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Effect of tree species on methane and ammonium oxidation capacity in forest soils

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Abstract

High and low affinity methane oxidation potentials were measured for soils under five fully replicated land-use treatments over an entire calendar year. Simultaneous measurements of soil nitrification potential in replicate soil samples were also made. Both high and low affinity CH_4 oxidation were significantly reduced in the nitrate-rich soils under alder, compared to the other four vegetation treatments (oak, Norway spruce, Scots pine and grass). However, the effect of land-use was less for high affinity methanotrophy than for low affinity CH_4 oxidation. Nitrification rates were highest in alder soils, with the greatest potential for NH_4^+ oxidation occurring in the top 5 cm of the soil. No significant relationship between potential nitrification rate and low affinity CH_4 oxidation was seen. However, a significant negative relationship between nitrification and high affinity CH_4 oxidation was identified. We found vegetation type to be a key determinant of soil-mediated CH_4 and NH_4^+ oxidation, but found no evidence for significant CH_4 oxidation by nitrifying bacteria.

Keywords: Methanotrophs; Nitrifiers; Nitrate inhibition; Greenhouse gas; Grassland; Norway spruce; Oak; Alder; Scots pine

1. Introduction

The largest biological sink for the powerful greenhouse gas methane (CH_4) is soil. Current estimates of the size of the soil CH_4 sink are of the order of 30–40 Tg y^{-1} (Mosier et al., 1998; Houweling et al., 1999). Soil mediated CH_4 oxidation takes two distinctive forms depending on the extant concentration of CH_4 (Bender and Conrad, 1992). The first involves oxidation of CH_4 by methanotrophic bacteria at or near atmospheric concentrations (~ 1.8 μl l^{-1}). These 'high affinity' methanotrophs have not been defined phylogenetically, and have not been isolated, despite their importance to the global CH_4 budget. Methane oxidation in the laboratory in soils with high affinity methanotrophs is characterised by an initially very rapid decrease in CH_4 concentration, down to just a few hundred nanoliters CH_4 l^{-1}, followed by a slower oxidation rate (Bender and Conrad, 1993). The second form of soil-mediated CH_4 oxidation is that of 'low affinity, high capacity' methanotrophy, characteristic of the known methanotrophs in culture collections. These methanotrophic bacteria utilise CH_4 at concentrations many times greater than that in the atmosphere, becoming saturated only at 1–10 ml CH_4 l^{-1}. Both groups are extremely important to the global CH_4 budget as, while high affinity methanotrophs are responsible for direct uptake of atmospheric CH_4, the high capacity methanotrophs remove much of the CH_4 produced in source areas such as landfill sites or CH_4 seeps, before it can reach the atmosphere (Conrad and Rothfuss, 1991; King, 1992).

Nitrifying bacteria (NH_4^+ oxidising bacteria—AOB) in soils are also known to have the ability to oxidise CH_4 during the process of NH_4^+ oxidation, while methanotrophs have been found to oxidise NH_4^+, albeit at much lower rates than the AOB. Indeed, the nitrifier *Nitrosococccus oceanus* apparently has a half saturation constant (k_m) for CH_4

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oxidation similar to that of known methanotrophs (see Bédard and Knowles, 1989). However, most studies indicate little, if any, potential for CH_4 oxidation by soil nitrifiers (Jiang and Bakken, 1999; Klemedtsson et al., 1999). There are numerous reports of a significant land-use effect on soil-mediated nitrification (e.g. Rhoades and Coleman, 1999; Verchot et al., 2001; Krave et al., 2002). What is not clear, though, is the extent to which such land-use effects are shared between high and low affinity CH_4 oxidation in soils and the activity of AOB.

Land-use is also known to be a key determinant of soil mediated CH_4 oxidation. Conversion of forested land for agriculture may significantly reduce the soil's capacity to act as a sink for CH_4 (Mosier et al., 1991; Dobbie and Smith, 1996). Similarly, changes in land-use which affect the soil water content, pH and nutrient chemistry have all been shown to affect CH_4 oxidation capacity (e.g. Steudler et al., 1989; Nesbit and Breitenbeck, 1992; Dunfield et al., 1993; Willison et al., 1995). In preliminary experiments in 1998 Reay et al. (2001a) showed how five vegetation types (alder, oak, Norway spruce, Scots pine and grassland) affected the CH_4 oxidation capacity of temperate soils in an experimental plot in Northwest England. However, one aim of our program was to assess land–use effects on both the high and low affinity CH_4 oxidation potential–the capacity of soils under various vegetation types to act as sinks for CH_4 at near atmospheric and saturating concentrations, respectively. Assuming that high and low affinity CH_4 oxidation are representative of physiologically distinct populations of methanotrophs, would changing vegetation type have a differential effect on their relative CH_4 oxidation potentials?

We hypothesised that the soil CH_4 oxidation capacity would be significantly reduced in the alder treatment, relative to soils in the oak, Norway spruce, Scots pine and grassland treatments, given the elevated NO_3^- concentrations of the alder soils. Though in situ the soils in question are never likely to be exposed to saturating CH_4 concentrations ($>10{,}000$ μl $CH_4\,l^{-1}$), by so exposing the soils we aimed to elucidate their relative CH_4 oxidation capacities as dependent on vegetation type, and then to compare this response to that of the high affinity methanotrophy likely to dominate under field conditions.

Finally, we wished to examine the relationship between CH_4 and NH_4^+ oxidation capacities, given the possibility of significant co-oxidation of CH_4 by soil nitrifiers based on previous studies. Did either high or low affinity CH_4 oxidation show a clear relationship with NH_4^+ oxidation capacity in the same soil?

Here we present the findings of a fully replicated, year-long study of vegetation effects on high and low affinity CH_4 oxidation potentials, and NH_4^+ oxidation potentials in temperate forest soils. Additionally, we have compared depth profiles of CH_4 and NH_4^+ oxidation in soils of different tree species over several seasons and have derived large-scale estimates of the size of sink for atmospheric and saturating CH_4 concentrations which the different soils constitute.

2. Materials and methods

2.1. Site description

All soil samples were collected at the Gisburn experiment of Forest Enterprise's Bowland Forest in Lancashire, UK. This is a fully replicated, randomised plot experiment established in 1955, clear felled in 1989 because of windthrow problems and plots replanted exactly as previously. Prior to 1955 the site consisted of poorly drained sheep grazings dominated by *Festuca*, *Agrostis* and *Deschampia*. The site slopes gently to the south-west, is 260–290 m above mean sea level and 35 km from the coast of northwest England.

The experiment has triplicated half acre (0.2 ha) plots of both pure and mixed stands of sessile oak (*Quercus petraea* (Mattuschka) Liebl.), alder (*Alnus glutinosa* (L.) Gaertn.), Norway Spruce (*Picea abies* (L.) Karst), Scots Pine (*Pinus sylvestris* (L.)), and unforested control plots containing a species-poor rough pasture of *Festuca–Agrostis* with *Nardus stricta*, *Deschampsia* and *Juncus* spp. Plots of each treatment are distributed randomly in three blocks. This study examined only the pure stands of the above tree species and the grassed control plots. The experiment has never been fertilised. During initial planting the soil was shallow-ploughed at 1.5 m spacing to improve drainage and the trees were planted on the ridges. Key soil characteristics of the five treatments over the course of our investigation (1998–2000) are given in Table 1. Typical soil profiles consisted of several centimetres of leaf litter in the forested plots; a shallow layer ($\sim$1 cm) of leaf litter-derived humus; an organic-rich A horizon of around 20 cm in depth; and an underlying B/C horizon of sandy clay.

2.2. Sample collection and preparation (Reay et al., 2001a)

From November 1998 to November 1999, quadruplicate 10 cm vertical cores (15 cm dia.) were taken every 2 months from the five vegetation treatments in each of the three experimental blocks, with the 0–5 cm depth interval of the A horizon of each sample being used for laboratory measurements of CH_4 and NH_4^+ oxidation. Additionally, quadruplicate 30 cm cores were taken on a seasonal basis from the five vegetation treatments in experimental block two, the top 20 cm of which was divided into 5 cm intervals. Additional soil cores were periodically taken for measurements of bulk density. In the laboratory, soil samples were sieved (4 mm mesh) to remove stones and roots and to homogenise the four replicate cores used for each sample. Soil samples were stored for up to a maximum of 2 weeks at 4 °C before experimentation. Preliminary experiments showed that such storage had no significant effect on CH_4