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Beyond nitrogen: The importance of phosphorus for CH_4 oxidation in soils and sediments

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ABSTRACT

Wetlands, lakes and agricultural soils are important sources and sinks of the greenhouse gas methane. The only known methane sink of biological nature is the oxidation by methanotrophic microorganisms, these organisms therefore provide an important ecosystem service. To protect this ecosystem service, it is important to maintain methanotrophic microorganism diversity, especially under increased anthropogenically-induced environmental pressures, such as imbalanced input of nutrients to ecosystems. There is therefore an urgent need to understand how N and P affect the structure and activity of methane oxidizing communities. Numerous research studies have already shown variable effects of N-addition on methane oxidation: small additions tend to stimulate methane oxidation, whereas large additions are inhibitory. There is however still a large knowledge gap concerning effects of P on methane oxidation. Here, we present data on the relation between methane oxidation and various measures of P in 50 drainage ditches, and summarize literature reporting relations between P and methane oxidation in wetlands and soils. Additionally, we review experiments on effects of P, N and N + P addition on both low affinity and high affinity methane oxidation. In our set of drainage ditches, as well as studies on wetland and permafrost soils, P content is positively correlated to methane oxidation, though it also co-correlates with many other variables. However, results from P-additions in rice paddies, agricultural soils, landfills, peat bogs, permafrost soils and forests were more variable: sometimes inhibiting (2 studies), other times stimulating methane oxidation (4 studies), and sometimes showing no effect (5 studies). Two studies report increased methanotroph (*pmoA*) abundance following P-fertilization, but little is known about effects of P on methanotroph community structure and its consequences for methane consumption. By mining methanotrophic genomes for genes involved in N and P-related processes, we demonstrate that variability in N/P related traits (influencing acquisition, uptake and metabolism) does not reflect DNA-based phylogeny. This review points to a need for better mechanistic understanding of the effects of P on methane oxidation, and the role of traits of methanotrophic community members in regulating this process.

1. Introduction

Humans have changed the availability of nitrogen (N) and phosphorus (P) in the environment. This has caused an imbalance in nutrient availability, which has cascading effects in the ecosystem (Sterner and Elser, 2002). For example, in Western Europe, atmospheric nitrogen deposition has shifted nutrient-poor terrestrial ecosystems from historic N-limitation to human-induced P-limitation (Berendse et al., 1993; Vitousek et al., 2010). Although various studies have shown effects of such altered N:P availability on the community composition and trophic interactions of eukaryotes (Sterner and Elser, 2002), little is known about stoichiometric effects on microbes, and the associated biogeochemical consequences. A process of particular biogeochemical importance is the microbial oxidation of methane in lakes, wetlands, rice paddies and soils. With a 34 times higher warming potential than CO_2, and a 2.5-fold increase of its atmospheric concentrations since pre-industrial times, methane has become the second most important long-lived greenhouse gas (Denman et al., 2007; IPCC, 2013; WMO, 2014). Following a period of stable atmospheric methane levels in the period between 1999 and 2006, concentrations are rising again since 2007, reaching 1824 ppb in 2013 (WMO, 2014). The only known biological sink for methane is its oxidation to CO_2 by aerobic and anaerobic methane oxidizing microorganisms (methanotrophs). Historically, aerobic methane oxidizing bacteria (MOB) have been classified as types I, II and X, based on physiological, biochemical and phenotypical characteristics. Nowadays MOB are preferentially classified based on phylogeny; either belonging to the classes of Gammaproteobacteria (hereafter referred to as Gamma-MOB, also known as type I or X methanotrophs), the Alphaproteobacteria (hereafter: Alpha-MOB, also known as type II

Abbreviations: MOB, methane oxidizing bacteria; Alpha-MOB, alphaproteobacterial MOB; Gamma-MOB, gammaproteobacterial MOB; MMO, methane monooxygenase; PMO, potential methane oxidation.

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methanotrophs), or to the phyla Verrucomicrobia and NC10 (Stein et al. 2012). MOB belonging to the latter phylum represent a special case, creating their own oxygen under anoxic conditions (Ettwig et al., 2010). Within aerobic MOB we can furthermore distinguish organisms capable of oxidizing methane at atmospheric concentrations (i.e., in forest soils), the so-called 'high-affinity' MOB, from the regular 'low-affinity' MOB which are active at the higher methane concentrations occurring in wetlands, lakes and rice paddies (Dunfield et al., 1999).

Because MOB are the sole known organisms capable of transforming methane to CO_2 and many of the ecosystems in which they are present are under strong environmental pressure, methane oxidation is a potentially vulnerable ecosystem service (Ho et al., 2013a). Important factors regulating methane oxidation in soils and sediments are CH_4, O_2 and nutrient availability, which are influenced by soil or sediment type and land-use, including agricultural practices such as fertilization and tillage (Borrel et al., 2011; Hanson and Hanson, 1996; Hütsch, 1998). Because human activities change nutrient inputs to soils and sediments, there is a strong interest in functioning and resilience of methanotrophic communities under changing nutrient availability. Despite the numerous studies that have been conducted to investigate impacts of N fertilization (see Aronson and Helliker, 2010 for a meta-analysis), little is known about the effect of P availability and N:P stoichiometry on methane oxidation. Such effects act at different levels of organization. On one hand, bottom-up effects on individual cell physiology impact cell growth and functioning, which effects can cascade to ecosystem functioning through populations and communities. On the other hand, effects on communities and populations can influence the genomes of organisms involved, through which consequently all upper levels will be affected (M. Cherif, personal communication.).

In this review we assessed the available literature on effects of N and P on methane oxidation and complement these with recently obtained data on the relationship between N and P with methane oxidation in a reference set of 50 drainage ditch sediments. We discuss the different ways in which N and P concentrations and N:P ratios can affect biological methane oxidation and discuss potential driving mechanisms at multiple organizational scales. We focus mainly on aerobic methane oxidation.

2. Effects of N and P on methane oxidation rates in soils and sediments

To determine known effects of N and P on methane oxidation, we performed a database search for records on methane oxidation and either a form of N, P, or both (Table 1). A quick search revealed an order of magnitude difference between the number of records containing information on methane oxidation and N and those with information on P. Only 47 records contained the words 'nitrogen' and 'phosphorus' in the text, clearly indicating a knowledge gap. These 47 records form the basis of this literature review.

2.1. Field observations

Methane oxidation has been studied intensively in environments where methane production rates are high, such as in peat, rice paddies, wetlands and waste water treatment systems (Basiliko et al., 2007; Ho et al., 2013b; Krause et al., 2013; Zheng et al., 2013), and in environments harboring large organic carbon stores such as permafrost soils. These latter soils form a potential staggering source of methane due to climate change (Gray et al., 2014; Mackelprang et al., 2011). The uptake and oxidation of atmospheric methane in upland soils (e.g., forests, grasslands) has also been thoroughly studied (Dunfield, 2007; Kolb, 2009). Only few studies assessing methane oxidation in methane producing and consuming habitats have addressed both potential relations with N as well as P. These studies, performed in wetland, upland (forest, grassland) and arctic permafrost soils, are discussed below.

Table 1
Web of Science (Thompson Reuters) database search results. 'CH_4 ox.' = methane oxidation.

Web of Science search query[a]	CH_4 ox.	+N	+P	N + P
TOPIC: ("methane oxidation" OR "CH_4 oxidation")	+	+	+	+
AND TOPIC: (nitrogen OR NO_3 OR nitrate OR NH_4 OR ammonium OR urea)		+		+
AND TOPIC: (phosphorus OR PO_4 OR phosphate OR TP)			+	+
# Records	3808	765	80	47

[a] August 2014, *Timespan*: All years, *Search language* = Auto, all including: "*NOT* TOPIC: (catalyst OR catalysis OR catalysts) *NOT* TITLE: (catalyst OR catalysis OR catalysts)".

In a study of US wetlands, P-eutrofied sites displayed 2-fold higher methane oxidation, and 4 orders of magnitude higher methanotroph numbers than unimpacted sites. Furthermore, impacted and unimpacted sites had distinct communities, both containing Gamma-MOB, whereas Alpha-MOB were only observed in the impacted sites, which also showed higher methanogenic activity (Chauhan et al., 2012). In upland forest soils contrasting results were found, ranging from no relation between methane oxidizing communities and N and P concentrations in beech-maple forest soils (Burke et al., 2012) to stimulating effects of methane uptake in tropical forest soils (Zhang et al., 2011). In arctic permafrost soils (lowland and upland), soil P was positively related to methanotroph abundance (dominated by Gamma-MOB at all sites), and experiments showed that indeed methane oxidation potential was limited by P (Gray et al., 2014).

2.2. Methane oxidation in drainage ditch sediments

High rates of methane production and oxidation can occur in the sediment of drainage ditches that receive runoff from fertilized agricultural fields. In Fig. 1 the relation between potential CH_4 oxidation (PMO) and P concentrations is shown for a set of 50 Dutch drainage ditches. Phosphate and total P concentrations in sediment porewater, in ditchwater and in the sediment show a significant positive correlation with PMO. Of these variables, phosphate concentrations in the sediment porewater, which is the most easily accessible form of P for sediment microorganisms, show the strongest correlation to PMO. However, the correlation between P contents and methane oxidation rates does not necessarily point to a causal relation. In this particular dataset, PMO correlated significantly with 53 out of 95 environmental variables that were measured for all 50 ditches (for more detail, see SI 1). This multitude of significant correlations can be explained by the fact that many variables co-vary with the organic matter content of the sediments (e.g., total C and N content, water content, particle size distribution). In addition, organic matter content generally correlates with not only easily-measured variables such as P, but also with specific substrate area, leading to a higher mass exchange and more niches for methanotrophic bacteria at higher organic matter contents (Amanullah et al., 1999; Streese and Stegmann, 2003). Conversely, in environments with prolonged, high methane availability, such as landfill-cover soils, MOB biomass itself causes an increase in soil organic matter content — and therefore N and P contents (Kightley et al., 1995).

When using field observations to determine the effect of nutrients on methane oxidation, two additional difficulties arise. First, nutrient availability can have many indirect effects on methane oxidation. For example, N and P impact plant growth, which can affect the conditions for methane cycling in the root zone. Lu et al. (1999) for example detected higher pore water CH_4 concentrations and higher CH_4 emissions in P-limited rice paddy soils, which could either indicate that methanotrophs are limited by P, or methanogenesis is increased due to indirect effects of P-limitation of the plants, such as changes in excretion of root-exudates. Second, although bioavailability of N is fairly straightforward, bioavailability of P may change with environmental conditions, for example by binding to metals, mediated by pH and oxygen content. Although Richardson and Simpson (2011) note that 'bioavailable P' is a term suited for plants, but not for microorganisms, that can potentially use P from all pools, microorganisms will at least need to invest more