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Characterisation of bacterial populations in Arctic permafrost soils using bacteriohopanepolyols

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ABSTRACT

Bacteriohopanepolyols (BHPs) are biomarkers providing taxonomically and environmentally diagnostic information. BHPs may help to unravel the composition of bacterial communities residing in recent as well as ancient permafrost soils and sediments and also provide information on associated environmental conditions. However, detailed data on their distribution in the heterogeneous Arctic environment are scarce. The distribution and structural diversity of BHPs were studied in the annually thawing (active) layer of three different sites in the polygonal tundra of the Lena Delta in the Siberian Arctic. Variations between permafrost structures and soil horizons caused by differences in the physical and chemical soil properties were observed. C and N content is significantly correlated with the BHP composition so that the highest BHP concentrations and greatest structural diversity occur in the uppermost organic soil horizons, which consist mainly of fresh or little degraded plant material. Furthermore, statistical analyses reveal that higher abundances of adenosylhopane-type soil marker BHPs are linked to higher soil pH values. Small scale environmental controls on BHP distributions are reflected by amine-functionalised BHPs from methanotrophic bacteria only occurring in the water-saturated, oxygen-depleted polygon centres and by soil marker BHPs, which are significantly more abundant in the well aerated polygon rims than in the centres. In contrast, C-2 methylated BHPs, putative indicators of plant-bacterial interactions, are present in all soil horizons and permafrost structures and their relative distribution is not systematically linked to soil properties. Overall, lipid-based results agree with published 16S rRNA based community structure assessments highlighting the usefulness of BHPs to represent bacterial populations in recent and ancient permafrost soils.

1. Introduction

Permafrost soils are a very distinct habitat for life given their sub-zero temperatures and significant temperature fluctuations (Gilichinsky et al., 1995). Nonetheless, microorganisms have adapted to these harsh conditions through metabolic regulation (Jansson and Tas, 2014 and references therein). Bacterial activity and cell growth have been reported at ambient permafrost temperatures of down to −25 °C (Mykytczuk et al., 2013). Generally, bacteria seem to occur in higher diversity and higher abundance when compared to both archaea and fungi (Steven et al., 2008; Yergeau et al., 2010). The most frequently observed bacterial phyla (based on 16S rRNA sequencing) are Proteobacteria, Firmicutes, Chloroflexi, Acidobacteria, Actinobacteria and Bacteroidetes (Jansson and Tas, 2014).

One means to study bacterial biomass is the analysis of their membrane lipids. Phospholipid fatty acids (PLFAs) are the main constituents of the bacterial bilayer membrane. However, PLFAs are degraded within days to weeks after cell death and, thus, reflect the viable microbial community (Kaur et al., 2005) and do not allow tracing of bacterial biomass through space and time. Bacteriohopanepolyols (BHPs) are pentacyclic triterpenoids, which are produced almost exclusively by bacteria, although not all bacteria, while they are absent in archaea (Ourisson and Albrecht, 1992). In contrast to PLFAs, the degradation products of BHPs can be preserved in sedimentary records (e.g., Brocks et al., 1999). BHPs are believed to help organisms adapt to physiological stress by modulating the fluidity and organisation of the bacterial membrane

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(Rohmer et al., 1984; Kannenberg and Poralla, 1999; Rohmer, 2008; Welander et al., 2009; Sáenz et al., 2012). To date a suite of structurally diverse side chains have been identified of which some are proposed to provide taxonomic and/or physiological information (Rohmer, 1993; Talbot and Farrimond, 2007). For example, some amine-functionalised BHPs such as 35-aminobacteriohopane-31, 32,33,34-tetrol (aminotetrol; **Ia**, see Appendix for structures) and 35-aminobacteriohopane-30,31,32,33,34-pentol (aminopentol; **Ib**) are characteristic for aerobic methanotrophic bacteria and are found in many species and environments (Neunlist and Rohmer, 1985a; Cvejic et al., 2000; Talbot and Farrimond, 2007; Zhu et al., 2010; van Winden et al., 2012; Talbot et al., 2014). However, low levels of aminotetrol (**Ia**) and in one case trace levels of aminopentol (**Ib**) have been found in some species of sulfate-reducing bacteria of the genus *Desulfovibrio* (Blumenberg et al., 2006, 2009, 2012). BHPs methylated at the C-2 position (**II**) have previously been used as markers for cyanobacteria (e.g., Summons et al., 1999; Zhang et al., 2007; Talbot et al., 2008) although this interpretation has been questioned as the *hpnP* gene required for C-2-methylation has also be identified in alphaproteobacteria and in at least one acidobacterium (Welander et al., 2010; Ricci et al., 2014). The C-2 methylation in alphaproteobacteria appears to be particularly common in species involved in plant–microbe interactions and to be an indicator for this specific environmental niche rather than a taxonomic marker (Ricci et al., 2014).

The BHP adenosylhopane (**Ic**) has been reported to be the precursor to all other side chain extended BHPs (Bradley et al., 2010). Adenosylhopane (**Ic**) together with several related structures also containing a cyclised side chain (**Id, Ie**) and their C-2 methylated homologues (**IIc**, **IId**, **IIe**) are also potential environmental markers rather than taxonomic markers. These compounds are abundant in soils while occurring only in minor concentrations in marine and lacustrine sediments (Talbot and Farrimond, 2007; Cooke et al., 2009; Xu et al., 2009; Blumenberg et al., 2010; Rethemeyer et al., 2010; Kim et al., 2011; Sáenz et al., 2011; Taylor and Harvey, 2011; Zhu et al., 2011; Doğrul Selver et al., 2012; Wagner et al., 2014). Adenosylhopane (**Ic**) and its related structures (hereafter referred to as soil marker BHPs) have also been studied in Arctic environments where they have been used as indicators for the export of terrigenous organic matter into Arctic rivers and the Arctic Ocean (van Dongen et al., 2008; Cooke et al., 2009; Taylor and Harvey, 2011; Doğrul Selver et al., 2015). The Arctic studies mainly investigated marine and riverine samples, while information from the alleged terrigenous source – permafrost soils – remains scarce. To date only two studies of BHPs in Arctic soils have been published. Rethemeyer et al. (2010) studied BHPs in Arctic permafrost soils from Svalbard in which a larger and more diverse bacterial community was observed in the organic horizons compared to the underlying mineral soils. Doğrul Selver et al. (2015) investigated three Yedoma (ice complex) samples within the Siberian Kolyma River catchment and found low structural BHP diversities dominated by soil marker BHPs. So far, no study has been performed in the organic-rich and extremely heterogeneous Arctic tundra even though these regions contribute significantly to the terrestrial organic matter pool (Ciais et al., 2013) – including BHPs – found in Arctic rivers and the Arctic Ocean (Dittmar and Kattner, 2003). Accordingly, understanding BHP distributions in these polygonal tundra soils is crucial for understanding the BHP records obtained from such Arctic riverine and marine samples off tundra areas. Here, we investigated BHP distributions in the seasonally thawing surface layer, the active layer, of characteristic polygonal tundra soils in the Siberian Arctic in order to (a) evaluate their spatial variability and (b) to characterise the bacterial communities present and compare these results with other methods including PLFA analyses and DNA/RNA sequencing.

2. Study area

The Lena Delta in Siberia, Russia, is the largest Arctic river delta covering approximately 32,000 km^2 (Are and Reimnitz, 2000). It is located in the zone of continuous permafrost under an Arctic continental climate characterised by low mean annual precipitation (125 mm), low mean annual air temperatures (−12.5 °C), and a large seasonal temperature amplitude between summer (July 10.1 °C) and winter (February −33.1 °C; Boike et al., 2013).

The Lena Delta consists of over 1000 islands including Samoylov Island and Kurungnakh Island (Fig. 1). Samoylov Island belongs to the recent active delta region (1–12 m a.s.l.) and is made up of Holocene fluvial sediment. It is characterised by ice wedge polygonal tundra with thermokarst lakes and an active flood plain. Ice wedges form in polygonal patterns through seasonal frost cracking repeatedly pushing material upwards to form elevated rims surrounding depressed centres (e.g., Fiedler et al., 2004). Kurungnakh Island (30–60 m a.s.l.) consists of a lower, 15–20 m thick Paleo-Lena River sand unit overlain by a ca. 20 m thick late Pleistocene ice-rich, fine grained permafrost sequence (ice complex; Schirrmeister et al., 2011). The ice complex formation, often synonymously called 'Yedoma', is covered by a 2–3 m thick unit of Holocene aeolian silty sand in which polygonal tundra developed with small, 3–5 m wide, ice wedges (Morgenstern et al., 2011; Schirrmeister et al., 2011; Zubrzycki, 2013).

The soils on Samoylov and Kurungnakh Islands belong to the order of Gelisols (Soil Survey Staff, 2010) with polygon rims dominated by Glacic Aquiturbels and depressed polygon centres characterised by Typic or Ruptic Historthels with sandy loam to silt loam soil texture (Table 2; Zubrzycki et al., 2012). Mosses, grasses, sedges, and dwarf willow shrubs dominate the vegetation at both study sites with different distributions on polygon rims and centres (Boike et al., 2013).

3. Material and methods

3.1. Sampling

Three sampling sites were chosen according to their morphological differences (Table 1): a polygon in a relatively recently developed thermokarst basin (KUB) and a polygon on the elevated (55 m a.s.l.) upland (KUU) on Kurungnakh Island as well as a polygon developed on typical modern fluvial deposits on Samoylov Island (SA). In comparison to the aeolian origin of the KUU polygon, the KUB polygon developed on aeolian and lacustrine sediment of a former thermokarst lake, which drained about 5.7 ka BP (Morgenstern et al., 2013). At all sites, the polygons had diameters of ca. 9–13 m. Both the depressed, water saturated polygon centres (C) and the several decimetres elevated and relatively dry polygon rims (R) were sampled at the end of the summer, i.e. at maximal thaw depth of the active layer in August 2009 and 2010. Samples were taken from the characteristic horizons of the active layer (Table 2), which was about 29–43 cm thick; shallower in polygon rims and deeper in centres. Soil horizons were defined according to US Soil Taxonomy (Soil Survey Staff, 2010). At site SA, a sample of the uppermost still frozen permafrost was also retrieved from the polygon rim (SA-R_{Bjjf}).

All samples were stored in pre-combusted glass jars and kept frozen until analysis. Prior to analysis, samples were freeze dried and ground.

3.2. Bulk soil analysis

Total carbon and nitrogen contents were determined on 5–10 mg soil using a Vario MICRO cube elemental analyser