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Aerobic and anaerobic microbial activities in the foreland of a receding glacier

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ABSTRACT

The foreland soils of a receding glacier were investigated for both aerobic and anaerobic microbial activities. Estimation of microbial biomass via substrate induced respiration, and determination of dehydrogenase activity, dimethylsulfoxide reduction and ammonification were performed to describe soil microflora and its activity. These parameters distinctly increased along the chronosequence from the youngest to the oldest soil. Additionally, these properties showed remarkably higher values in the samples collected at the end of the growing season indicating distinct seasonal changes. The determination of methane emission by the three soils incubated at 10, 37 and 50 °C clearly pointed to higher methanogenic activities within the thermophilic temperature range. Our results also show that water saturation in order to simulate spring snow melt led to increased emissions of methane due to reduced oxygen availability. Methane release was generally low in the primary soil, slightly increased as soil formation proceeded and in all soils was distinctly higher at the end of the growing season. Potential methane consumption also increased along the foreland and during the year. Overall methanotrophic activity greatly exceeded methanogenic activity, and the net CH_4 consumption distinctly increased along the chronosequence.

1. Introduction

Due to the increasing atmospheric temperatures during the past 150 years, alpine glaciers, environments which are known to strongly respond to climatic changes, have lost significant portions of their ice covers (Patzelt and Bortenschlager, 1979; Raffl, 1999). New sites composed of barren moraine material become exposed to the air and various other factors which altogether drive the succession and soil formation at these areas. Glacier forelands include only recently deglaciated sites of bare moraine material and soils that have been ice-free for time periods up to 150 years and thus these sites can be considered as time series. Therefore, glacier forelands provide valuable experimental sites to gain insight into primary succession as well as soil formation (Begon et al., 1990; Kaufmann, 2001).

Various studies on this topic have examined the establishment of plant communities (del Moral and Jones, 2002; Nagl and Erschbamer, 2010) and faunal succession (Hodkinson et al., 2003; Kaufmann, 2001). Recently, increased attention has been paid to the investigation of soil microbes within these harsh developing habitats (Sigler and Zeyer, 2002; Tscherko et al., 2003; Deiglmayr et al., 2006; Barcena et al., 2010, 2011; Lazzaro et al., 2012). An important objective of these studies was to determine the contribution of different functional groups to nutrient cycles via assessment of soil enzyme activities such as protease, urease, and so forth (Tscherko et al., 2003). Others focused on the description of microbial community structures using various molecular approaches (e.g. Sigler and Zeyer, 2002). In particular, also the foreland of the receding Rotmoosferner was a site of interest in such studies with special regard to the community structure and successional patterns of *Crenarchaeota* which were found to occur in three phases (Nicol et al., 2005). Others have recognized a decrease in the species richness of nitrate reducing bacteria along with increasing soil age (Deiglmayr et al., 2006).

However, up to now little attention has been paid to the investigation of methanogenic archaea and methanotrophic bacteria in these alpine environments and if so, merely their abundance and not their activities were measured. Both functional groups of microorganisms are important key players within the methane and thus C cycle by either the production (acetoclastic and hydrogenotrophic methanogens) or the oxidation (methanotrophic bacteria) of the greenhouse gas methane (CH_4). Up to our knowledge there are only two studies, both conducted in Greenland, which examined the role of glacier foreland soils in methane budget (Barcena et al., 2010, 2011) and which concluded that these soils are net methane sinks. However, these results were not

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directly linked to temperature, water content, other soil microbiological properties nor to the process of soil formation (Barcena et al., 2010).

Due to this lack of information we decided to investigate the activities of anaerobic methanogenic archaea as well as methanotrophic bacteria across the chronosequence soils of the receding Rotmoosferner (Ötz Valley, Austria) in respect to soil age and general microbial activities. Besides microbial standard methods describing abundance and activity of microorganisms we used assays that determine the potential for consumption and emission of CH_4 by these soils as well as quantitative PCR (qPCR) targeting the archaeal 16S rRNA gene. The results should help to understand how organisms and activities engaged in CH_4 cycle can establish within these high altitude alpine soils and how the activities change during the phases of soil formation.

A further objective of the present study was to investigate a possible seasonality of microbial activities within the glacier foreland. Recent investigations from our institute proved a surprising high microbial activity in these high alpine soils during winter (Kuhnert et al., 2012) and preliminary investigations made us suggest that seasonal variations might exceed some effects of soil age but were not paid a justified attention till now.

2. Materials and methods

2.1. Study site and soil sampling

The study sites were situated on the glacier foreland of the receding Rotmoosferner (46°50′N, 11°03′E) in the Tyrolean Ötz Valley (Austria) at 2280–2450 m above sea level. The foreland starts at the margin of the receding glacier and is terminated by the moraine of 1858. The soils outside the respective moraine are ice-free for more than 5000 years. All soils of the Rotmoos Valley are influenced by the basement rocks of the Ötztal–Stubai Complex and the Schneeberg Complex (Schwienbacher and Koch, 2010). Therefore, the moraine material is mainly composed of paragneis and mica schists derived from the Ötztal–Stubai Complex, but also of mica schists containing marble, garnet, hornblende and amphibolites representing the main material of the Schneeberg Complex (Krainer, 2010). Comprehensive studies in terms of soil formation, plant succession and the development of soil invertebrates were performed previously (Erschbamer et al., 1999; Kaufmann, 2001; Raffl, 1999). Early successional stages consist of pioneer plant species such as *Saxifraga aizoides*, *Saxifraga oppositifolia* (Nagl and Erschbamer, 2010), *Linaria alpina* as well as *Artemisia genipi* (Raffl, 1999). Further soil development leads towards the establishment of a typical alpine tundra community (Nagl and Erschbamer, 2010).

Due to the retreat of the glacier each sampling site represents a particular soil age. Soils were sampled at three different sites. Site S1 (6 years) was collected near the margin of the receding glacier, S2 represents an intermediate stage with an approximate age of 140 years and S3 is a mature soil with an age of several thousand years. If necessary, the plant material was removed in order to collect the soil material representing the A horizon. We collected the uppermost 5 cm of the A horizon of at least five replicates. Within each site the replicates were taken 1–3 m apart from each other. The fresh soil material from each site was pooled, passed through a sieve (2 mm mesh size) and stored at 4 °C prior to the experiments. Soil sampling was performed approximately ten days after snow melt in July 2010 (start of the growing season) and in October 2010 at the very end of the plant growing season. Selected soil properties are listed in Table 1.

Table 1
Selected soil properties of the Rotmoos glacier foreland according to soil age and sampling date. Values are given as means ($n = 3$), standard deviations are depicted in parenthesis. Soils from site S1, S2 and S3 were 6, 140 and several thousand years old.

Soil	Sampling	pH	OM%[a]	NH_4^+[b]
S1	July 10	6.99 (0.03)	0.77 (0.06)	2.82 (0.03)
S2	July 10	6.64 (0.03)	2.16 (0.02)	6.75 (1.14)
S3	July 10	4.25 (0.01)	14.70 (0.12)	8.85 (0.22)
S1	October 10	7.31 (0.01)	0.70 (0.06)	2.40 (0.08)
S2	October 10	6.71 (0.10)	4.96 (0.15)	5.63 (0.43)
S3	October 10	4.67 (0.10)	16.05 (0.43)	4.85 (0.05)

[a] OM, organic matter.
[b] NH_4^+, ammonium-N [μg g^{-1} dry soil].

2.2. Physicochemical soil parameters

Sieved samples of each soil were used for pH determinations. Measurements were performed in triplicate for each soil site and sampling date by mixing soil in 10 mM $CaCl_2$ (1:13.5) and determining pH after 2 h of incubation at room temperature (Schinner et al., 1996). The dry weight was assessed from drying 10 g of sieved soil at 105 °C overnight.

Organic matter was also determined in three replicates per soil sample and sampling date. We used oven dried (105 °C, overnight) soils that were subsequently combusted for 4 h at 550 °C. The loss of mass after combustion served as a measure for the organic material that was present within the soils (Schinner et al., 1996). Ammonium nitrogen was determined after the protocol described in Schinner et al. (1996) after extraction in KCl solution (2 M).

2.3. Microbial biomass

Analysis of microbial biomass (C_{mic}) was performed using substrate-induced respiration (SIR). CO_2, evolved after the amendment of glucose, was measured by an infrared gas analyzer (IRGA). For the calculation of C_{mic} the formula of Anderson and Domsch (1978) was applied. 1 ml of CO_2 produced corresponds to 40 mg of microbial biomass. For the measurement we used 70–90 g of fresh soil material that was mixed thoroughly with 10 mg of glucose g^{-1} dry soil. Triplicate samples were subsequently placed in gastight plastic columns, incubated at 22 °C for 2–3 h and measured 2 h after glucose amendment.

2.4. Enzyme activities

Various soil enzymes were estimated to assess the microbial activities of the three soils. Determination of dehydrogenase activity (DHA), ammonification (AM) and dimethylsulfoxide (DMSO) reduction were performed as recommended in Schinner et al. (1996). For DHA determination, sieved soils were mixed with triphenyltetrazolium chloride (TTC), a compound which is used as an alternative intracellular electron acceptor by the majority of soil microbes (Ottow, 2011). After an incubation of 16 h at 25 °C the end product triphenylformazan (TPF) was extracted with acetone and quantified photometrically at 546 nm.

For the determination of ammonification soils were incubated under anoxic conditions according to the assay described in Schinner et al. (1996). The basic principle of this assay is the conversion of organic nitrogen to NH_4^+ during an incubation period of seven days at 40 °C. NH_4^+ nitrogen can subsequently be detected colorimetrically at 660 nm.

We assessed dimethylsulfoxide reduction by using a 10% (v/v) DMSO solution as a substrate. 5 g of sieved soil was incubated with 1.25 ml DMSO solution at 40 °C for 4 h. The dimethylsulfide (DMS)