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Review

Ecology of aerobic methanotrophs in controlling methane fluxes from wetlands

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ABSTRACT

Methane (CH_4) is a critical greenhouse gas, with wetlands and flooded rice soils contributing >38% of the global emissions of CH_4. A key process that offsets CH_4 production is biological oxidation by methanotrophs that can consume as much as 90% of the CH_4 produced in aerobic soils. The objective was to review the literature on the biochemical pathways, ecology of methanotrophs, research methods, and environmental and management controls on CH_4 oxidation in wetlands. Methanotrophs have been extensively studied using phospholipid fatty acids (PLFA) but much less so using nucleic acid analysis or with the powerful stable-isotope probing technique of ^{13}C-PLFA analysis. Of the environmental factors that affect CH_4 oxidation, temperature, water content and redox potential are the most important whereas a wide range of soil pH enables oxidation. Methane oxidation varies with season as functions of temperature and plant community shifts (changes with growth stage of C input chemistry and oxygenation from aquatic rhizospheres). Indirect evidence suggests there is greater CH_4 oxidation in pulsing than permanently flooded soils based on observations that static wetlands have greater emissions than pulsing wetlands. Basic research is needed on: the role of inorganic N species in controlling CH_4 oxidation pathways; phylogenetic analysis of methanotrophs; and environmental and edaphic effects on methanotroph growth and activity. Research is needed to develop wetland systems that optimize CH_4 oxidation relative to wetland type and environments and hydrology while maintaining and/or promoting other ecosystem services (e.g. C sequestration, pollution remediation, wildlife habitat, flood control).

Contents

1. Introduction 9
2. Methanogenesis 9
3. Types of methane oxidation and occurrence 10
   3.1. Aerobic methane oxidation 10
   3.2. Anaerobic methane oxidation 10
4. Biochemistry of aerobic methanotrophy 11
   4.1. Obligate methanotrophs 11
   4.2. The methane monooxygenase enzyme system 11
   4.3. Facultative methanotrophs 12
5. Classification of aerobic methanotrophs 12
   5.1. Classification of aerobic methanotrophs based on methane affinity 12
   5.2. PLFA-based classification of methanotrophs 12
      5.2.1. Competitive distribution of the Type I and Type II methanotrophs 13
6. Ecology of aerobic methanotrophs 13
7. Fate of C metabolized by methanotrophs 14
8. Methods to study methanotrophs 14
   8.1. Nucleic acid based approaches 14
   8.2. Phoshpholipid analysis 15

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9. Estimation of methane oxidation rates using isotopic fractionation methods 15
10. Environmental controls on methane oxidation 15
10.1. Temperature and pH 15
10.2. Hydrology and redox potential 16
10.3. Inorganic nitrogen 16
10.4. Seasonal dynamics 17
10.5. Methane concentrations 17
11. Conclusions and future research needs 18
References 18

1. Introduction

There is a broad consensus in the scientific community that human activity is affecting the global climate (IPCC, 2007). Methane (CH_4) is a critical greenhouse gas contributing to global climate change, in part, because it absorbs infrared radiation (IR), nearly 25 times more efficiently than carbon dioxide (CO_2) (Ramaswamy et al., 2001). The atmospheric concentration of CH_4 as of 2005 was 1774 ppb, far exceeding the natural range for the past 650,000 years (IPCC, 2007). Atmospheric CH_4 is largely (70–80%) of biological origin as shown in Table 1.

Recent estimates of the global atmospheric CH_4 budget have revealed unexpected variations in CH_4 concentration such that its growth appears to have declined almost to a standstill in the past three decades (Heinman, 2011). Potentially contradictory studies by Kai et al. (2011) and Aydin et al. (2011) have attempted to answer the puzzling behavior of this atmospheric trace gas. Comparing Table 2 to Table 1 would suggest that CH_4 levels in the atmosphere are going down because total CH_4 oxidation is 577 Tg yr^{-1} compared to 530 Tg yr^{-1} production of CH_4. Even though CH_4 sinks are quite well understood, the apparent discrepancy showing reduced concentrations of atmospheric CH_4 has been attributed to the uncertainties in our understanding of the relative contributions of the various CH_4-generating processes. What this further underscores are the challenges in obtaining accurate field measurements for either CH_4 oxidation or genesis.

Methane oxidation is environmentally beneficial because the radiative absorption potential of CO_2 is lower than that of CH_4. During the microbial oxidation of CH_4 (methanotrophy), carbon (C) in CH_4 is either converted to CO_2 or assimilated into the cellular biomass of the aerobic methane-oxidizing (MO) bacteria (methanotrophs). Aerobic methanotrophy is the key process that counteracts CH_4 emissions from submerged environments such as wetlands, peat bogs, landfills (Table 2) (Segers, 1998; Wagner et al., 2003). Additionally, aerobic methanotrophs consume 43%–90% of the CH_4 produced in aerobic soils being consumed by microbial oxidation (Roslev and King, 1995, Le Mer and Roger, 2001; Hao et al., 1988) which is estimated to be 40 Tg y^{-1} (Reeburgh et al., 1993). Globally, the CH_4 oxidation sink in soils reportedly consumes 7–10% (Table 2) of the net total annual global emission of CH_4, and is roughly equal to the annual increase in atmospheric CH_4 (Watson et al., 1990).

The net flux of CH_4 from a given environment is a balance between the two opposing processes: production by methanogenic archaea and consumption by methanotrophic bacteria and/or archaea. The global CH_4 cycle consists of both atmospheric (mainly chemical) and terrestrial (mainly biological) processes (Reeburgh et al., 1993). Although the soil sink strength for CH_4 is relatively small, its absence would result in an increase in the atmospheric CH_4 concentration by approximately 1.5 times (Duxbury, 1994; Whalen, 2005).

Wetlands are the largest natural source of CH_4 with average estimates of 145 Tg y^{-1}, compared to the next highest sources, energy generation (95 Tg y^{-1}) and ruminant animals (93 Tg y^{-1}) (Table 1). Additionally, it is important to note that rice production is a significant source of CH_4 because of the large areas grown under flooded conditions worlwide. Flooded rice paddies and wetland systems constitute approximately 38% of the total average CH_4 production globally.

Most of the research that has been done on CH_4 oxidation is limited mainly on upland aerobic soils. To our knowledge there are no comprehensive reviews on methanotrophs and CH_4 oxidation relevant to flooded soils. This is important for information synthesis, understanding the state of the research and determination of the gaps in knowledge on methanotrophy in flooded environments. Therefore, the objective of this paper is to review information on the ecology of methanotrophs, their role in regulation of CH_4 consumption from diverse ecosystems with a focus on flooded soils (freshwater wetlands and rice paddies), the biochemical basis of the proposed pathways of CH_4 oxidation, and the techniques used to study methanotrophs in different ecological systems which is important to direct future research on methanotrophy. This review is significant, particularly for constructed wetlands, flooded rice soils, and possibly natural wetlands because these systems can or are being managed for water regimes, nutrients, and plant species; factors that could be optimized to promote CH_4 oxidation. The second objective is to establish a basis to develop management systems to promote CH_4 oxidation of flooded soils. A brief overview of methanogenesis is included to facilitate an overall understanding of the CH_4 cycle.

2. Methanogenesis

Methanogenesis occurs when microorganisms from the domain Archaea called methanogens use C in CO_2 or, use other low molecular weight organic compounds such as one having a methyl group (see below) via alternative biochemical pathways, as an electron acceptor for the production of CH_4. CH_4 production requires extremely reduced conditions, with a redox potential below −200 mV, a condition after other terminal electron acceptors (e.g. O_2, NO_3^-, and SO_4^{2-}) have been reduced (Mitsch and Gosselink, 2007). Wetlands, because of their large surface area and extremely reducing conditions are a major source of CH_4 with estimates of 25% of the annual emissions on a global basis (Mitsch and Gosselink, 2007).

Twenty-six genera and more than 60 species of methanogens have been recorded (Huttunen et al., 2003; Lee et al., 2009; Shin et al., 2008; Talbot et al., 2008). Methanogens have long been classified based on the terminal electron donors that include the simple compounds of: $H_2 + CO_2$, acetate, formate, methylated compounds (methanol, methylamines, dimethylsulfur), and primary and secondary alcohols (Hanson and Hanson, 1996). This forms the basis of defining the five trophic groups of methanogens. The two major pathways of CH_4 production in most environments where organic matter decomposition is significant (digesters, freshwater sediments, submerged soils) are acetotrophy and CO_2 reduction.