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15. Global Warming and Carbon Dynamics in Permafrost Soils: Methane Production and Oxidation

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Abstract

The Arctic plays a key role in the Earth's climate system, because global warming is predicted to be most pronounced at high latitudes, and one third of the global carbon pool is stored in ecosystems of the northern latitudes. The degradation of permafrost and the associated intensified release of methane, a climate-relevant trace gas, represent potential environmental hazards. The microorganisms driving methane production and oxidation in Arctic permafrost soils have remained poorly investigated. Their population structure and reaction to environmental change is largely unknown, which means that also an important part of the process knowledge on methane fluxes in permafrost ecosystems is far from completely understood. This hampers prediction of the effects of climate warming on arctic methane fluxes. Further research on the stability of the methane cycling communities is therefore highly important for understanding the effects of a warming Arctic on the global climate. This review first examines the methane cycle in permafrost soils and the involved microorganisms. It then describes some aspects of the potential impact of global warming on the methanogenic and methanotrophic communities.

15.1 Introduction

A better understanding of the global terrestrial carbon cycle has become policy imperative, both nationally and worldwide. The Kyoto Protocol recognizes the role of terrestrial systems as carbon sinks and sources. Terrestrial and sub-marine permafrost is identified as one of the most vulnerable carbon pools of the Earth system (Osterkamp 2001; Zimov et al. 2006). About one third of the global soil carbon is preserved in northern latitudes (Gorham 1991), mainly in huge layers of frozen ground, which underlay around 24% of the exposed land area of the northern hemisphere (Zhang et al. 1999). This carbon reservoir is of global climatic

importance, in particular due to the currently observed climate changes in the Arctic (IPCC 2007; see Chapters 1 and 15.4).

Thawing of permafrost could release large quantities of greenhouse gases into the atmosphere, thus further increasing global warming and transforming the Arctic tundra ecosystems from a carbon sink to a carbon source (Oechel et al. 1993). Trace gas fluxes from permafrost ecosystems are influenced by a number of biotic and abiotic parameters (Figure 15.1). The decomposition of soil organic matter and the generation of greenhouse gases results from microbial activity which is affected by habitat characteristics (soil parameters) and by climate-related properties (forcing parameters). The way of gas transport determines the ratio between methane and carbon dioxide emission to the atmosphere. However, the processes of carbon release, their spatial distribution and their climate dependency are not yet adequately quantified and understood.

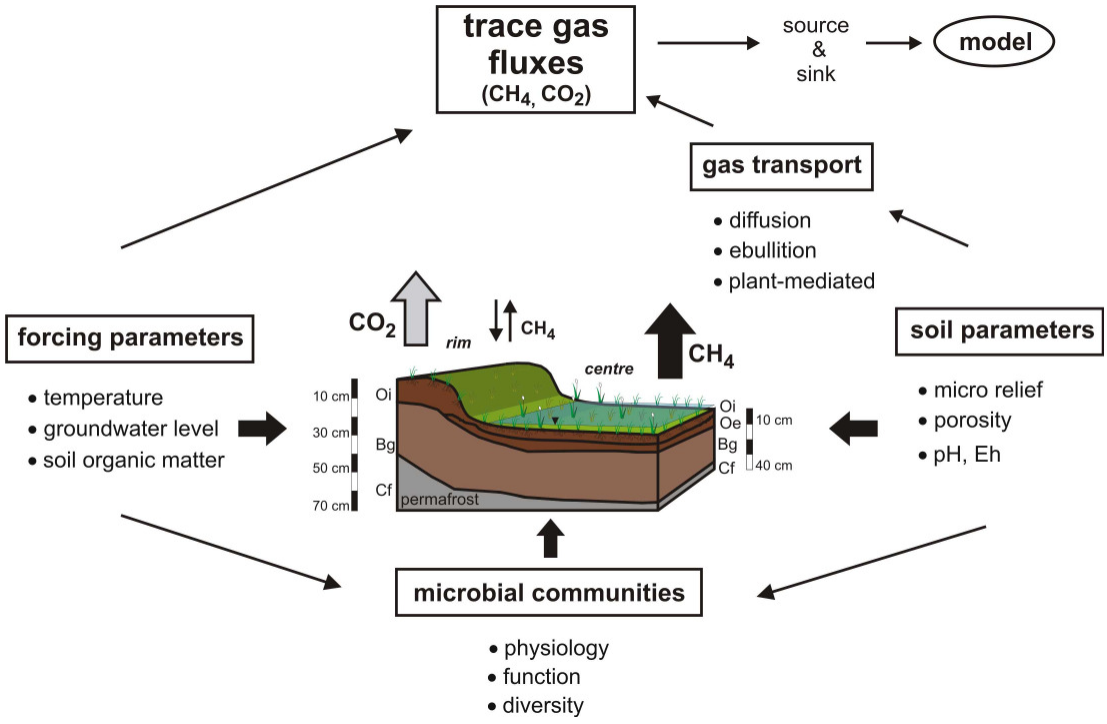

Fig. 15.1 Schematic view of the process variables influencing the formation, transport, and release of climate-relevant trace gases in permafrost soils.

The world-wide wetland area has a size of about 5.5 x 10^6 km^2 (Aselman and Crutzen 1989). About half of it is located in high-latitudes of the northern hemisphere (> 50°N). The atmospheric input of methane from tundra soils of this region was estimated to vary between 17 and 42 Tg CH_4 yr^{-1} (Whalen and Reeburgh 1992; Cao

et al 1996; Joabsson and Christensen 2001), corresponding to about 25 % of the methane emission from natural sources (Fung et al. 1991).

In the last decades, numerous studies on methane fluxes were focused on tundra environments in Northern America and Scandinavia (e.g. Svensson and Rosswall 1984; Whalen and Reeburgh 1988; Bartlett et al. 1992; Liblik et al. 1997; Reeburgh et al. 1998; Christensen et al. 2000). Since the political changes in the former Soviet Union in the early nineties, the large permafrost areas of Russia were integrated into the circum-arctic flux studies (e.g. Christensen et al. 1995; Samarkin et al. 1999; Panikov and Dedysh 2000; Tsuyuzaki et al. 2001; Wagner et al. 2003; Corradi et al. 2005; Kutzbach et al. 2007; Wille et al. 2008). All these studies revealed temporal and spatial variability of methane fluxes, ranging between –1.9 and 360 mg CH_4 m^{-2} d^{-1}. To understand these dramatic fluctuations, some studies focused on the environmental conditions and soil characteristics, comprising the water table position, soil moisture and temperature, type of substrate and vegetation as well as availability of organic carbon (e.g. Torn and Chapin 1993; Vourlitis et al. 1993; Bubier et al. 1995; Oberbauer et al. 1998; Joabsson et al. 1999; Yavitt et al. 2000). These factors influence the methane dynamics of tundra environments. Although 80 to 90% of total methane emissions originate from microbial activity (Ehhalt and Schmidt 1978), only a few investigations dealt with methane production and methane oxidation caused by microbiological processes in the course of carbon dynamics (Slobodkin et al. 1992; Vecherskaya et al. 1993; Samarkin et al. 1994; Schimel and Gulledge 1998; Segers 1998; Frenzel and Karofeld 2000; Høj et al. 2005; Wagner et al. 2005; Liebner and Wagner 2007; Metje and Frenzel 2007).

This review first examines the processes of the methane cycle in permafrost soils. It then describes the methane-cycling microorganisms including possible impacts of global warming on their structure and function.

15.2 Methane Cycle in Permafrost Soils

The carbon pool estimates for permafrost soils vary between 4 and 110 kg C m^{-2} (e.g. Schell and Ziemann 1983; Tarnocai and Smith 1992; Michaelson et al. 1996). These large variations can be attributed to different soil types (from mineral to peaty soils) and varying depths of measurements (from the upper few centimeters to 1 m depth). Permafrost soils can function as both a source and a sink for carbon dioxide and methane (Figure 15.2). Under anaerobic conditions, caused by flooding of the permafrost soils and the effect of backwater above the permafrost table, the mineralization of organic matter can only be realized stepwise by specialized microorganisms of the so called anaerobic food chain (Schink and Stams 2006). Important intermediates of the organic matter decomposition are hydrogen, carbon dioxide and acetate, which can be further reduced to methane (methanogenesis) by

methanogenic archaea (see Chapter 15.3.1). The fermentation of carbon by microorganisms runs much slower than the oxidative respiration. As a result of the prolonged anaerobic conditions and low *in situ* temperatures of permafrost soils organic matter accumulates (peat formation) in these environments.

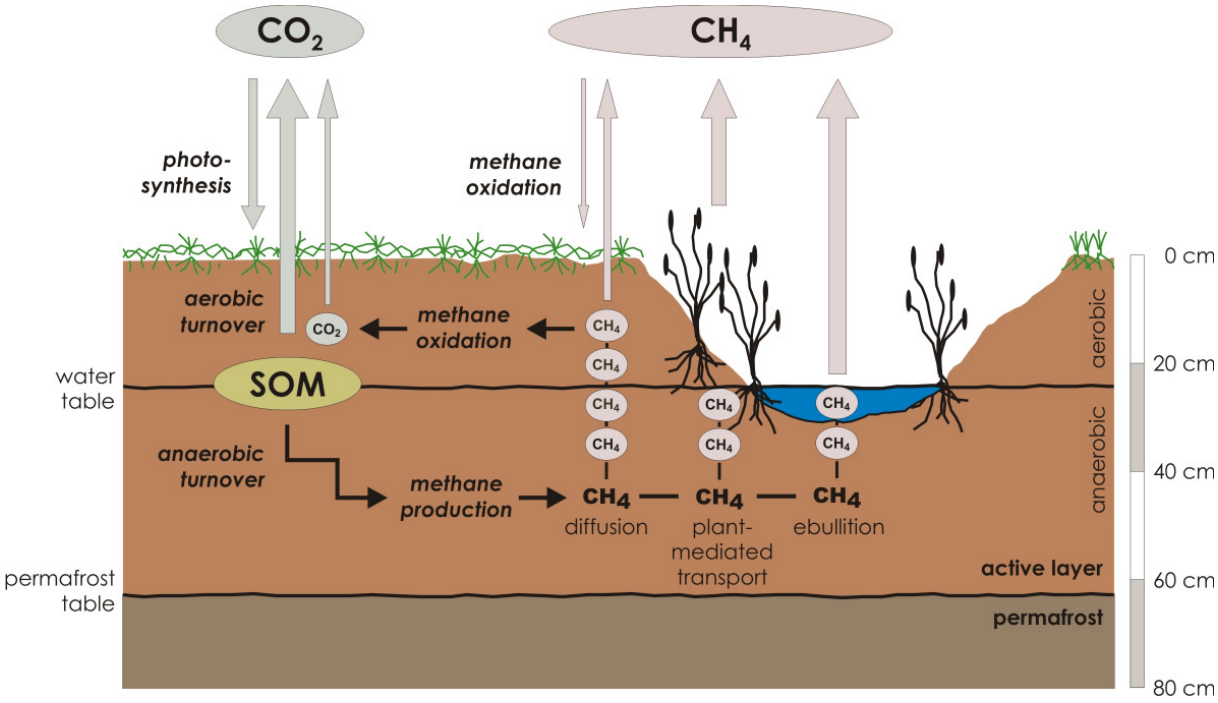

Fig. 15.2: The carbon cycle in permafrost soils: Permafrost soils can be both a source and a sink for CO_2 and CH_4. Under aerobic conditions soil organic matter (SOM) is respired to CO_2, whereas under anaerobic conditions SOM is decomposed via a sequence of microbial processes to CH_4. Methane fluxes from anaerobic soil horizons to the atmosphere results from diffusion (slow), ebullition (fast), and through plant-mediated transport (bypassing the oxic soil layer). Therefore, the way of transport determines the amount of methane that is re-oxidized by microorganisms in aerobic soil horizons. Photosynthesis poses as an important sink for CO_2 in permafrost environments. Thereby biomass is produced. In contrast, the consumption of atmospheric methane (negative methane flux) in the upper surface layer of the soils plays only a minor role for the methane budget. The thickness of the arrows reflects the importance of the above processes.

Nervertheless, the quantity of organic matter provides no information on its quality. This, however, determines the availability of organic compounds as energy and carbon sources for microorganisms (Hogg 1993; Bergman et al. 2000; see also Chapter 17). For this purpose the humification index (HIX, dimensionless) for instance, is a criterion for organic matter quality and can, therefore, give suitable

information with regard to microbial metabolism (Zsolnay 2003). It was demonstrated that the availability of organic carbon in permafrost soils decreased with increasing HIX (Wagner et al. 2005). It was further shown that the HIX increased continuously with depth in Holocene permafrost sediments (Wagner et al. 2007). This indicates that the organic carbon is less available for microorganisms with increasing depth because of the higher degree of humification. Therefore, beside the quantity also the quality of soil organic matter should be taken into account in consideration of permafrost environments as a huge carbon reservoir.

Wherever oxygen is present in permafrost habitats (upper oxic soil horizons, rhizosphere), methane can be oxidized to carbon dioxide by aerobic methane oxidizing bacteria (see Chapter 15.3.2). Between 76 % and up to more than 90 % of the methane produced in wetlands was oxidized by these specialists before reaching the atmosphere (Roslev and King 1996; Le Mer and Roger 2001). Hence, the biological oxidation of methane represents the major sink for methane in arctic permafrost environments.

Vegetation is another important factor occupying a central position for microbial processes and the transport of methane. Plants can have both enhancing and attenuating effects on methane emission. Through the aerenchyma of vascular plants, oxygen is transported from the atmosphere to the rhizosphere, thus stimulating methane oxidation in otherwise anoxic soil horizons (Van der Nat and Middelburg 1998; Popp et al. 2000). In opposite direction, the aerenchyma is a major pathway for methane transport from the anoxic horizons to the atmosphere, bypassing the oxic/anoxic interface in the soil, where methane oxidation is most prominent. It was shown that up to 68% of the total methane release from wet permafrost soils is transported through sedges like *Carex aquatilis* (Kutzbach et al. 2003). Furthermore, the vegetation provides the substrates for methanogenesis such as decaying plant material and fresh root exudates (Whiting and Chanton 1992; Joabsson et al. 1999).

15.3 Microbial Communities of the Methane Cycle

The biological formation and consumption of methane are carried out by very specialized microorganisms, methanogens and methanotrophs. Thereby, methane production results solely from the activity of members of the kingdom *Euryarchaeota*, the so called methanogenic archaea (methanogens). The group of microorganisms capable to consume methane (methanotrophs), however, is more complex comprising obligate aerobic members of the phyla *Proteobacteria* (Bowman et al. 1999), and *Verrucomicrobiaea* (Dunfield et al. 2007; Pol et al. 2007), as well as anaerobically methane oxidizing archaea in marine habitats (e.g. Boetius et al. 2000), and bacteria of a yet unknown phylum carrying out methane oxidation in the

presence of very high nitrate and methane concentration in freshwater habitats (Raghoebarsing et al. 2006). The dominant methane consuming microorganisms in permafrost soils are those of the *Proteobacteria* phylum. Because of the pronounced distribution of methanogenic archaea and methanotrophic *Proteobacteria* in Arctic permafrost soils (reviewed by Wagner 2008, Fig. 15.3) and their significance for the global methane budget, these two groups are of particular attention in this review.

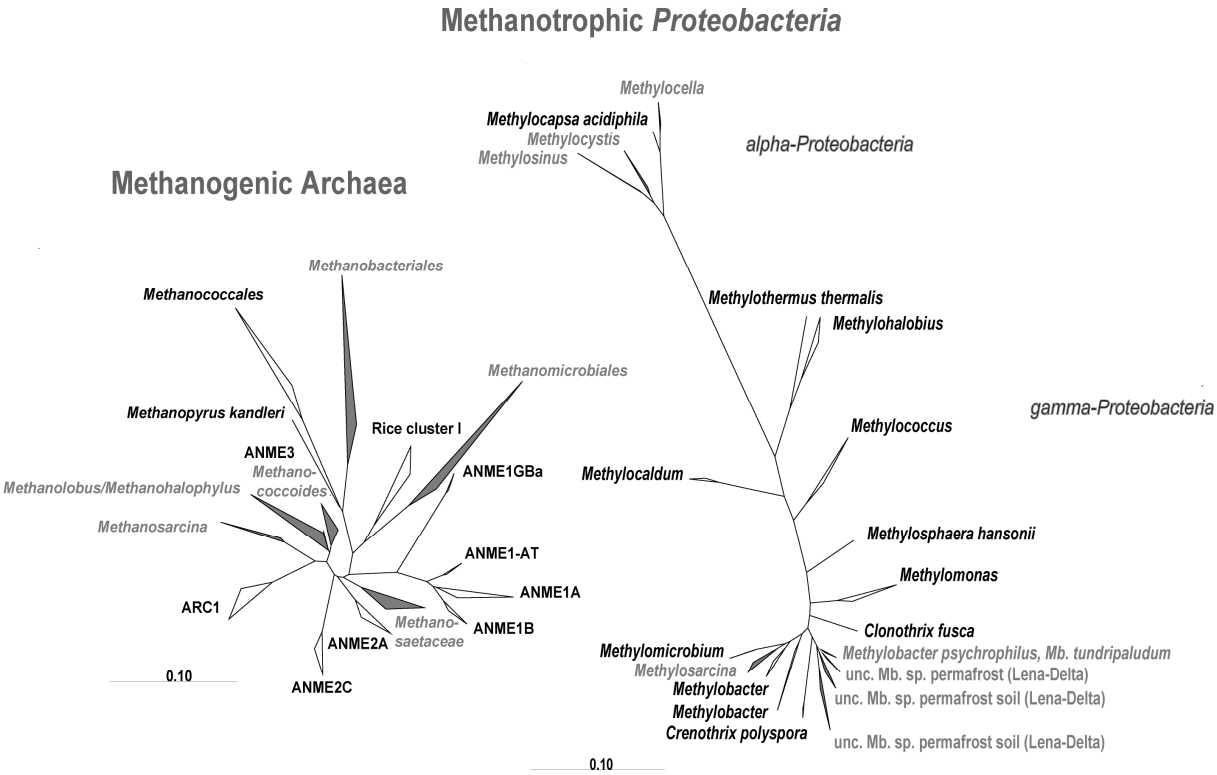

Fig. 15.3 Phylogenetic relation (based on 16S rRNA gene sequences) of methanogenic archaea and aerobic methanotrophic bacteria. Grey squares illustrate groups including sequences from arctic tundra environments. Trees represent maximum likelihood trees using the PhyML algorithm (Guindon and Gascuel, 2003) and the ARB software package.

15.3.1 Methanogenic Archaea

Methanogenic archaea represent a small group of strictly anaerobic microorganisms (Hedderich and Whitman 2006). They can be found either in temperate habitats like paddy fields (Grosskopf et al. 1998), lakes (Jurgens et al. 2000; Keough et al. 2003), freshwater sediments (Chan et al., 2005), in the gastrointestinal tract of animals (Lin et al. 1997), or in extreme habitats such as hydrothermal vents (Jeanthon et al. 1999), hypersaline habitats (Mathrani & Boone 1995) or permafrost soils and

sediments (Rivkina et al. 1998; Kobabe et al. 2004). In cold environments, two main pathways of energy-metabolism dominate: (i) the reduction of CO_2 to CH_4 using H_2 as a reductant and (ii) the fermentation of acetate to CH_4 and CO_2 (Conrad 2005). However, only a few psychrophilic (cold-adapted) strains of methanogenic archaea have been described so far (Simankova et al. 2003; Cavicchioli 2006).

Although permafrost environments are characterized by extreme climate conditions, it was recently shown that the abundance and composition of the methanogenic population is similar to that of communities of comparable temperate soil ecosystems (Wagner et al. 2005). The highest cell counts of methanogenic archaea were detected in the active layer of permafrost, with numbers of up to 3 x 10^8 cells g^{-1} soil (Kobabe et al. 2004). Methanogenic archaea represented between 0.5% and 22.4% of the total cell counts. Phylogenetic analyses revealed a great diversity of methanogens in the active layer, with species belonging to the families *Methanobacteriaceae*, *Methanomicrobiaceae*, *Methanosarcinaceae*, and *Methanosaetaceae* (Høj et al. 2005; Metje and Frenzel 2007; Ganzert et al. 2007; Fig. 15.3). Other sequences detected were affiliated to the euryarchaeotal Rice Cluster II and V (Hales et al. 1996; Grosskopf et al. 1998; Ramakrishnan et al. 2001) as well as to the Group I.3b of the uncultured Crenarchaeota (non-methanogenic archaea; Ochsenreiter et al. 2003). Environmental sequences from the Laptev Sea coast form four specific permafrost clusters (Ganzert et al. 2007). Permafrost Cluster I was recovered mainly from cold horizons (with temperatures of less than 4°C) of the active layer and was related to *Methanosarcinacea*. Permafrost Clusters II and III were related to *Methanomicrobiales* and Permafrost Cluster IV was related to Rice Cluster II. It was hypothesized that these clusters comprise methanogenic archaea with a specific physiological potential to survive under harsh environmental conditions. The phylogenetic affiliation of the sequences recovered in this study indicated that both hydrogenotrophic and acetoclastic methanogenesis exist in permafrost soils. Recent studies on perennially frozen permafrost deposits from the Lena Delta (Siberia) revealed significant amounts of methane which could be attributed to *in situ* activity of methanogenic archaea (Wagner et al. 2007). Another study on frozen ground on Ellesmere Island reported an archaeal community composed of 61% Euryarchaeota (methane producing archaea) and 39% Crenarchaeota, suggesting the presence of a diverse archaeal population also in the perennially frozen sediments (Steven et al. 2007).

Methanosarcina spec. SMA-21, which is closely related to *Methanosarcina mazei*, was recently isolated from a Siberian permafrost soil in the Lena Delta. The organism grows well at 28°C and slowly at low temperatures (4°C and 10°C) with H_2/CO_2 (80:20, v/v, pressurised at 150 kPa) as substrate. The cells grow as cocci, with a diameter of 1-2 µm. Cell aggregates were regularly observed (Fig. 15.4 a). *Methanosarcina* SMA-21 is characterized by an extreme tolerance to very low temperatures (-78.5°C), high salinity (up to 6 M), starvation, desiccation and oxygen

exposure (Morozova and Wagner 2007). Furthermore, this archaeon survived for three weeks under simulated thermo-physical Martian conditions (Morozova et al. 2007; see also Chapter 22).

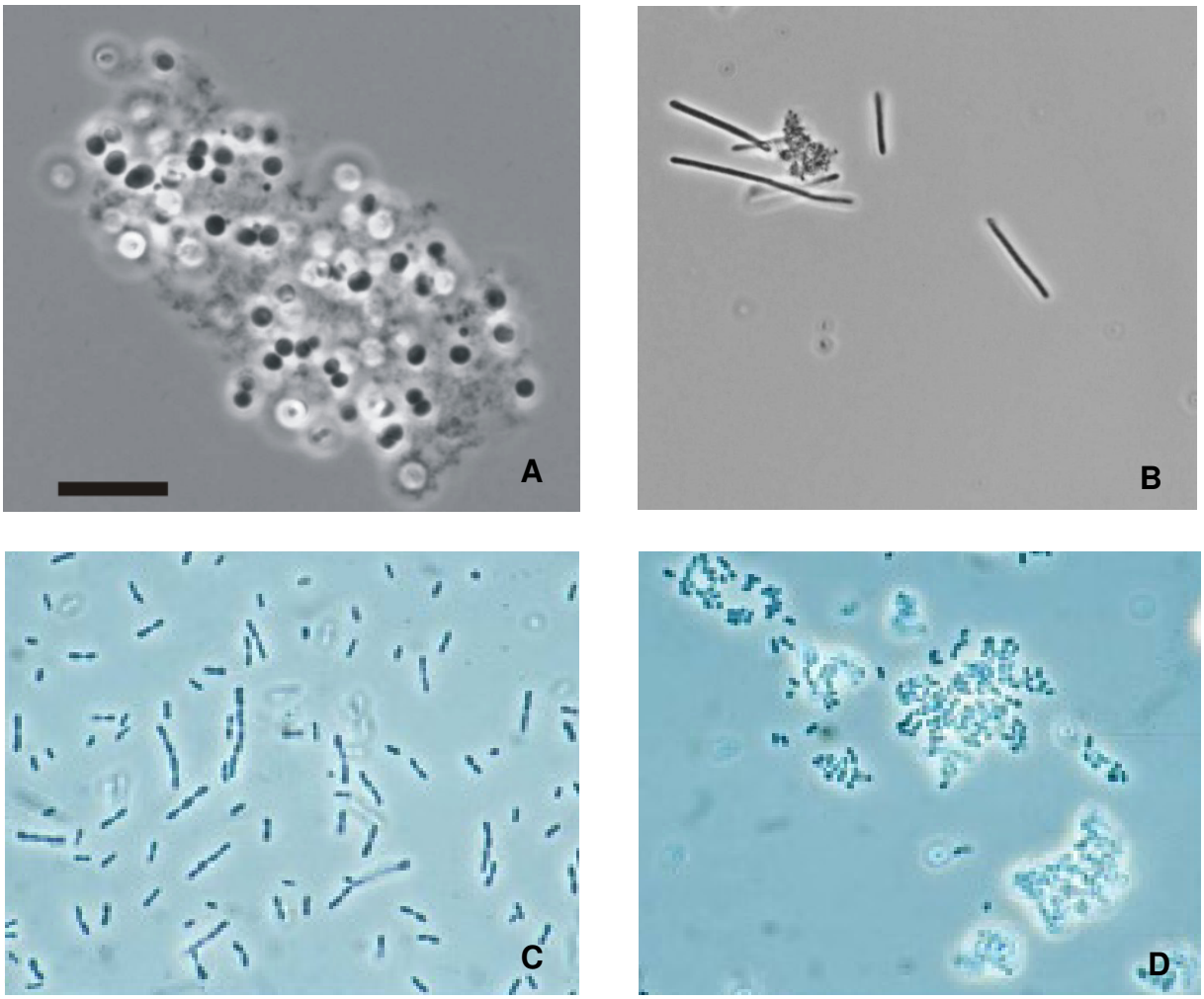

Fig. 15.4 Methane-cycling microorganisms isolated from permafrost environments: (**A**) *Methanosarcina* sp. SMA-21 (D. Wagner and D. Morozova, AWI; bar: 10µm); (**B**) permafrost strain SMA-23 (D. Wagner and D. Morozova, AWI); (**c**) *Methylobacter tundripaludum* (Wartiainen et al. 2006a); (**d**) *Methylocystis rosea* (Wartiainen et al. 2006b)

Methanogenic activity was observed at low *in situ* temperatures with rates of up to 39 nmol CH_4 h^{-1} g^{-1} soil in the active layer of permafrost (Wagner et al. 2003; Høj et al. 2005; Metje and Frenzel 2007). The highest activities were thereby measured in the coldest zones of the profiles. Furthermore, it could be shown that methane production is rather limited by the quality of soil organic carbon than by the *in situ* temperature (Wagner et al. 2005; Ganzert et al. 2007). Another important

factor affecting methanogenic communities in permafrost soils is the water regime. Along a natural soil moisture gradient, changes in archaeal community composition were observed, which suggest that the differences in these communities were responsible for the large-scale variations in methane emissions observed with changes in soil hydrology (Høj et al. 2006).

15.3.2 Methane Oxidizing Proteobacteria

Based on their function as the major sink for methane in arctic permafrost affected wetlands and tundra, methane oxidizing *Proteobacteria* are also of importance for the greenhouse gas (GHG) budget of these environments.

Methane oxidizing *Proteobacteria* represent a subset of methylotrophic bacteria. Through the activity of their specific enzyme, methane monooxygenase, they are specialized to utilize methane as single carbon and energy source (Hanson and Hanson, 1996). The group of methane oxidizing *Proteobacteria* comprises the three families *Methylococcaceae, Methylocystaceae, and Beijerinckiaceae* (Bowman 1999; Dedysh et al. 2000; 2001; 2002; 2004). The only exception is *Crenothrix polyspora*, a filamentous, sheathed microorganism recently discovered to be methanotrophic (Stoecker et al. 2006). *Methylococcaceae* include the genera *Methylobacter*, *Methylomonas*, *Methylomicrobium*, *Methylosarcina*, *Methylosphaera*, *Methylohalobius*, *Methylosoma*, *Methylothermus*, *Methylococcus*, and *Methylocaldum* (Hanson and Hanson 1996; Bowman et al. 1997; Wise et al. 2001; Heyer et al. 2005; Tsubota et al. 2005; Rahalkar et al. 2007). They belong to the gamma-subdivision of the *Proteobacteria* phylum and are termed type I methanotrophs, except for the last two, which are also known as type X methanotrophs. The families *Methylocystaceae*, and *Beijerinckiaceae* include the genera *Methylosinus*, *Methylocystis*, *Methylocella*, and *Methylocapsa* (Hanson and Hanson 1996; Bowman et al. 1999; Dedysh et al. 2000; 2001; 2002; 2004). Members of the *Methylocystaceae* and *Beijerinckiaceae* are termed type II methanotrophs and belong to the alpha-subdivision of the *Proteobacteria* phylum. Except for their phylogeny, type I and type II methanotrophs can also be distinguished by their carbon assimilation pathway, the structure of their intracytoplasmic membranes, their resting stages, G+C-content, the constitution of their methane monooxygenase, and by their major phospholipid fatty acids (PLFAs).

Several studies revealed that methanotrophs are abundant and active also under very harsh environmental conditions of cold environments (review by Trotsenko and Khmelenina 2005). Viable methane oxidizers were even detected in deep Siberian permafrost sediments with ages of 1000-100,000 years (Khmelenina et al. 2001). Numerous psychrophilic and psychrotrophic methanotrophs, primarily affiliated to the type I group, are known such as *Methylobacter psychrophilus*, isolated from Siberian tundra (Omelchenko et al. 1996), *Methylobacter*

tundripaludum, isolated from Arctic wetland soils (Fig. 15.4, Wartiainen et al. 2006a), *Methylosphaera hansonii*, isolated from Antarctic, marine salinity, meromictic lakes (Bowman et al. 1997), and *Methylomonas scandinavica*, isolated from deep igneous rock ground water (Kaluzhnaya et al. 1999). Type I methanotrophs were also recovered to dominate in arctic permafrost affected soils (Wartiainen et al. 2003; Wagner et al. 2005; Liebner and Wagner 2007). Within the type II group, *Methylocystis rosea*, isolated from an Arctic wetland soil (Fig. 15.4, Wartiainen et al. 2006b), and representatives of the acidophilic genera *Methylocella* and *Methylocapsa* were reported to be psychrotrophs (Dedysh et al. 2002; 2004).

Methane oxidizing *Proteobacteria* were shown to be highly abundant in permafrost soils of the Lena Delta, Siberia, with cell numbers ranging between 3 x 10^6 and 1 x 10^8 cells g^{-1} soil and contributing up to 10 % to the total number of microbial cells (Liebner and Wagner 2007). In the same area, specific clusters of methane oxidizing *Proteobacteria* closely related to *Methylobacter psychrophilus* and to *Methylobacter tundripaludum* were detected indicating a micro-diverse community on the species level (Liebner et al. 2008). Also, highly divergent functional gene sequences of these methanotrophs were found in soils of the high Canadian Arctic (Pacheco-Oliver et al. 2002). In contrast, the diversity of methane oxidizing *Proteobacteria* in an arctic wetland on the island of Svalbard was observed to be restricted to only two genera (Wartiainen et al. 2003), whereas most methanotrophic *Proteobacteria* were detected in a Russian sub-arctic tundra (Kaluzhnaya et al. 2002). Still, diversity and composition of methane oxidizing bacteria in permafrost soils are only poorly explored. Also, it remains unknown whether psychrophilic or cold-adapted mesophilic methantrophs are responsible for methane oxidation at low and subzero temperatures in permafrost sediments (Trotsenko and Khmelenina 2005). A recent study, though, observed a shift between a mesophilic methanotrophic community near the surface and a psychrophilic methanotrophic community near the permafrost table of Siberian permafrost soils (Liebner and Wagner 2007). This indicates that depending on the environmental conditions both mesophilic as well as psychrophilic methanotrophs are active in Siberian permafrost soils.

15.4 Methane-cycling Communities under Global Climate Change

Arctic surface temperatures on average increased to a greater extent than those of the rest of the earth (IPCC 2001), causing a particular susceptibility of arctic permafrost to degradation. Global warming could degrade 25 % of the total permafrost area by 2100 (Anisimov et al. 1999). Also, Nelson et al. (2001) predicted a high potential of large areas of Siberian permafrost to be degraded, which would primarily lead to a thickening of the seasonally thawed layer (active layer). In the period 1956-1990, the active layer in Russian permafrost already increased by on

average 20 cm (IPCC 2007). By the end of the 21st century, an increase of mean annual ground temperature by up to 6 °C and of active layer depth by up to 2 m is expected for East Siberia (Stendel et al. 2007). Although the estimated size of the carbon pool in Arctic permafrost affected tundra varies between 190 and, in more recent studies, approximately 900 Gt, it accounts for at least 13-15 % of the global carbon pool in soils (Post et al. 1982; Zimov et al. 2006). Thawing of 10 % of the total Siberian permafrost carbon reservoir was suggested to initially release about 1 Pg carbon followed by respiration of about 40 Pg carbon to the atmosphere over a period of four decades (Dutta et al. 2006). Model calculations suggest that methane currently emitted from Arctic permafrost environments may enhance the greenhouse effect with a portion of approx. 20 % (Wuebbles and Hayhoe 2002). Palaeoclimate reconstruction combined with biogeochemical biomarker analysis, for example, revealed an increase in production and release of methane from the terrestrial biosphere during the Palaeocene-Eocene thermal maximum, a period of intense global warming 55 million years ago (Pancost et al. 2007). It was also shown that an increase of the permafrost temperature in Holocene permafrost deposits of northern Siberia would lead to substantial rise in microbiologically produced methane (Wagner et al. 2007). Serious concerns are thus associated with the potential impact that thawing permafrost may have on the global climate system through release of greenhouse gases (Friborg et al. 2003; Christensen et al. 2004; Wagner et al. 2007). Methane flux models do indeed predict increasing methane emissions in latitudes above 60° N by 19-25 % (Cao et al. 1998; Walter et al. 2001; Zhuang et al. 2004). These estimates are challenged, though, by other studies suggesting that increasing methane fluxes from Russian permafrost regions will change atmospheric methane concentrations by only 0.04 ppm (2.3 %) leading to 0.012 °C temperature rise globally (Anisimov 2007).

Models on modern methane emissions from arctic wetlands determine methane production and methane oxidation rates primarily as functions of substrate availability, substrate concentration, and temperature as well as indirectly of water table and thaw depth (Walter et al. 2001; Zhuang et al. 2004; Anisimov 2007). Changes of these parameters will consequently lead to short-term alterations of methane production and methane oxidation rates. Whether, however, the currently observed global climate change will effectively alter modern methane fluxes from arctic permafrost affected wetlands will particularly depend on its long-term impact on the methane cycling communities and their ability to adapt to the new environmental conditions. This ability is very likely dependant on the level of specialisation and diversity of the indigenous microbial communities. It was observed that an increase of temperature and precipitation altered the community structure and relative abundance of methane oxidizers in rice, forest and grassland soils (Horz et al. 2005; Mohanty et al. 2007). Also, the overall relative abundance and diversity of methanogenic archaea in a high Arctic peat from Spitsbergen increased with

increasing temperature, in accordance with a strong stimulation of methane production rates (Høj et al. 2008). In contrast, the population structure of methanogenic archaea in a permafrost affected peat in Siberia remained constant over a wide temperature range (Metje and Frenzel 2007). Also, a psychrophilic and little diverse methanotrophic community as detected near the permafrost table of Siberian polygonal tundra soils (Liebner and Wagner 2007; Liebner et al. 2008) will likely require more time for resilience than the diverse mesophilic-psychrotolerant methanogenic community detected in permafrost soils of the same region (Ganzert et al. 2006).

There is, however, a lack of experimental research investigating the long-term effect of simulated climate change on the methane cycling communities in permafrost soils, which would be essential to prove or disprove the previously mentioned assumptions. Also, an account of the entire plant-microbe-animal system and the interactions between metabolic networks, which are important for methanogenesis is missing in modern methane flux models (Panikov 1999). Due to this poor knowledge it is worthy to consider microbial communities in the scope of global climate change in general. Simulating the affects of warming on the competition between psychrophilic and mesophilic sub-populations of *Pseudomonas*, for example, displayed a high degree of stability of this artificial community (Panikov 1999). Psychrophiles dominated the bacterial community under cold conditions, and an increase in temperature by 5 °C did not affect their domination. Further warming of another 5 °C resulted in a rapid 50 % substitution of psychrophiles by mesophiles over two years finally reaching a stable coexistence between the two sub-populations. In the same model, the main effect of rising temperatures on the carbon balance of the ecosystem was a considerable activation of organic matter decomposition due to higher production of hydrolytic enzymes. Experimental setups revealed a rather low direct impact of rising temperatures on the decomposition of soil organic matter but rather attributed increased decomposition rates most strongly to be due to changes in local substrate characteristics and vegetation type (Zhang et al. 2005; Bokhorst et al. 2007). Still, a warming induced shift in the microbial community structure was again observed at least in the first study.

To summarize, there is an urgent need for modelling the response of methane cycling communities in permafrost regions to global climate change on the one hand and to validate these models by empirical data on the other hand. This is not only due to the importance of these communities for the atmospheric methane budget and thus for the global climate. It is also inevitable given the close connection between physiology and function of these communities in permafrost soils that allows for a general understanding of how important is the stability of microbial communities for the GHG budget of arctic permafrost affected wetlands.

15.5 Conclusions and Future Perspectives

Permafrost soils and sediments are unique systems in the context of biogeochemical cycling of carbon, particularly due to the enormous amount of organic carbon stored in these environments. Recent studies demonstrate the close relationship between apparent methane fluxes and the modes and intensities of microbiological processes of methane production and oxidation in permafrost ecosystems. Methane producing and consuming microorganisms are widespread, highly active and abundant in permafrost soils, despite the harsh environmental conditions they are exposed to. The permafrost environment forces an adaptation of the methane cycling communities to low temperature conditions often yealding species, which have not been detected in temperate ecosystems so far. In addition to soil characteristics and climate conditions, the activity and physiology of these well adapted microbial communities dictate trace gas fluxes in permafrost soils. The future development of permafrost environments as a source of methane, therefore, primarily depends on the response of the methanogenic and methanotrophic microorganisms to a changing environment.

Anticipating this response, however, is difficult as the sensitivity of microbial communities to permafrost degradation is completely unknown. At first, there is lack of experimental and theoretic studies on what determines microbial stability in general and in particular in permafrost environments. At second, the consequences of thawing permafrost on hydrology and morphology that indirectly influence microbial communities and its activity are very difficult to predict.

International projects such as ACD (Arctic Coastal Dynamics) and CALM (Circumpolar Active Layer Monitoring), which examine the impact of global warming on permafrost environments should thus be linked more closely to microbiological process studies and biodiversity research. Microbial parameters important for the assessment of carbon turnover (e.g. cell numbers, activities, biodiversity and stability of microbial communities) should be analysed at observation areas in the Arctic, where long-term monitoring programs are undertaken. The evaluation of microbial ecology and its correlation to climatic and geochemical data represent the basis for an understanding of the role of permafrost soils in the global system, in particular in terms of feedback mechanisms related to fluxes of material and greenhouse gases in the scope of a warming Earth.

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