective CH₄ mitigation strategies.

Effects of agricultural management strategies on CH₄ cycle

Agricultural activities shape the CH₄ production and consumption processes by altering the physical, chemical and biological properties of soils. Therefore, the selection and implementation of appropriate agricultural management strategies play critical roles in mitigating agriculture-derived CH₄ emissions. This section discusses the effects of key management practices (such as water management organic matter and fertilization management, tillage, and plant and cropping management) on the soil CH₄ cycle, their underlying microbial mechanisms and potential for optimization, considering their interrelationships.

Water management is one of the most effective strategies for controlling CH₄ emissions in agricultural systems involving flooding such as rice cultivation. Traditional continuous flooding quickly leads to anaerobic soil conditions, which favor methanogenic activity and result in high CH₄ emissions (Frolking et al., 2002; Van Groenigen et al., 2011). In contrast, alternative water management techniques that allow for periodic soil aeration greatly alter this balance. Practices, such as AWD or midseason drainage, allow O₂ entry into the soil profile, thereby suppressing methanogenic activity, while simultaneously stimulating the activity of aerobic methanotrophs (Le Mer and Roger, 2001). Previous studies and meta-analyses have demonstrated that controlled water management practices can substantially reduce CH₄ emissions, often by 30–70% or more, compared to continuous flooding (Linguist et al., 2012; Jiang et al., 2019). However, a potential side effect of these water-saving methods is the increased risk of nitrous oxide (N₂O) emissions, another potent greenhouse gas, due to the repeated wetting-drying cycles stimulating nitrification-denitrification processes (Zou et al., 2005; Lagomarsino et al., 2016). This necessitates careful consideration of the trade-offs between CH₄ and N₂O when optimizing water management strategies.

Alongside the water regime, organic matter management has a strong influence on CH₄ fluxes, as organic materials are the primary source of substrates for methanogens. The direct incorporation of fresh plant residues with easily decomposable

carbon, such as rice straw, substantially stimulates methanogenic activity and increases CH₄ emissions (Yagi and Minami, 1990; Wang et al., 1992; Neue et al., 1996). Alternative practices, such as removing straw from the field or applying it after composting, can lead to lower emissions compared to direct incorporation (Sander et al., 2014). Similarly, using composted manure instead of fresh manure is an effective method to reduce CH₄ production, as the labile carbon fraction is largely decomposed aerobically during composting (Watanabe et al., 2009; Pramanik and Kim, 2014; Kong et al., 2019). The application of biochar, a product of biomass pyrolysis, has shown variable effects on CH₄ emissions; in some cases, it may reduce emissions by improving soil aeration, altering redox conditions, releasing potentially toxic compounds for methanogens or providing habitat for methanotrophs (Wang et al., 2012; Jeffery et al., 2016); however, the net effect depends heavily on biochar properties and soil conditions (Zhang et al., 2012). Notably, the effectiveness of biochar depends heavily on the feedstock used. For example, rice husk- and straw-derived biochars often enhance soil aeration and reduce methanogenesis in paddy soils, while wood-derived biochars are typically more stable and primarily act by improving soil structure (Zhang et al., 2012). Manure-based biochars are nutrient-rich and may stimulate both crop growth and microbial activity, though in some cases they can provide additional labile carbon that temporarily increases CH₄ emissions (Nguyen et al., 2020). Sewage sludge biochars, although less common, have been reported to reduce CH₄ emissions by supplying mineral surfaces that favor methanotrophic colonization (Zhou et al., 2023). These differences highlight that the effects of a biochar cannot be generalized without reference to its feedstock origin. While essential for soil health, the management of organic matter must be carefully optimized to consider its impact on CH₄ emissions.

Fertilization management influences the CH₄ cycle in complex ways, particularly the type and application method of nitrogenous fertilizers. High application rates of NH₄⁺ based fertilizers can inhibit methanotrophic activity, possibly through competition for the MMO enzyme or O₂ depletion during nitrification, thus reducing CH₄ consumption (Bender and Conrad, 1994; Hütsch, 2001). Conversely, fertilizers containing NO₃⁻ or SO₄²⁻ can suppress CH₄ production under anaerobic conditions by serving as alternative electron acceptors or competing with methanogens (Klüber and Conrad, 1998; Malyan et al., 2019). Therefore, the choice of the form of the fertilizer is essential. Furthermore, using slow-release

fertilizers or nitrification inhibitors has potential to mitigate the negative impact on methanotrophs and control N_2O emissions (Weiske et al., 2001; Malla et al., 2005). Balanced fertilization regimes, including not just N but also P and K, might optimize CH_4 emissions indirectly by improving overall plant health and root activity (Babu et al., 2006). Fertilization strategies interact strongly with other management practices, particularly water management and organic matter additions, to determine the net greenhouse gas balance.

Tillage practices influence CH_4 fluxes by modifying the soil physical environment, particularly through changes in aeration and water retention. While conventional tillage may temporarily enhance CH_4 oxidation by aerating the soil, it can lead to a long-term decline in organic matter. Conservation tillage or no-till systems improve soil health. However, they have might increase CH_4 production, especially in the initial years or in poorly drained soils, due to increased moisture retention and surface accumulation of organic matter (Six et al., 2002; Baggs et al., 2003). Although the CH_4 oxidation capacity might improve over the long term as the soil structure improves and microbial communities adapt in no-till systems, such adaptation can be slow (Jacinthe and Lal, 2006). The net effect of tillage must be evaluated in conjunction with climate, soil type and other management practices such as residue management.

Plant and cropping management also play a role. Different plant cultivars vary genetically in root structure, exudation patterns and O_2 transport capacity via aerenchyma, resulting in inter-varietal differences in CH_4 emissions (Aulakh et al., 2001; Gutierrez et al., 2013). Selecting cultivars with lower emission potential (Wang et al., 1999) or adopting alternative planting methods, such as “direct seeded rice”, instead of

traditional transplanting (Pathak et al., 2011; Jain et al., 2014) can contribute to CH_4 mitigation that often is associated with reduced soil disturbance and altered water management. Although most studies have been conducted in rice-based systems, similar principles apply in other cropping systems. For example, upland maize and wheat fields in temperate regions generally act as net CH_4 sinks due to active methanotrophic communities (Kizilova et al., 2013; Judd et al., 2016), while sugarcane and soybean systems in tropical regions can produce substantial CH_4 fluxes when organic residues accumulate (Tavares et al., 2018). In addition, peat soils under cultivation in northern Europe and North America are recognized as important agricultural CH_4 sources (Oh et al., 2020).

As evident from the diverse effects of individual management strategies summarized in Table 2, there is no single approach that effectively mitigates agricultural CH_4 emissions. Often, the impact of different management strategies is interdependent and shaped by local environmental conditions, soil properties and socio-economic factors. For example, the effectiveness of water management can depend on the type of fertilizer applied and the amount of organic matter present. Similarly, the success of biological interventions, such as inoculations and *Azolla* use (discussed in Sections 4 and 5), is closely linked to existing soil management practices and microbial community structure. Therefore, the most effective mitigation strategies will likely rely on site-specific, optimized systems that integrate various approaches (water organic matter, nutrients, tillage, crop selection, biological interventions), maximizing synergies and minimizing adverse side effects (such as increased N_2O emissions and yield penalties). Understanding these complex interactions and developing optimized strategies is a central focus of this review.

Table 2 Summary of reported effects of key agricultural management strategies.

Treatment	Practice/Comparison	Effect on CH_4 emission	Key findings/Notes	References
Water Management	Midseason drainage vs Continuous flooding	-17% to -56% (example: -35.6%)	Significant CH_4 reduction but increases N_2O emissions (trade-off).	Zou et al. (2005)
Water Management	Alternate wetting and drying vs Continuous flooding	-30% to -70%	General reported range, N_2O trade-off likely.	Linguist et al. (2012), Jiang et al. (2019), I et al. (2016)
Straw	Straw incorporation (+N) vs No straw (+N)	Increase (example: +285%)	Provides substrate for methanogens.	Cai et al. (2007), Yagi and Minami (1990), Wang et al. (1992), Neue et al. (1996)
Straw	Removal/Burning/ Composting vs Incorporation	Decrease (qualitative)	Reduces available substrate.	Sander et al. (2014)
Manure	Manure (M) vs PK control	+20.4% Increase	OM input increases CH_4 .	Kong et al. (2019)
Manure	NPK + Manure (NPKM) vs PK control	+101.2% Increase	Combined NPK and Manure effect.	Kong et al. (2019)

Table 2 Continued

Treatment	Practice/Comparison	Effect on CH ₄ emission	Key findings/Notes	References
Manure	Composted manure vs Fresh/Air-dried manure	Decrease (qualitative)	Composting decomposes labile C aerobically.	Watanabe et al. (2009), Pramanik and Kim (2014)
Biochar	Biochar application (overall)	-28% (meta-analysis mean)	Highly variable effect depending on conditions.	Jeffery et al. (2016)
Biochar	Biochar in paddy soils	-30% (meta-analysis mean)	Potential in flooded systems.	Jeffery et al. (2016)
Fertilization	NPK vs PK control	+67.4% Increase	N and P additions stimulate CH ₄ .	Kong et al. (2019)
Fertilization	NH ₄ ⁺ -based vs NO ₃ ⁻ /SO ₄ ²⁻ -based N	Higher CH ₄ with NH ₄ ⁺ (qualitative)	NO ₃ ⁻ /SO ₄ ²⁻ can suppress methanogenesis.	Cai et al. (2007), Klüber and Conrad (1998), Malyan et al. (2019)
Fertilization	Nitrification inhibitors (dicyandiamide (DCD)/3, 4-dimethylpyrazole phosphate (DMPP)	Variable/minor effect on CH ₄	Mainly targets N ₂ O; may slightly reduce NH ₄ ⁺ inhibition of CH ₄ oxidation.	Malla et al. (2005), Weiske et al. (2001)
Tillage	No-Till vs Conventional Tillage	Variable (potential initial increase; slow oxidation recovery)	Complex effects, site-specific.	Six et al. (2002), Baggs et al. (2003), Jacinthe and Lal (2006), Bayer et al. (2012)

vs = versus.

Conclusion

The soil CH₄ cycle is a complex biochemical process that makes a dominant contribution to global climate change, with agricultural ecosystems playing a major role. The net CH₄ flux from soils depends on the delicate balance between CH₄ production by methanogenic archaea under anaerobic conditions and CH₄ consumption by methanotrophs under aerobic (and in some cases sub-oxic) conditions. This balance is regulated dynamically by soil moisture, O₂ status, temperature, pH, Eh, substrate availability and microbial community composition.

Agricultural practices substantially alter CH₄ emissions by influencing these environmental factors and microbial communities through water management, fertilization, tillage and crop choices. For example, water management strategies, such as AWD or continuous flooding, strongly influence CH₄ fluxes. Likewise, the fertilization regime—including fertilizer type, timing and application rate—directly affects methanotroph and methanogen activity. Biological interventions such as microbial inoculants (including methanotrophs, *Azolla*-cyanobacteria systems), or biostimulants are emerging as promising strategies (Xu et al., 2017; Malyan et al., 2021; Rani et al., 2021), though their performance may depend strongly on tillage practices (conventional, reduced or no-till). This review has highlighted that these factors rarely operate in isolation but interact synergistically or antagonistically. For example,

the benefits of AWD may be contingent on the fertilization regime, or the success of microbial inoculants may vary under different tillage conditions. Hence, sustainable CH₄ mitigation requires system-based solutions that integrate multiple practices rather than single interventions.

Although substantial progress has been made, several important research needs must be addressed to advance CH₄ mitigation in agricultural systems. Long-term, multi-site field trials across diverse agro-ecological zones are essential to validate proposed management strategies under real farming conditions. Equally critical are mechanistic studies of microbial inoculants, particularly the survival, adaptation and performance of high-affinity methanotrophs capable of oxidizing CH₄ at atmospheric concentrations (Tveit et al., 2019). Another key priority is the integrated assessment of management interactions and trade-offs, especially the balance between CH₄ reduction and the potential risk of elevated N₂O emissions (Yang et al., 2019). Beyond these top priorities, further attention should be given to microbial consortia approaches that combine methanotrophs with N-fixing or phosphorus-solubilizing partners (Malyan et al., 2021), as well as to the conservation of native soil microbial diversity to safeguard the long-term CH₄ sink capacity of agricultural soils.

In conclusion, advancing sustainable CH₄ mitigation in agriculture requires moving beyond single-factor strategies toward system-based approaches. Addressing the identified gaps will depend on interdisciplinary research that links

microbial ecology with agronomy, integrates field evidence with socio-economic considerations and evaluates potential trade-offs in a holistic manner. Such an outlook will ensure that promising laboratory findings are translated effectively into robust field-scale practices, ultimately strengthening agriculture's contribution to climate change mitigation.

Conflict of Interest

The authors declare no relevant financial or non-financial interests.

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