

Review

Methanotrophy: A Biological Method to Mitigate Global Methane Emission

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Abstract: Methanotrophy is a biological process that effectively reduces global methane emissions by utilizing microorganisms that can utilize methane as a source of energy under both oxic and anoxic conditions, using a variety of different electron acceptors. Methanotrophic microbes, which utilize methane as their primary source of carbon and energy, are microorganisms found in various environments, such as soil, sediments, freshwater, and marine ecosystems. These microbes play a significant role in the global carbon cycle by consuming methane, a potent greenhouse gas, and converting it into carbon dioxide, which is less harmful. However, methane is known to be the primary contributor to ozone formation and is considered a major greenhouse gas. Methane alone contributes to 30% of global warming; its emissions increased by over 32% over the last three decades and thus affect humans, animals, and vegetation adversely. There are different sources of methane emissions, like agricultural activities, wastewater management, landfills, coal mining, wetlands, and certain industrial processes. In view of the adverse effects of methane, urgent measures are required to reduce emissions. Methanotrophs have attracted attention as multifunctional bacteria with potential applications in biological methane mitigation and environmental bioremediation. Methanotrophs utilize methane as a carbon and energy source and play significant roles in biogeochemical cycles by oxidizing methane, which is coupled to the reduction of various electron acceptors. Methanotrophy, a natural process that converts methane into carbon dioxide, presents a promising solution to mitigate global methane emissions and reduce their impact on climate change. Nonetheless, additional research is necessary to enhance and expand these approaches for extensive use. In this review, we summarize the key sources of methane, mitigation strategies, microbial aspects, and the application of methanotrophs in global methane sinks with increasing anthropogenic methane emissions.

Keywords: ecology; greenhouse gases; microbes; enteric fermentation; methanotrophs; serine pathway and ribulose monophosphate pathway



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1. Introduction

Global warming is one of the threats of utmost importance to the globe, and this issue is gaining in popularity because of heat trapping pollutants such as water vapor, fluorinated gases, carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O); these especially are accumulating in the atmosphere, leading to global warming over last three decades [1]. CO₂ (79.4%), CH₄ (11.4%), ozone (O₃), fluorinated gases (3.0%) [hydrochlorofluorocarbons (HCFCs), chlorofluorocarbons (CFCs), sulfur hexafluoride (SF₆), hydrofluorocarbons (HFCs), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs)], and nitrous oxide (N₂O) (6.2%) are involved in this phenomenon and are referred to as greenhouse gases, which

are able to last from decades to centuries, trapping heat and causing the atmosphere to heat up [2]. In total, the amount of heat-trapping gases in the atmosphere is leading to a radiative force of 3.84 W/m^2 on the Earth's surface. This is about 500 times the amount of electricity used globally and represents approximately 1.5% of the sunlight that is absorbed by Earth [3]. Warming is leading to increasing temperatures globally, which in turn are fueling high-intensity heat waves. These greenhouse gases create a negative impact by changing total global temperature, which is a risk for the human race and the environment.

Among potent greenhouse gas, the most potent is methane, which is influential in trapping heat and accounts for 20% of global greenhouse gases. Although methane remains in the atmosphere for a shorter span (12 years) and is emitted less than CO_2 , it is more than 28 times as potent as CO_2 at trapping heat in the atmosphere [4]. Methane is much more powerful in confining heat in the atmosphere by absorbing infrared rays that emit most of the heat energy; hence, its contribution to global warming has been the greatest [5]. A recent report suggested that natural gas hydrate, a type of frozen methane, is a highly concentrated form of carbon that is stable only under specific temperature and pressure conditions. It is found in low-temperature and moderate-pressure environments, such as the sediments of deepwater continental slopes and beneath permafrost in high-latitude regions [6]. Research from Kennicutt et al. [7] on the continental slope of the northern Gulf of Mexico has changed our comprehension of the biological and chemical processes in the deep ocean. A community of organisms similar to those found in hydrothermal vents was recently discovered at the base of the Florida Escarpment. These organisms are nourished by hydrogen sulfide-rich hypersaline water seeping onto the seafloor. Interestingly, in a report by de Bruin et al. [8], the Cenozoic deltaic deposits offshore of the Netherlands have revealed numerous acoustic anomalies, commonly appearing as bright spots in seismic data. These bright spots are effective indicators of resource potential, drilling hazards, and seabed methane emissions when accompanied by shallow gas. While vertical seismic noise trails (chimneys) are typically regarded as evidence that shallow gas originates from the migration of deeper thermogenic gas, geochemical and isotope analyses consistently suggest that the gas is of microbial origin and generated in situ within the Cenozoic strata. The "chimneys" that have been observed are likely transmission effects, which are artifacts that do not depict the migration paths of gases [8]. According to Yurganov et al. [9], an analysis of satellite data reveals that the amplitude of the seasonal methane cycle in the Kara Sea has risen significantly since the start of the 21st century. This rise can be attributed to a decrease in ice concentration in the region. It is estimated that the annual emission of methane from the Arctic seas accounts for 2/3 that of land emissions. The Barents and Kara seas contribute approximately 1/3 to 1/2 of the annual emissions from the Arctic seas. A study by Bulavina et al. [10] examines the theoretical and practical aspects of how sea ice melt and methane migration affect chlorophyll-a concentrations, which serve as a proxy for phytoplankton productivity and community development during the spring stage of a succession cycle. It was discovered that low concentrations of chlorophyll-a in the edge zone prevented the spring flowering stage of the phytoplankton community from occurring. As a result, it was not possible to determine the potential impact of methane hydrate release on chlorophyll-a concentration.

Methane emissions occur during the production and transport of coal, natural gas, oil, and also with other environmental processes. In addition, emissions result from the decay of organic matter in municipal solid waste (MSW), landfills, livestock (mainly cattle) manure storage systems, and wastewater treatment systems. Different fossil fuel industries, including oil, gas, and coal, constitute a major portion of total emissions [11]. In summary, human activities in three sectors, fossil fuels (35%), waste (20%), and agriculture (40%), account more than half of global methane emissions. Capturing and reducing methane emissions from these sources and other anthropogenic activities is essential. To solve this issue, many mitigation strategies and practices are available and used across the world [11]. Many of these technologies and practices reduce other volatile and hazardous air pollutants along with methane. Reducing methane emissions is integral to meeting climate change,

energy, and health security. Considerable reductions can be achieved either by ending or reducing activities, such as changing the use of coal and gas as energy sources and minimizing ruminant emissions. Various existing methane mitigation practices involve the retrieval and use of methane as a fuel. Precise technologies and mitigation methods differ according to emission sources, owing to their different characteristics and emission processes.

The expensive nature of chemical technologies used on an industrial scale has renewed interest in biological methane activation, which offers higher conversion efficiencies and a lower environmental impact. Methanotrophs are a group of methane-oxidizing bacteria that activate aerobic biological methane. These bacteria can grow aerobically or anaerobically and activate methane at ambient temperatures and pressures [12,13]. Studies have shown that landfill soil covers possess active consortia of methanotrophic bacteria, and one third or more of the nearby emerging methane ($37.5 \pm 3.5\%$) is oxidized by methanotrophs in these covers. Therefore, bacterial methane oxidation is a feasible option for low-cost methane mitigation [11].

2. Sources of Methane Generation

Methane is emitted from a variety of anthropogenic activities, including agricultural activities, stationary and mobile combustion, landfills, certain industrial processes, wastewater treatment, oil and natural gas systems, coal mining, and also from natural sources [4,14–16]. Other sources are ruminants, livestock, and decaying organic matter in wetlands [17].

Methane is a promising target for reducing atmospheric greenhouse gas warming [18]. The concentration of methane in the atmosphere is determined by an equilibrium between the methane generated on the Earth's surface, which serves as its source, and the methane that is eliminated or removed, primarily through atmospheric chemical processes, which serve as its sink. As the air in the tropics ascends, it carries methane upwards through the troposphere, which is the lowest layer of Earth's atmosphere, extending 4–12 miles (6.4–19 km) above the surface. This layer is followed by the lower stratosphere, where the ozone layer is located, and then the upper portion of the stratosphere [19]. Since 2007, atmospheric methane began growing by about 6 ppb/year and an acceleration in the growth rate was observed around 2014 [20]. A preliminary analysis by the National Oceanic and Atmospheric Administration (NOAA) revealed that the annual increase in atmospheric methane during 2021 was estimated to be approximately 17 parts per billion (ppb), thus creating the greatest annual record increase since regular quantification began in 1983 [21]. Atmospheric methane levels averaged 1891.62 ppb in 2021 and were highest in January 2022, i.e., 1908.74 ppb [22,23]. The chart below represents global methane emissions from 1990 to 2020 [22]. Methane (CH₄) emissions peaked at 11.3 billion metric tons of carbon dioxide equivalent (GtCO₂e) in 2022, representing approximately 21 percent of the world's total greenhouse gas emissions for that year [24]. It is important to note that methane emissions have increased by over 32 percent since 1990 (Figure 1; [24]).

The chart below shows a comparison of the top methane emitters, as of 2021. The world's five top methane emitters are China, India, the United States, Russia, and Brazil, which together account for approximately half of all methane emissions worldwide [24,25]. Worldwide, human-caused methane emissions are predicted to increase by almost nine percent from the levels expected in 2020, to 10,220 MMTCO₂ E by 2030 (Figure 2, [24,26]).

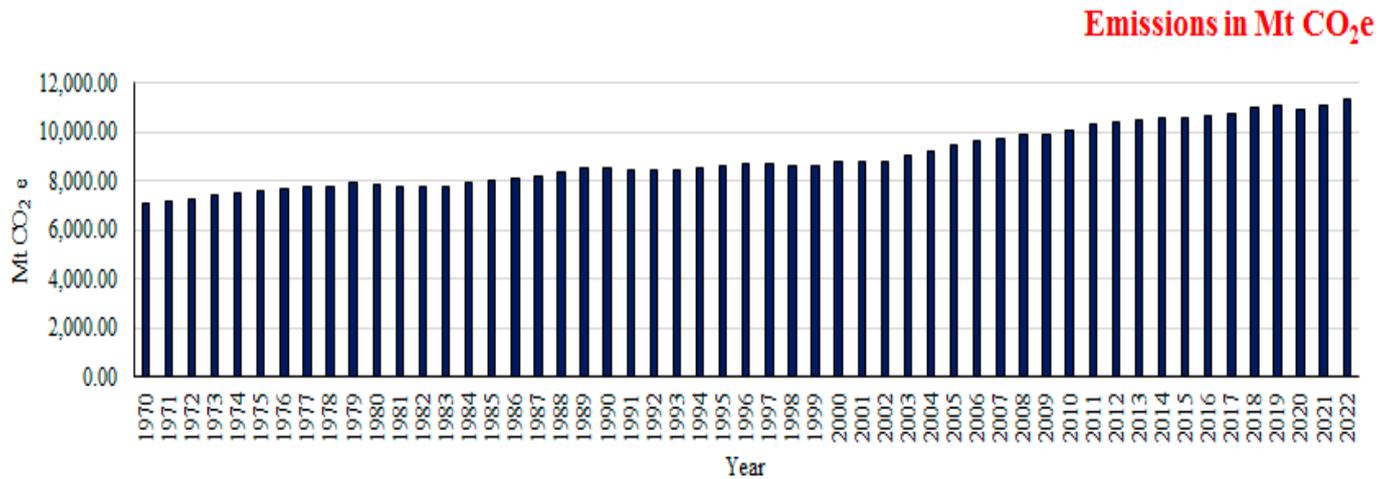


Figure 1. Worldwide methane emissions (in million metric tons of carbon dioxide equivalent) annually from 1970–2022 [24].

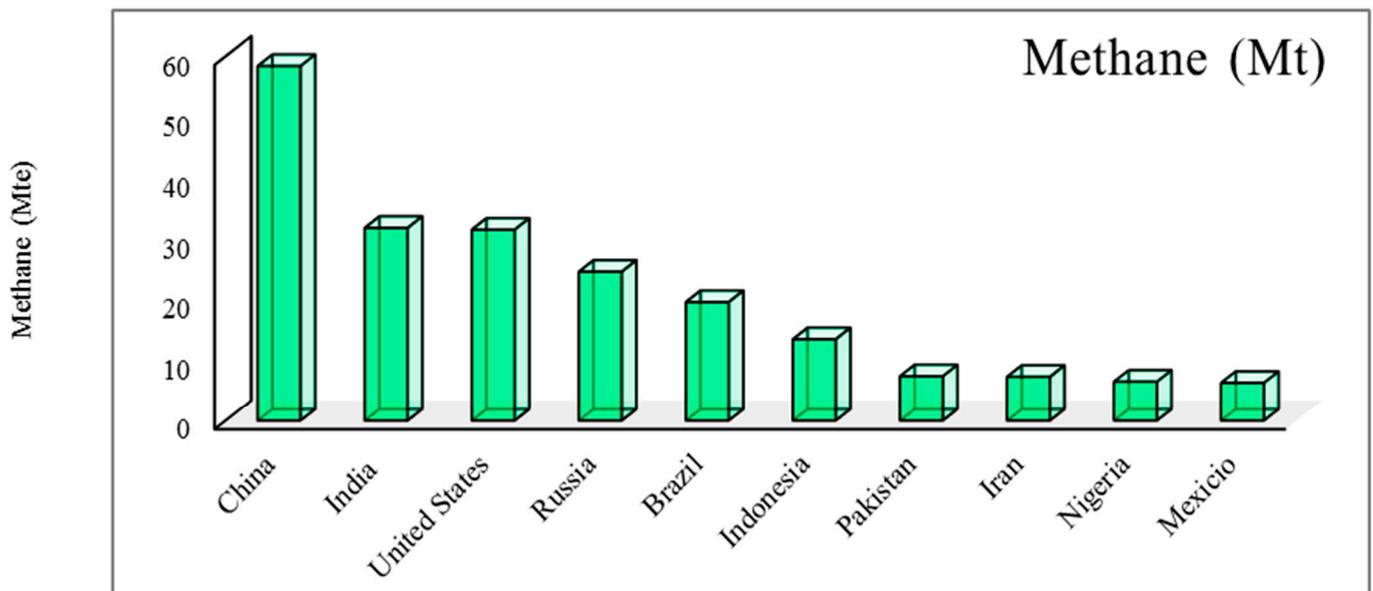


Figure 2. Top methane emitters as per 2021–2022 (<https://www.iea.org/reports/global-methane-tracker-2022/overview>, accessed on 5 April 2024; [27]).

Environmental changes that originate from human activity are considered to be anthropogenic changes in the environment, where urban areas, that is, cities, are the major source of methane emissions [28], which are influenced directly or indirectly in nature [29]. Natural processes contribute to approximately 40% of methane emissions, with wetlands being the most significant natural source [30]. There are some sources from which methane emissions are initiated at large levels, and a few of them are listed below (Figure 3).

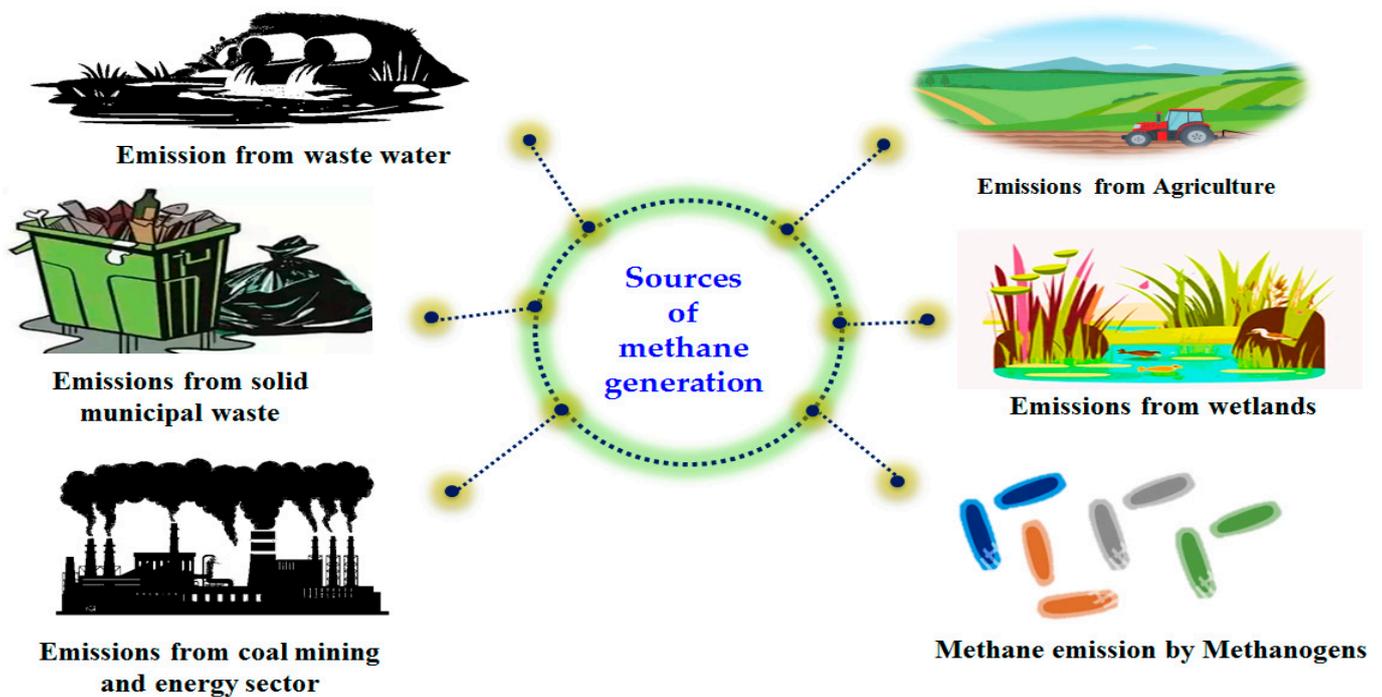


Figure 3. Major sources of methane emissions.

2.1. Emissions from Waste Water

Municipal and industrial wastewater and their sludge, that is, their residual solid byproducts, when subjected to anaerobic conditions, result in organic material methane emissions [31]. The influent entering a wastewater treatment plant contains a significant quantity of dissolved methane produced in the sewer system [32,33]. The production of dissolved methane takes place in different zones of wastewater treatment plants with anaerobic conditions and in areas such as sludge digesters, storage tanks, and buffer tanks, where a larger quantity of sludge results in a high range of anaerobic decomposition, which in turn results in the high-volume emission of methane. The production of methane from wastewater is expressed as up to 75% of CO₂-equivalents [32]. High levels of methane emissions are caused by anaerobic conditions; on the other hand, methane emissions from treatment plants can be lessened by aerobically oxidizing methane-bearing activated sludge [34]. Daelman et al. [35] reported the outcomes of a one-year evaluation of methane emissions from a full-scale municipal wastewater facility with sludge digestion. The findings indicated that the methane emissions made a slightly greater contribution to the greenhouse gas footprint than the CO₂ emissions, resulting from direct and indirect fossil fuel consumption for energy requirements. This value exceeded the quantity of CO₂ emissions that was averted by utilizing biogas. It was observed that around 80% of the methane entering the activated sludge reactor was biologically oxidized [35]. Here, methane, in addition to its potential for heat and power generation, is a renewable fuel that can produce various high-quality chemicals. However, its global use in wastewater treatment plants is limited, with most facilities primarily utilizing it for heat and power production [36]. The utilization of methane resources can be significantly facilitated by the bioconversion process, which is promoted by *Methylosinus trichosporium* OB3b. According to Lee et al. [37], the bioconversion ratio can exceed 60% when this microorganism is used, resulting in the high production of value-added chemicals. Furthermore, the application of micro-bubble and nano-bubble aeration techniques can lead to an even greater bioconversion of methane, which is particularly desirable [36,38–40]. However, the utilization of cogeneration engines aims to assist in achieving the state's climate action objectives, specifically by reducing greenhouse gas emissions to at least 45 percent below 1990 levels by 2035 and at least 80 percent below 1990 levels by 2050. At numerous wastewater treat-

ment facilities, methane is commonly wasted through the practice of burning or flaring, thereby releasing greenhouse gases like carbon dioxide and methane into the atmosphere. In contrast, cogeneration engines convert methane into renewable energy, thereby reducing emissions [41,42].

2.2. Emissions from Solid Municipal Waste

Methane emissions resulting from solid municipal waste, often referred to as landfill gas, represent a substantial contributor to greenhouse gas emissions. Solid waste generation by households is considered municipal solid waste, which is the third largest human-influenced source of methane emissions [43,44]. Biodegradable components or materials are ones which go through anaerobic decomposition in landfills and generate about 50–60% methane gas, with other small traces of non-methane organic compounds and other gases emitting as landfill gases [43,44]. The database utilized for this study [45] comprised 2107 municipal solid waste landfills across China's cities and towns in 2007. The findings indicate that CH₄ emissions from these landfills amounted to 1.186 million metric tons in 2007. The considerable variation in CH₄ emissions when compared to the 2005 figure of 2.20 million metric tons can be largely attributed to discrepancies in the statistical data, such as the number of landfills and the quantity of waste disposed of in these landfills. Another study by Lando et al. [46] calculated methane emissions at the Tamangapa landfill and predicted methane emissions from the Tamangapa landfill over the following decade using the 2006 IPCC Waste Model. The findings revealed that the waste production in Makassar City in 2016 was 0.449 kg/person/day, with organic waste being the most prevalent type of waste. The potential methane emissions at TPA Tamangapa Makassar in 2016 were 2.24 Gg/year, and the projection for 2026 was 4.968 Gg/year. However, an expanding global population with enhanced purchasing power is leading to heightened levels of consumption and waste generation. In the fastest-growing regions, including sub-Saharan Africa, South Asia, and the Middle East and North Africa, the disposal of solid waste is often unmanaged, posing significant risks to public health and increasing methane emissions [47]. In 2020, global human-caused methane emissions from municipal solid waste landfills alone had the same warming effect as approximately 4.4 billion metric tons of CO₂ over a 20-year time horizon [47]. This is equivalent to the annual emissions from roughly 950 million passenger vehicles [47]. A substantial portion of waste in India is biodegradable, and when disposed of in dumpsites or landfills, it continues to emit methane for years, even after the landfill has been decreased [48].

2.3. Emissions from Coal Mining and Energy Sectors

Methane emissions from the extraction, processing, transportation, and combustion of coal in the mining and energy sectors contribute significantly to global warming [49]. These emissions occur primarily during these processes and are a potent greenhouse gas [50]. Methane emissions from the energy sector are annually calculated to be 1774.50 MtCO₂eq, where the total methane emission value constitutes 28.65% [51]. As coal is transformed from biomass under the influence of biological and geological actions, it causes the production of methane gas and coal, and the methane formed is stored inside the layers of coal rock [50]. Coal formation and its extraction result directly in the production and emission of methane gas, respectively, and when the pressure within a coalbed is reduced due to different activities such as faulting, mining, or natural erosion, it results in the release of methane gas [52]. It is observed that in 2022, the energy industry worldwide was accountable for almost 135 million metric tons of methane emissions, a slight increase from the previous year. Specifically, coal, oil, and natural gas operations each contributed approximately 40 million metric tons to the total, while end-use equipment leaks accounted for nearly 5 million metric tons [53]. Approximately 10 million metric tons of emissions are caused by the incomplete combustion of bioenergy, primarily from the conventional use of biomass. The energy sector is accountable for nearly 40% of all human-caused methane emissions, coming in second only to agriculture [53]. In 2019, methane emissions from coal mining

and abandoned coal mines in the United States contributed to approximately 8% of total methane emissions. This sector ranked as the fifth-largest emitter of methane [54].

2.4. Emissions from Agriculture

Within human activities, the agricultural sector is among the biggest sources of methane from a variety of sources, including the cultivation of rice, manure management, and enteric fermentation, which lead to high levels of methane emissions in turn, making the agricultural sector contribute towards high levels of methane emissions [55]. Two-thirds of all anthropogenic methane emissions are from agricultural activities [56]. Methane emissions from enteric fermentation constitute a large percentage of the total emissions, followed by emissions from rice cultivation, other agricultural activities, and manure management. Among livestock, ruminants are at the top, being one of the highest emitters of enteric methane [57].

Methanogenic archaeobacteria are responsible for methane production in ruminants, which are mainly present in the rumen, and the growth of microbes associated with the rumen is influenced by diet and other nutrition-related characteristics, including the amount of intake, feeding strategies, quality of fodder, and concentrate ratios [58].

The process of enteric fermentation revolves around ruminant livestock, where livestock constitutes a crucial part of the agricultural sector in encouraging high levels of methane emissions under human-influenced activities [59]. Additionally, emissions from manure storage are a possible source of CH₄. Ruminants possess a special digestive organ called the rumen which helps in combining fibrous roughage or plant materials. As it undergoes the process of enteric fermentation, the low-grade plant material feed is digested by the ruminants in a breakdown carried out by bacteria; the process defined here is known as methanogenesis, and methane is generated as a waste product in this process [60]. Malerba et al. [61] conducted a large-scale assessment of methane emissions from agricultural ponds in the United States and Australia. They found that in the United States, there are approximately 2.56 million agricultural ponds covering an area of 420.9 square kilometers and emitting around 95.8 thousand metric tons of methane per year. In Australia, there are roughly 1.76 million agricultural ponds covering an area of 291.2 square kilometers and emitting about 75.1 thousand metric tons of methane annually. Agriculture is the leading anthropogenic source of CH₄, releasing 145 teragrams (Tg) of CH₄ into the atmosphere each year [62]. The primary sources of these emissions are enteric fermentation, manure management, rice cultivation, and residue burning. There is considerable opportunity to reduce CH₄ from these sources, with bottom-up mitigation potentials of approximately 10.6, 10, 2, and 1 Tg of CH₄ per year from rice management, enteric fermentation, manure management, and residue burning, respectively. Other studies have estimated even higher potentials for reducing CH₄ emissions, such as 4.8 to 47.2 Tg of CH₄ per year from enteric fermentation and 4 to 36 Tg of CH₄ per year from improved rice management. Therefore, it is crucial to focus on mitigation actions that target the reduction of all three main anthropogenic greenhouse gases, including CH₄ [62].

2.5. Emissions from Wetlands

Wetlands play a crucial role in emitting methane and nitrous oxide, the latter of which is a greenhouse gas with a global warming potential 300 times that of carbon dioxide and which serves as the primary ozone-depleting substance released in the 21st century. Furthermore, wetlands can also function as a sink for greenhouse gases [63]. A crucial source of atmospheric methane, which comprises approximately 21% of the total atmospheric methane budget, is wetlands. Northern wetlands constitute 34% of the total, where water depth, soil water content, type of vegetation, and temperature conditions are certain factors responsible for methane production and oxidation in wetlands [64–67]. The carbon and oxygen from wetland plants are responsible for methanogenesis and decomposition, respectively [68–70]. It is observed that Amazonia releases 46.2 ± 10.3 teragrams (Tg) of methane annually, which constitutes approximately 8% of global emissions [63]. The data

indicate that there is no discernible change in this emission trend over time. In terms of sources, carbon monoxide analysis reveals that 17% of emissions originate from biomass burning, while the remaining 83% is primarily attributed to wetlands [63].

The following graph represents the sources of methane contribution (Figure 4).

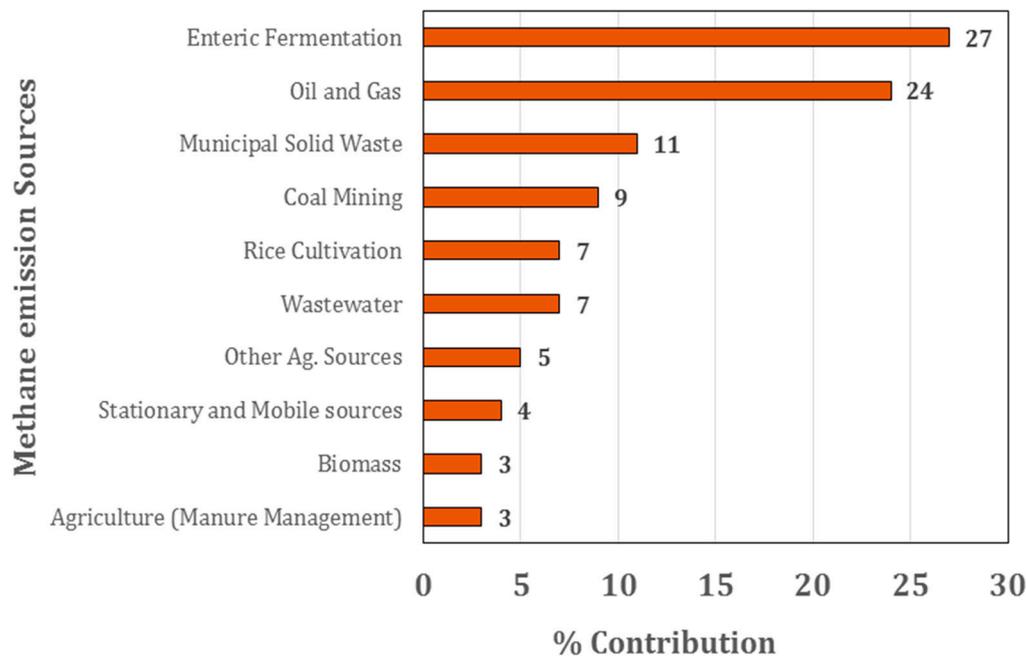


Figure 4. Contribution of various sources of methane generation [71].

2.6. Methane Emission by Methanogens

The ecosystem is a special case for methane emissions, where a unique species of microorganisms called methanogens reside that behave as environmental inhabitants, which greatly contribute to the emission of methane in the atmosphere [72–74]. Methane is a byproduct of the digestive process in the rumen and hindgut of animals, specifically in the *Euryarcheota* phylum of *Archaea*. In livestock, ruminants are the primary producers of methane, as they are capable of generating it during the normal digestion of feed [75,76].

Methanogens possess great diversity in their phylogenetic and ecological branches [61]. Methanogenic archaea and methanogens are both anaerobic organisms. They derive their metabolic energy from the conversion of substrates such as hydrogen, carbon dioxide, and formate to methane [77]. Hence, this category of microorganisms has recently become a very important part of the study of methane emissions globally. Lee et al. [78] conducted a study on methane emissions in a flooded rice ecosystem, including the investigation of methanotrophs, methanogens, and soil chemical properties. After rice transplantation, methane emissions increased significantly from 7.2 to 552 mg day⁻¹ m⁻², and this increase was positively correlated with the transcripts of *pmoA* and *mcrA* genes, as well as the transcript/gene ratios of *mcrA*, temperature, and total organic carbon. The study found that *Methylocystis* decreased rapidly after rice transplantation, whereas *Methylosinus* and unclassified *Methylocystaceae* remained relatively constant throughout rice cultivation. The normalized *mcrA/pmoA* transcript ratios were found to be promising parameters for predicting the net methane fluxes emitted from rice paddy soils. According to the findings of Angle et al. [79], *Candidatus Methanotheroxillum paradoxum* is a widely distributed organism in ecosystems that emit methane, indicating its global importance. Additionally, it is estimated that up to 80% of methane emissions in wetlands are due to methanogenesis in oxygenated soils. Here, methanogens are the sole group of microorganisms on earth that generate substantial amounts of methane. Cattle, for instance, produce methane through enteric fermentation (accounting for 85 to 90% of the total) and fecal excretion. In the case of cattle, a significant portion (95%) of the methane generated in the rumen is expelled through

eructation (i.e., burping) and the intestines, while only a small fraction (5%) is excreted through the anus [80,81]. The trend and legal obligation of mitigating greenhouse gas emissions will likely directly impact the improved efficiency of livestock systems, including animal nutrition, productivity, handling, and management. Research on the development of mitigation strategies and their practical applications has been conducted globally [82].

3. Mitigation Measures of Methane

The problems related to methane mitigation are very wide and complex in nature. As it deals with searching, identifying, and evaluating emissions, but because of swift advancements in technical branches, it becomes much simpler to identify and cut emissions [4,83]. Various mitigation approaches have been developed to diminish methane production from ruminants, such as animal interference, microbiome manipulation, diet selection, dietary feed additives (e.g., methane inhibitors, plant secondary metabolites, essential oils, lipids, and algae), probiotics, genetic selection, defaunation, supplementation of fats, oils, organic acids, and plant secondary metabolites [84]; however, sustainable mitigation strategies are yet to be established [12]. Nevertheless, an approach that is progressive, such as probiotics, involving methane measurements and mitigation strategies with an emphasis more on the biological reduction of methane emissions that occur due to direct-fed microbes, could be considered as a methane mitigation approach towards sustainability [85–87]. Researchers have developed numerous nutritional technologies to minimize CH₄ production, including direct inhibition techniques [88], feeding ruminants with additives [89], propionate enhancers [90], methane oxidizers [91], probiotics [92], defaunation [93], and manipulation of ruminant diets and hormones [84,94]. The study conducted by Abdelbagi et al. [92] aimed to evaluate the impact of probiotics and encapsulated probiotics on enteric methane production and in vitro nutrient digestibility in ruminants. The probiotics utilized were from the group of lactic acid bacteria. The study involved three dietary treatments and three replicates: control diet, probiotics addition, and encapsulated probiotics addition. The results demonstrated that both probiotics and encapsulated probiotics significantly decreased ($p < 0.05$) methane production by 6.1% and 33.1%, respectively, compared to the control diet. Additionally, both probiotics and encapsulated probiotics increased ($p < 0.05$) total gas production compared to the control.

Another perspective for reducing enteric methane emissions is to take into account the enhancement of milk yield in dairy animals, which can be done only when milk production is made constant and by maintaining a reduced number of animals [95]. Reduction strategies related to manure management focus on emissions generated from liquid systems, as these systems have large amounts of methane emissions that can be viably reduced [95,96]. Multiple drainages of fields during the rice-growing season reduce the capacity of the soil, which decreases methane emissions from wet rice [96,97]. Another method is the constant percolation of water over fields [98]. This measure results in methane oxidation in water, which keeps methane emissions low [91,99–101]. Methane emissions can also be reduced by reducing the content of carbon-based compounds in the soil [2,102]. Methane production is minimal under dry, aerobic conditions, which is why switching from liquid to dry management systems helps in reducing methane emissions generated by liquids [51,103]. Methane emissions from natural gas, oil systems, and coal mining constitute most of the emissions in the energy sector (Figure 5). Thus, it is important to reduce methane emissions from the energy sector (Figure 5). Methane emissions from natural gas and oil systems can be reduced by using options in these systems, such as the following:

- ✓ Installation of vapor recovery units to capture light hydrocarbon vapors that vent out from crude oil storage, followed by conversion of methane to CO₂.
- ✓ Installation of Flash Tank Separators in the production, processing, and transmission units. They can recover methane from tri-ethylene glycol for fuel or sale, thus minimizing venting with water vapor.
- ✓ Using low-bleed pneumatics or dried air systems eliminates the methane emissions caused by high-bleed pneumatics.

- ✓ Direct leak detection surveys of facilities to identify and repair leak sources [51].

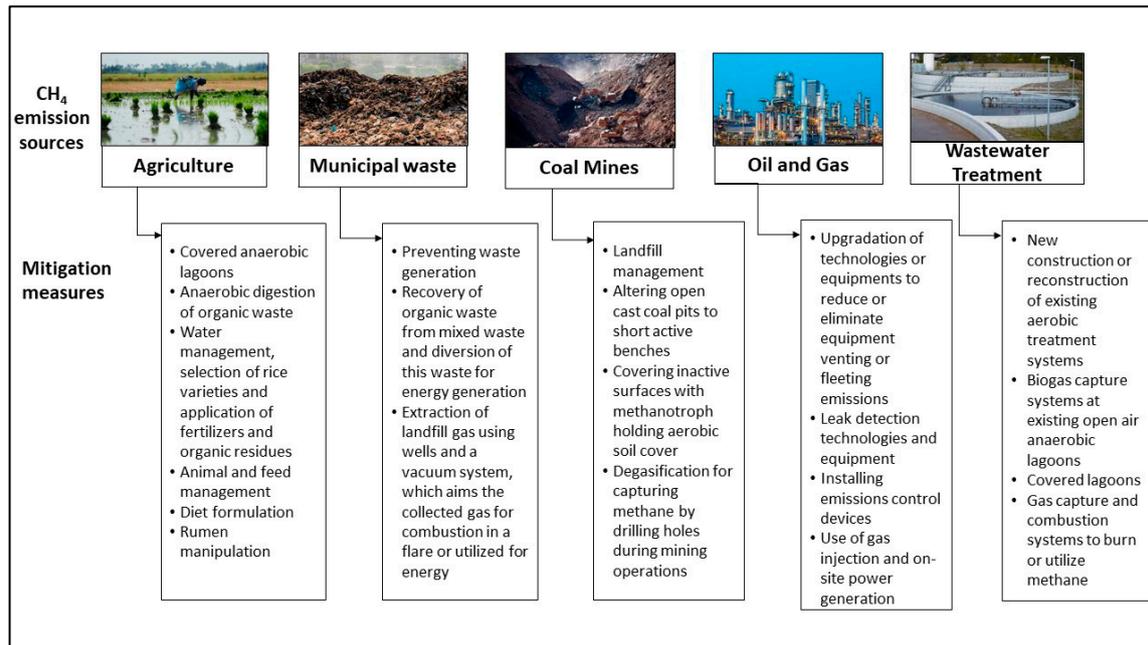


Figure 5. Methane emission sectors and their mitigation measures.

Reducing methane emissions from coal mines is quite possible, as methane must be primarily extracted from coal mines for use in different applications [80,104]. These applications comprise a basic conversion of methane into CO₂, which can decrease the greenhouse effect by 20 times [105]. Gases with a high methane content are recovered from coal mines to manage production activities efficiently. Recovered gas contains approximately 95% methane, which is further used in various industries [106]. Another biological mitigation approach is methanotrophy, that is, the use of methanotrophic bacteria for methane remediation [107]. Methanotrophs utilize methane as a carbon and energy source and can convert methane into valuable compounds (Figure 5).

4. Methanotrophy

Microbiological oxidation is a method through which a notable amount of methane can be eliminated from the environment by methanotrophic bacteria and is known as methanotrophy. These organisms oxidize methane to gain energy under aerobic and anaerobic conditions using a range of diverse electron acceptors. Methanotrophy was first reported as an oxygen-dependent process in 1906. For a century, aerobic methanotrophy has been thought to be the only biological pathway to oxidize methane, and all methanotrophs belong to the Proteobacteria phylum [107,108]. In the late 1960s, Whittenbury provided a taxonomic framework for methanotrophs. It is based on cell morphology, intracellular membrane structure, carbon assimilation pathways, and cell wall components, and classifies methane oxidizers into type I and type II methanotrophs. Type I are Gammaproteobacteria (with families Methylococcaceae and Methylothermaceae) with the genera *Methylomonas*, *Methylobacter*, and *Methylococcus*, whereas Type II are Alphaproteobacteria (with families Methylocystaceae and Beijerinckiaceae) with *Methylosinus* and *Methylocystis* genera [109,110]. Several new genera of methanotrophs have been reported, including extremophiles such as *Methylosphaera*, *Methylocaldum*, *Methylothermus*, *Methylohalobius*, *Methylocella* and *Methylocapsa* [111]. Mostly, competition occurs between type I and II methanotrophs, which rely on CH₄ and O₂ concentrations along with the presence of nitrogen. Prior studies have indicated that type I methanotrophs prefer environments

with abundant O₂ and limited CH₄, while type II methanotrophs favor environments with high CH₄ concentrations and limited O₂ [112].

Some Methanotrophs belong to the Phylum Verrucomicrobia (family Methylococcoides), which contains the bacterium Methylococcus. This species uses the Calvin cycle to assimilate carbon from CO₂ as it cannot use RuMP and serine cycles because of the lack of their main enzymes. All methanotrophs belonging to Gammaproteobacteria, Alphaproteobacteria, and Verrucomicrobia were considered aerobic methanogens.

Findings from the past two decades have uncovered microorganisms beyond the Proteobacteria phylum, and even within the archaea domain, that can anaerobically oxidize methane using alternative electron acceptors such as sulfate, nitrite, nitrate, iron, and manganese. Later, a microbial consortium consisting of sulfate-reducing bacteria (SRB) and methanotrophic archaea facilitated sulfate-dependent anaerobic methane oxidation (S-dAOM). The methanotrophic archaea involved in this process are currently classified as ANME [4,5,11,113]. The following table compares some basic features of the two classes of methanotrophs, Gammaproteobacteria and Alphaproteobacteria, which belong to the phylum Proteobacteria (Table 1).

Table 1. Comparison of Type I and Type II methanotrophs [107].

Involved Characteristics	Gammaproteobacteria (Type 1 Methanotrophs)	Alphaproteobacteria (Type 2 Methanotrophs)
Arrangement within cell membrane:	Disc-shaped utricles in bundle forms	Coupled membrane along the periphery
Assimilation process: (Carbon compounds)	Undergo Ribulose monophosphate pathway	Undergo serine pathway
Type of organism include:	Paraphyletic	Oligotrophic
Species under category:	<i>Methylococcus capsulatus</i> , <i>Methylobacter marinus</i> , <i>Methylomonas methanica</i>	<i>Methylosinus trichosporium</i> , <i>Methylocystis minimus</i>

Habitats of Methylocotrophs: Methanotrophs are present in or near environments where methane is produced, although some methanotrophs can oxidize atmospheric methane. They reside in different habitats, including the open ocean and soils, and are associated with plant roots and leaf surfaces. Aerobic methanotrophs are metabolically versatile, making them ubiquitous in nature. Aerobic Methanotrophs present in the soil act as biological sinks for atmospheric methane. They are also present in oxic–anoxic interface environments such as rice paddies and peatlands [113]. Verrucomicrobia oxidize methane in extreme environments such as geothermal and volcanic environments while proteobacterial methanotrophs are found and actively involved in the oxidation of methane in environments with extreme conditions beside volcanic soils [114,115]. Methanogens and methanotrophs coexist widely in many habitats, benefitting from each other, and also possess a range of symbiotic relationships with eukaryotic organisms [116].

Methanotrophs can inhabit aerobic as well as anaerobic conditions, wherein the formaldehyde molecule is fixed by combining methane with oxygen and is then incorporated as cell material either by the serine or the RuMP pathway along with the release of carbon dioxide. A few methanotrophs (e.g., *Methylobacter*) can oxidize methane under microoxic conditions owing to the presence of high-affinity cytochromes (e.g., cytochrome bd ubiquinol-oxidoreductase). On the other hand, methanotrophs that inhabit anaerobic (anoxic) conditions oxidize methane using different electron acceptors. Some anoxic habitats include marine or lake sediments, oxygen-limited zones, anoxic water columns, rice paddies, and soil [111].

A remarkable diversity of methanotrophs has been revealed by different studies conducted in consideration of the environment. These works have been used to determine methanotrophs in different types of environments, such as landfill cover soils and wetlands, which indicates that their presence and numbers play an important role in methane cycling in many different environments, which helps mitigate the effects of this highly potent

greenhouse gas around the globe. Methanotrophs also have a symbiotic relationship with eukaryotes. Methanotrophs in marine sediments attenuate emissions of methane from hydrocarbon seeps on the seafloor in substantial amounts [117].

Gram-negative *Methyococcus capsulatus*, an obligate methanotroph, is an aerobic gamma-proteobacterium isolated by Foster and Davis [112]. This organism has been of interest for a wide range of studies. Specifically, studies have been conducted with a commercial interest in *M. capsulatus* as the major microbe used for the production of single-cell protein (SCP) as animal feed in the 1970s [113]. *Methyococcus capsulatus* expresses two different types of methane monooxygenases (MMOs): particulate/membrane-bound pMMOs and soluble sMMOs. Soluble MMO was active when *M. capsulatus* was grown at low-copper levels, whereas pMMO was primarily active at high levels [114].

4.1. Mechanisms of Methane Oxidation in Methanotrophic Bacteria

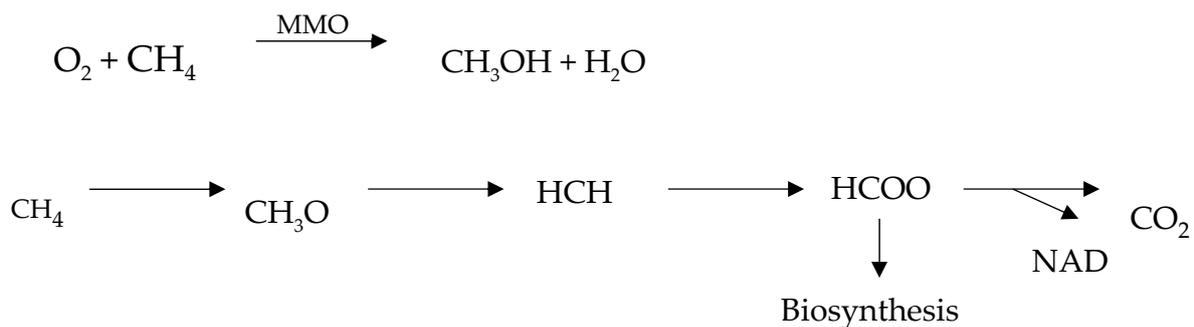
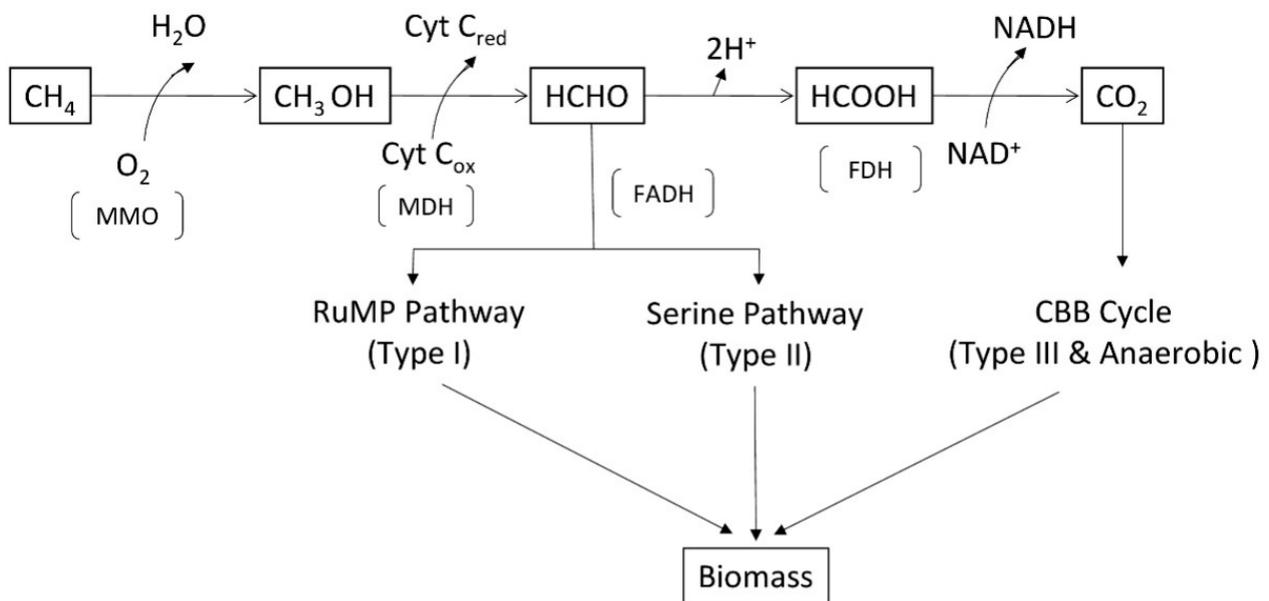
Methanotrophs rely on a key enzyme, methane monooxygenase (MMO), for methane oxidation. MMOs exist in two forms: iron-containing (membrane-associated) pMMOs and (soluble) sMMOs [118,119]. pMMO is a copper-containing enzyme, whereas sMMO is a non-haem iron-containing enzyme complex. This is because, when centrifuged, sMMO remains soluble, but pMMO sediments easily [110]. sMMO is produced in copper-controlled conditions, preferably $<0.89 \mu\text{mol g}^{-1}$ dry weight of cells [13,35]. All methanotrophs express pMMO in the presence of copper, except for the genera *Methylocella* and *Methyloferula*, whereas sMMO is present only in certain methanotroph strains [110,113]. Soluble methane monooxygenase (sMMO) is formed under low copper conditions, while the appearance of membrane proteins is associated with the addition of more copper, leading to pMMO, increased growth yields, and a loss of sMMO activity. The synthesis of sMMO by some methanotrophs may be a survival mechanism in copper-limited environments [110]. Under copper-limited conditions, some methanotrophs utilize sMMO, which is regulated by a mechanism termed the copper switch. Upon availability of copper, sMMO expression is downregulated by 2–3 orders [13].

Although MMO is mostly involved in the oxidation of methane, recent findings have revealed that it might also oxidize hydrocarbons and chlorinated compounds [62], indicating versatile substrate (e.g., ethane and propane) utilization by methanotrophic bacteria [120].

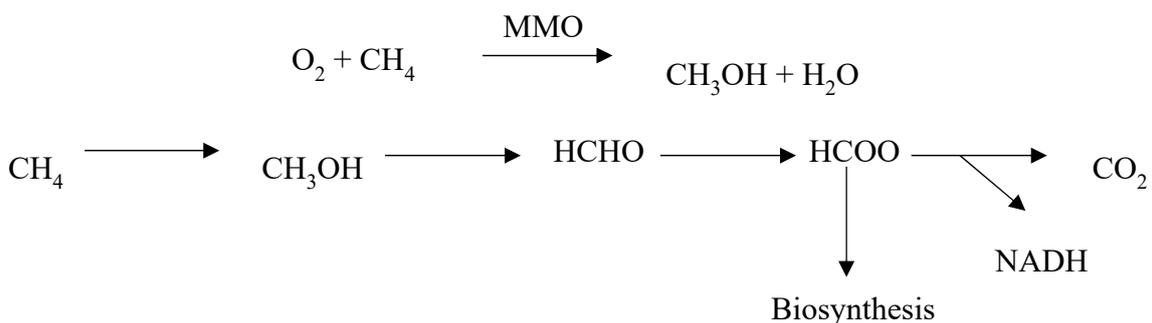
In the initial step of methane assimilation, MMOs incorporate oxygen from O_2 molecules into CH_4 . The requirement for oxygen at this stage indicates that these methanotrophs are obligate aerobes. MMOs exist in extensive internal membrane systems, which are methane oxidation sites. These different membrane arrangements, which are often distinguishing features among methanotrophs, are in type I disc-shaped vesicles arranged as bundles distributed throughout the cells, and in type II the membrane in pairs runs peripherally to the cells [107]. *Verrucomicrobia*, which also lack the key enzymes of the type I and type II pathways, have membrane vesicles, unlike previously mentioned.

In the major step of methanotroph metabolism, methane monooxygenase (MMO) enzymes convert methane to methanol. This process starts in the cell wall and periplasmic space where sources of energy are produced to fuel further reactions. Methanol generated from the first step is then converted to formaldehyde by the methanol dehydrogenase enzyme (MDH), followed by diverse metabolic pathways, depending on the type of methanotroph. Formaldehyde (HCHO) is either oxidized to CO_2 or used to prepare new cell materials. For C1 compound incorporation into the cell material, two distinct pathways exist: the serine pathway and the ribulose monophosphate pathway (RuMP). Type I methanotrophs adhere to the RuMP pathway, whereas type II methanotrophs follow the serine pathway. The Calvin Benson Bassham (CBB) cycle is followed by Type III anaerobic methanotrophs. The phylum *Verrucomicrobia* contains the bacterium *Methylacidiphilum*; *Methylacidiphilum* lacks the main enzymes of both the ribulose monophosphate and serine pathways. Thus, they use the Calvin cycle to assimilate carbon from CO_2 . Overall, methane

oxidation occurs, as shown in the following flowchart. The initial steps in this process occur in the periplasmic space of an organism.



MMO incorporates one oxygen atom from O₂ into a carbon compound. The following reaction occurs.



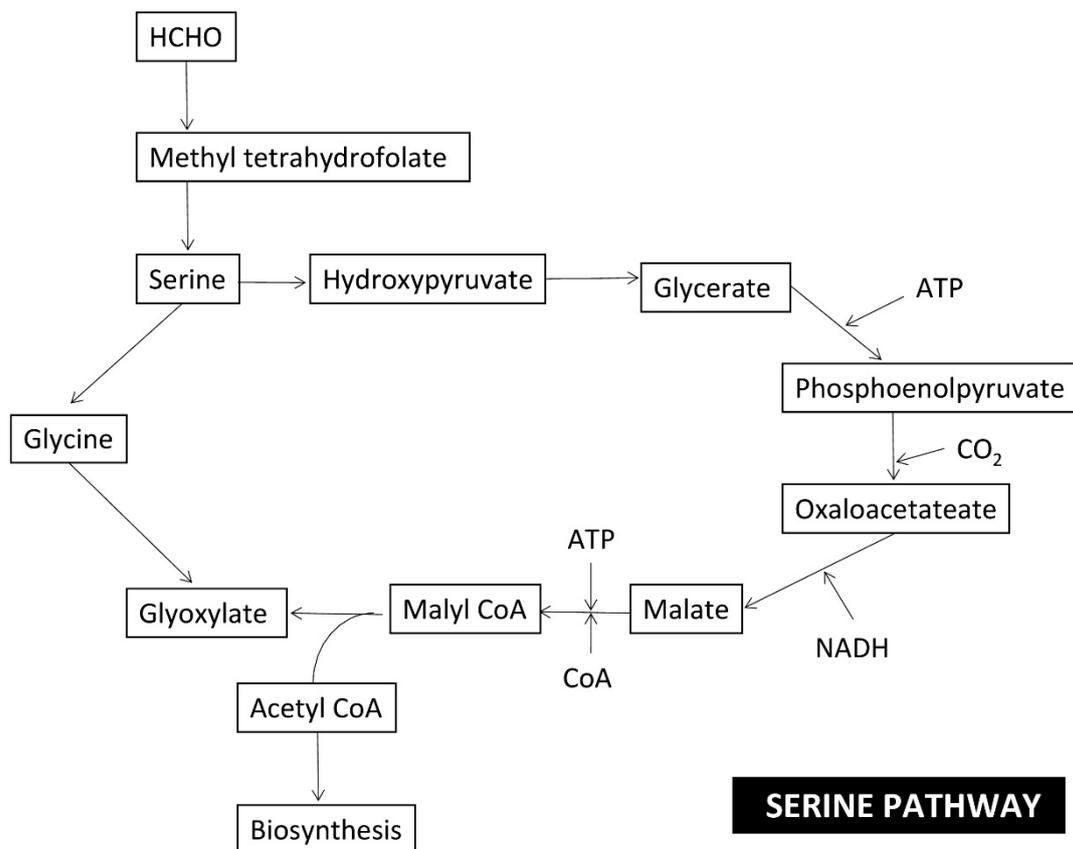
An oxygen atom is introduced into CH₄, resulting in the formation of methanol (CH₃OH). The second O atom is reduced to form H₂O. CH₃OH is oxidized by alcohol dehydrogenase to formaldehyde (HCHO) and NADH. This step is facilitated by periplasmic methanol dehydrogenase (MDH) [120]. The oxidation of formaldehyde to carbon dioxide produces most of the reducing power required for metabolism. During this process, formaldehyde is first converted to formate. Formate is oxidized to CO₂ by formate dehydrogenase in most methanotrophs [120]. Formaldehyde can also be absorbed to form intermediates used for the biosynthesis of cell material.

During these reactions, electrons flow in the membrane, generating a proton motive force. This proton motive forces ATPase to form ATP, which is then used by the organism. ATP is also required for further biosynthetic pathways. After the formation of HCHO (formaldehyde), further reactions depend on the type of methanotroph. Type I methanotrophs take up carbon compounds by ribulose monophosphate while type II methanotrophs absorb C1 intermediates; hence, they follow a different pathway called the serine pathway.

4.2. Serine Pathway (Type II Methanotrophs)

Type II methanotrophs follow the serine pathway for formaldehyde assimilation. This pathway requires one HCHO molecule as its initial carbon source. During the course of the cycle, CO₂ molecules are added. This CO₂ molecule is then added as a source of carbon. Reducing power is always required in the form of two molecules of NADH, and energy is provided by two ATP molecules. All of these external molecules are required for the synthesis of each molecule of the end product [110].

In the first step of the serine pathway, formaldehyde generates serine by reaction with glycine. This step is catalyzed by the serine hydroxy methyltransferase enzyme. Glyoxylate acts as an amino-group acceptor to produce hydroxypyruvate and glycine from serine. The hydroxypyruvate produced is further reduced to glycerate with the help of hydroxy pyruvate reductase [80]. Glycerate kinase acts as a catalyst for the addition of a phosphate group from ATP to produce 2-phosphoglycerate. The 2-Phosphoglycerate converts to phosphoenolpyruvate, followed by CO₂ fixation and oxaloacetate reduction to malate. The end product of this pathway is acetyl-CoA, a two-carbon molecule, which is used as the starting point for the development of new cell material.



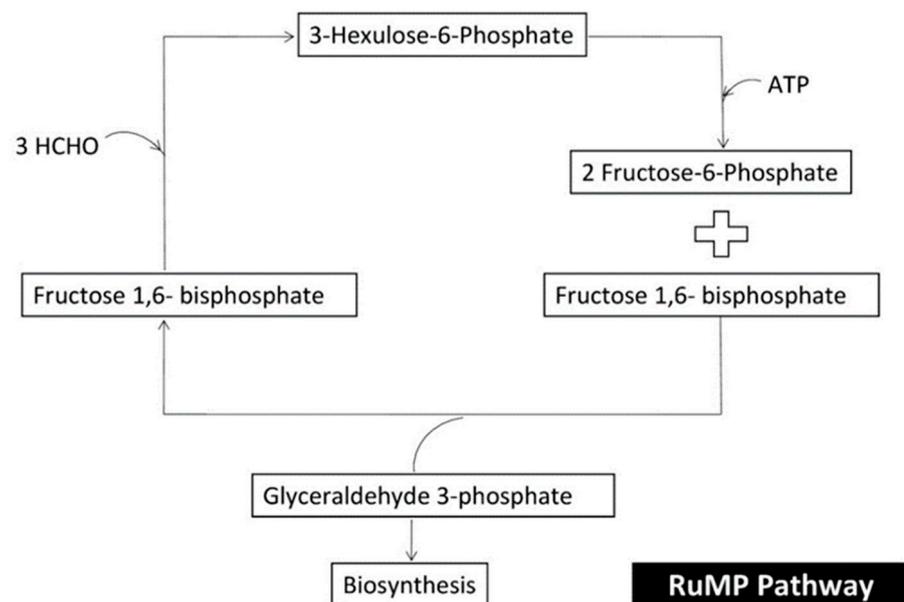
Overall Reaction:



4.3. Ribulose Monophosphate Pathway (Type I Methanotrophs)

The ribulose monophosphate pathway [110] is another pathway that is used for C1 incorporation. This pathway is more energetically efficient than the serine pathway. Here, all the carbon used in the formation of cell material is taken from HCHO, unlike the serine pathway, which includes HCHO as its carbon source in addition to CO₂ for another carbon. Reducing power (NADH) is not required in this pathway, as the three HCHO molecules are already at the same oxidation level as the cell material. Thus, all NADH produced from methane oxidation can be oxidized in the electron transport chain. Only one molecule of ATP was used as the energy source for every synthesized glyceraldehyde-3-Phosphate. The two key enzymes involved in RuMP Pathway are the HPS (Hexulose Phosphate Synthase) and HPI (Hexulose Phosphate Isomerase). HPS catalyzes the formation of Hexulose-6-phosphate from the merging of formaldehyde (HCHO) and ribulose monophosphate, and HPI is used in the next step to form fructose-6-Phosphate [120].

Two glyceraldehyde-3-Phosphate (G-3-Ps) can then be converted into glucose via the reverse glycolytic pathway. The main enzyme, hexulose phosphate synthase, merges one molecule each of HCHO and Ribulose-5-Phosphate. Hexulose-6-Phosphate isomerase is another enzyme used for the conversion of Hexulose-6-Phosphate into two reduced forms fructose-6-Phosphate and fructose-1,6-Phosphate. The end product of this reaction is Glyceraldehyde-3-Phosphate which is a three-carbon molecule. This molecule can then be the starting point for upcoming biosynthesis processes. The basic reactions in this pathway are represented and simplified in the flowchart below.



Overall Reaction:



5. Future Prospects and Applications of Methanotrophs

Methanotrophs are prevalent in controlling methane emissions in the environment by limiting methane release by utilizing them from the surroundings. Under different conditions, methanotrophs have different possibilities and potentials. On the anaerobic side, they play an important role in wastewater treatment, and as aerobic ones, they work biotechnologically to recover different sources from methane waste streams [113]. These aerobic methanotrophs also play a major role in degrading pollutants such as halogenated hydrocarbons [121–123]. Their roles and biotechnological implications help in methane mitigation, as methanotrophs utilize methane for their metabolic processes. In addition,

these microbes produce valuable bioproducts during metabolism that help achieve a bio-based circular economy. Bioremediation is a subject that has been under research in recent years and in which research is still being conducted. There are certain areas where the role of methanotrophs, which possess the ability to contribute to sustaining the environment beyond than their role in maintaining global methane emissions, is still under research.

6. Conclusions

The worldwide methane burden is escalating at an alarming rate, and human activities are responsible for two-thirds of the overall emissions. Among all man-made sources, 57% of the total man-made methane emissions are ascribed to livestock, waste, wastewater treatment, rice cultivation, and other similar activities, which underscores the necessity for more progress and comprehension of methane-reduction tactics. In addition, it is imperative to consider the microbial processes that occur during the methane cycle. Methanotrophs, a diverse group of microorganisms, have been identified as the sole biological sink for methane, suggesting that they are responsible for the oxidation of both aerobic and anaerobic methane in the environment. Aerobic methanotrophic bacteria belong to the phyla Verrucomicrobia and Proteobacteria, which oxidize methane using oxygen, whereas anaerobic methane oxidation is facilitated by anaerobic methanotrophs (bacteria and archaea) using alternative terminal electron acceptors. Methanotrophs possess unique enzymes such as MMOs and MDH that catalyze methane oxidation. The distinctive biology of methanotrophs holds the potential for the effective utilization and bioremediation of methane. The application of anaerobic and aerobic methanotrophs for methane mitigation in anthropogenically-influenced ecosystems should be explored for wastewater treatment and resource recovery from waste streams. Finally, the identification of major aspects of methanotrophs, such as their ecology, physiology, metabolism, and genomics, may help in capitalizing on the biotechnological benefits of methanotrophs in methane mitigation and in the transformation of methane into valuable products (single-cell proteins and biopolymers). Methanotrophs hold considerable promise for a wide range of environmental, energy-related, and biotechnological and microbiological applications, and it is anticipated that ongoing research efforts will uncover additional opportunities for their utilization in the future and in making a sustainable tomorrow.

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