



## **Depth Distribution of Net Methanotrophic Activity at a Mountain Birch Forest—Tundra Heath Ecotone, Northern Sweden**

Authors: Sjögersten, Sofie, Melander, Erik, and Wookey, Philip A.

Source: Arctic, Antarctic, and Alpine Research, 39(3) : 477-480

Published By: Institute of Arctic and Alpine Research (INSTAAR),  
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(06-009\)  
\[SJOGERSTEN\]2.0.CO;2](https://doi.org/10.1657/1523-0430(06-009)[SJOGERSTEN]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Depth Distribution of Net Methanotrophic Activity at a Mountain Birch Forest–Tundra Heath Ecotone, Northern Sweden

Sofie Sjögersten\*

Erik Melander† and

Philip A. Wookey‡

\*Corresponding author: Division of Agricultural and Environmental Sciences, School of Biosciences, University of Nottingham, Biology Building, University Park, Nottingham NG7 2RD, U.K.

sofie.sjogersten@nottingham.ac.uk

†Department of Earth Sciences, Uppsala University, Villavägen 16, 752 36 Uppsala, Sweden

‡School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, U.K.

## Abstract

Methanotrophy (the bacterial oxidation of CH<sub>4</sub>) in soils is the major biological sink for atmospheric CH<sub>4</sub>. Here we present results from a study designed to quantify the role of the physical diffusion barrier to CH<sub>4</sub>, through surface soils, as a factor affecting methanotrophy. We used the mountain birch forest–tundra heath ecotone in subarctic northern Sweden as our study system. Our results show that, although CH<sub>4</sub> fluxes were generally low (around  $-20 \mu\text{mol m}^{-2} \text{h}^{-1}$ ; a net flux from atmosphere to soil), the two adjacent communities responded in contrasting ways to *in situ* experimental reduction of the diffusion barrier (removal of the top 50 mm of soil): Uptake increased by 40% in forest soil in association with the removal, whereas it decreased marginally (by 10%) in tundra heath. Investigations of the depth-distribution of CH<sub>4</sub> oxidation *in vitro* revealed maximum rates at the top of the mineral soil for the forest site, whereas at the tundra heath this was more evenly spread throughout the organic horizon. The contrasting physicochemical properties and methanotroph activity in the organic horizons together explain the contrasting responses to the removal treatment. They also illustrate the potential role of vegetation for methane oxidation around this ecotone, exerted through its influence on the depth and properties of the organic horizons in these subarctic soils.

DOI: 10.1657/1523-0430(06-009)[SJÖGERSTEN]2.0.CO;2

## Introduction

Methane (CH<sub>4</sub>) is a potent greenhouse gas, contributing ca. 17% to climate warming (IPCC, 1990, 2001). Parts of the CH<sub>4</sub> budget are controlled by biological processes, for example CH<sub>4</sub> oxidation in aerobic soils (Mancinelli, 1995), and are estimated to amount to 5% of the global atmospheric CH<sub>4</sub> sink (Ehhalt et al., 2001). Soils in a wide range of ecosystems have been found to oxidize CH<sub>4</sub> (Mancinelli, 1995) including high altitude/latitude soils (Whalen and Reeburgh, 1990; Torn and Harte, 2006; Christensen et al., 1999). There are also indications that the CH<sub>4</sub> sink strength could increase in well-drained high latitude soils as a consequence of climate warming (Sjögersten and Wookey, 2002). However, the controls of high affinity CH<sub>4</sub> uptake in high latitude environments remain unclear. Despite the cold climate, neither temperature nor moisture seem to explain the fine scale spatial or temporal variation in uptake rates in mesic soils. This suggests more complex controls of CH<sub>4</sub> oxidation through, for example, the properties of the diffusion barrier, ammonium inhibition, and interaction with bacterivores (Mancinelli, 1995; Schlesinger, 1997; King, 1997). Indeed, one of the main constraints on CH<sub>4</sub> oxidization is the diffusion of CH<sub>4</sub> into microsites in the soil where the high affinity methanotroph population is active (Born et al., 1990; Dörr et al., 1993; Situala et al., 1995; Torn and Harte, 2006; Dong et al., 1998; Shrestha et al., 2004) and a thinning of the diffusion barrier could subsequently lead to increased CH<sub>4</sub> uptake (Dong et al., 1998; Saari et al., 1998) as long as other factors remain favorable. Furthermore, the depth distribution of methanotrophs is not well understood (King 1997), making it more difficult to identify the main controls on methanotrophic activity, and thus to predict the sink strength of CH<sub>4</sub> in high altitude/latitude soils.

In this study we chose the subarctic forest–tundra heath ecotone as a model system in order to evaluate the importance of

the diffusion barrier for high affinity CH<sub>4</sub> oxidation rates. In these ecosystems the organic horizon differs markedly between adjacent forest and tundra heath vegetation types, with generally thicker and denser organic horizons beneath the tundra heath (Sjögersten et al., 2003). This contrast allows us to quantify the effect of the organic horizon on CH<sub>4</sub> oxidation in two different soil types in close proximity. The specific objectives of this study were (1) to assess whether the diffusion barrier limited CH<sub>4</sub> uptake rates, and (2) to determine the depth-distribution of methanotrophic activity in mesic forest and tundra heath soils. Although we cannot rule out the process of methanogenesis in these soil profiles (thus the net CH<sub>4</sub> flux could be the product of both methanotrophy in aerobic soil, and methanogenesis in anaerobic zones or microsites), previous observations in this area confirm that mesic/well-drained soils are predominantly net methane oxidizers (Christensen et al., 1999; Sjögersten and Wookey, 2002).

## Methods

### SITE DESCRIPTION

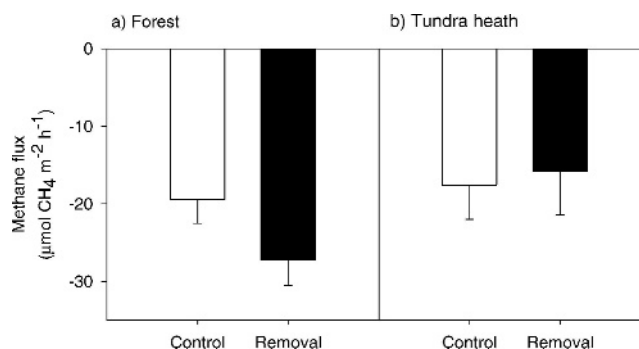
The two study sites were located at the mountain birch forest–tundra heath ecotone in the Abisko (Paddus) area at 560 m a.s.l., northern Sweden (68°21'N, 18°49'E); one site was within the mountain birch [*Betula pubescens* Ehrh. ssp. *czerpanovii* (Orlova) Hämet-Ahti] forest and the other on subarctic tundra heath, approximately 50 m apart. The January and July mean temperatures at the nearby Abisko Research Station, 341 m a.s.l., are  $-11.9$  and  $11^\circ\text{C}$ , respectively, and the annual precipitation is 304 mm. The study sites are mesic, and the soils are free-draining and classed as mature inceptisols/immature spodosols. The soil profile at the tundra site has a 10-mm-deep

fibric (O<sub>i</sub>) horizon underlain by a 122 mm hemic (O<sub>e</sub>) horizon, and beneath that a ca. 63 mm albic (E) horizon overlying the parent material (till). The soils at the forest site are comprised of a 10 mm O<sub>i</sub> horizon, underlain by a 38 mm O<sub>e</sub> layer and a 90 mm albic horizon on top of the original till. The vegetation at the tundra site is dominated by *Empetrum hermaphroditum*; the few percent that make up the rest of the vegetation include *Vaccinium uliginosum*, *V. vitis-idaea*, *Betula nana*, graminoids, *Arctostaphylos alpinus*, *V. myrtillus*, *Salix glauca*, *Loiseleuria procumbens*, *Tofieldia pusilla*, *Bartsia alpina*, bryophytes, and lichens. The forest site has a sparse mountain birch canopy, the understory is comprised of 21% litter (mainly birch), 32% *Empetrum hermaphroditum*, 13% *V. myrtillus*, 4% *V. uliginosum*, and 5% *A. alpinus*. Also present at the site were *Juniperus communis*, *Betula nana*, *Linnaea borealis*, *Lycopodium annotinum*, bryophytes, and lichens.

#### METHANE SAMPLING AND EXPERIMENTAL DESIGN

In order to quantify the impact of the organic horizon as a diffusion barrier we established a soil removal experiment during July 2001. Twenty plots in each community, representative of the area with respect to soil and vegetation, were selected for the experiment. At each site 10 of the 20 plots were randomly allocated a treatment, but this was not applied until two baseline measurements (on 16 and 25 July) confirmed that there were no significant ( $p > 0.3$ ) initial differences between plots. The treatment (applied on 25 July, after CH<sub>4</sub> sampling was completed) involved careful removal of the top 50 mm of the soil organic horizon. The soils were allowed to settle from the initial disturbance, and methane fluxes were then measured on three occasions within the following week. Methane fluxes were estimated by the closed-chamber technique, whereby an air-tight lid was placed on 100-mm-diameter collars that were inserted in the plots to form bases for the sampling (Sjögersten and Wookey 2002). Air samples (2 mL) were taken with syringes initially from the headspace air, and again after 1 h of incubation. These were analyzed the following day on a Perkin Elmer AutoSystem XL Gas Chromatograph. Soil moisture between 0–100 mm depth (ThetaMeter and probe: Delta-T Devices, Burwell, U.K.) and temperature at 100 mm (thermistor) were also measured adjacent to the collars as the CH<sub>4</sub> sampling was carried out.

To investigate further the depth distribution and activity of the methanotrophic community, both organic and mineral soil, as well as the transition between the two (i.e. the albic illuvial horizon in these profiles), were sampled for *in vitro* laboratory incubations. At each site, five representative plots were chosen for sampling, and from these soils were collected as 10 or 20 mm slices to ca. 250 mm depth, varying slightly depending on the nature of the horizon. The top of the organic horizon and the transition zone to the mineral soil were sampled as 10 mm slices of soil, and the rest of the profile as 20 mm slices at 20 mm intervals down the profile. The samples were passed through a 4 mm sieve in order to standardize and maximize the aeration, and hence the CH<sub>4</sub> oxidation of the different soil layers. For the incubations ca. 18 cm<sup>3</sup> of sieved soil were placed in clean glass serum bottles (41 cm<sup>3</sup>), and the samples were allowed to settle at 10°C for ca. 12 h. Subsequently, the bottles were ventilated with laboratory air for 3 h, septum stoppers were added, and initial air samples (2 mL) were taken immediately, followed by another set after 1 h. The gas samples were then analyzed on the GC as described above. Soil moisture was determined gravimetrically after drying at 120°C.



**FIGURE 1.** Methane fluxes in control plots and in plots where the top 50 mm of the organic horizon was removed, measured in (a) mountain birch forest and (b) tundra heath soils. Negative values indicate methane uptake by soils from the atmosphere. Mean values  $\pm$  SE are shown.

#### DATA ANALYSIS

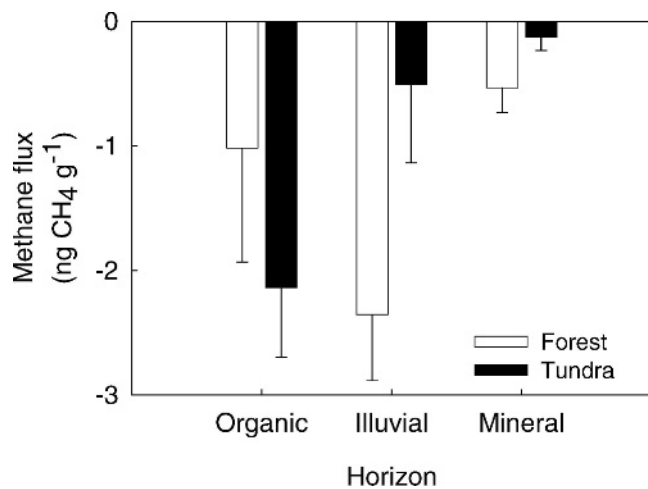
To identify systematic differences between the field sites and treatments, analyses were conducted on plot mean flux data following application of the soil removal treatment. Data were analyzed in SAS for Windows V. 8.2 using generalized linear mixed models (GLMM) with 'plot' as the random effect, vegetation type (site) and treatment (removal of organic material) as main effects, together with their interactions. Significant differences between means were thereafter tested with Tukey HSD (honest significant difference) *post hoc* analysis. The models were fitted by the method of residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell et al., 1996), and the residual variances were modeled as constant to the mean using PROC MIXED.

The results from the incubation experiment were analyzed in a similar way, but this time the data at each plot were grouped and averaged for the three main horizons, i.e. the organic, illuvial, and mineral, prior to the statistical analyses. A probability level of  $P = 0.1$  was set as the upper limit for reporting  $P$  and  $F$  values from the statistical analyses of CH<sub>4</sub> flux.

## Results

Both forest and tundra soils were weak net sinks of CH<sub>4</sub>;  $-24.6$  and  $-21.8 \mu\text{g m}^{-2} \text{h}^{-1}$ , respectively. The experimental removal of the organic horizon had contrasting effects on the CH<sub>4</sub> fluxes at the forest and tundra site (Fig. 1) as revealed by a site  $\times$  treatment interaction ( $F_{1,36} = 2.9$ ,  $P = 0.096$ ) and subsequent *post hoc* analysis ( $P = 0.06$ ). At the forest site the removal of the top organic layer was associated with a 40% increase in rates of CH<sub>4</sub> uptake, while at the tundra site CH<sub>4</sub> uptake was marginally (10%) lower. Average soil temperatures over the measurement period were 7.1 and 7.8°C at the tundra and forest sites, respectively. Soil moisture content was slightly higher ( $F_{1,36} = 14.3$ ,  $P < 0.001$ ) at the tundra site compared to the forest: 0.32 and 0.29 m<sup>3</sup> H<sub>2</sub>O m<sup>-3</sup>, respectively.

The laboratory incubation of the different profiles showed that the methanotrophic activity differed significantly between the horizons at the two different sites (Fig. 2). At the tundra heath site the highest CH<sub>4</sub> uptake was found in the organic horizon, while at the forest site, the illuvial transition zone between the organic and mineral horizon had the highest CH<sub>4</sub> oxidation rates. Soil moisture content varied significantly ( $F_{2,16} = 223.6$ ,  $P < 0.001$ ) between the organic and the mineral soil horizons, ca. 200 and



**FIGURE 2.** Depth distribution of methane uptake rates in soils from tundra heath and mountain birch forest. The illuvial layer is here a thin profile characterized by organic material transported into the mineral soil. Negative values indicate methane uptake. Mean values  $\pm$  SE are shown.

50%, respectively, but did not differ between forest and tundra soils.

## Discussion

The data presented here suggest that the upper 50 mm of predominantly organic soils in these profiles do, indeed, present a barrier to the diffusion of atmospheric CH<sub>4</sub> to sites where significant net methane oxidation by high-affinity methanotrophic bacteria occurs. This interpretation is consistent even with the contrasting response of CH<sub>4</sub> uptake in forest and tundra heath soil to the removal treatment.

Several studies of CH<sub>4</sub> fluxes in forests have reported maximum CH<sub>4</sub> oxidation at the top of the mineral horizons, while the organic horizons have not been considered sites of high activity (Crill, 1991; Torn and Harte, 1996; Koschorreck and Conrad, 1993; Schnell and King, 1994). By contrast, organic tundra soils studied by Whalen and Reeburgh (1990) supported an active methanotroph population. In our study, removal of the upper soil layer increased CH<sub>4</sub> oxidation at the forest site, while this was not noted at the tundra heath site. The 40% increase in CH<sub>4</sub> uptake in the forest compares with results from a similar removal of the organic horizon in a boreal forest system where CH<sub>4</sub> uptake rates increased by 50% (Saari et al., 1998). This suggests that CH<sub>4</sub> oxidation rates are more limited by diffusion at the forest site (where the maximum CH<sub>4</sub> oxidation occurs at the interface between the organic horizon and the mineral soil) than they are at the tundra heath. The contrasting nature of the soil profiles at the two sites, however, must be taken into account when interpreting the results. The removal of 50 mm of organic soil from the forest profiles effectively exposed the mineral albic horizons, where the *in vitro* measurements suggested that net methanotrophy was most active. If this treatment did not result in the development of any more adverse physical conditions for methanotrophs, then it seems a reasonable interpretation that *in situ* rates of net CH<sub>4</sub> oxidation would increase. Had this not occurred we might be led to conclude that removal of the organic horizons may have impaired methanotroph activity via mechanisms, which could include (1) increased desiccation stress, and/or (2) increased temperature variability near the surface of the

exposed albic horizon. These factors might, indeed, be important, but the data do not suggest that they outweighed increased methanotrophy. Furthermore, there was also net CH<sub>4</sub> oxidation in the organic horizons of the forest soil (Fig. 2), and if the role of these horizons as a diffusion barrier for CH<sub>4</sub> transport was weak, or insignificant, we might expect the soil removal treatment actually to have *reduced* net CH<sub>4</sub> oxidation.

In the tundra heath soils, by contrast, our treatment removed around 38% of the organic horizon, but this did not translate into any significant reduction in the rate of CH<sub>4</sub> uptake, even though the strongest net methanotrophy noted *in vitro* was in the organic horizons (Fig. 2). This result suggests that methanotrophy in the lower parts of the organic (O<sub>c</sub>) horizons might well have been constrained by poor CH<sub>4</sub> diffusion through intact profiles, and therefore been accelerated *in situ* with 50 mm of the upper soil removed. It is also important to note that although the CH<sub>4</sub> flux is substantially lower per unit mass in the tundra illuvial horizons (Fig. 2), the bulk density of these horizons is much higher (0.99 compared with 0.15 g cm<sup>-3</sup>), thus making their contribution to surface CH<sub>4</sub> fluxes proportionally higher (especially when constraints on CH<sub>4</sub> diffusion were reduced).

The higher methanotrophic activity in the organic layer in the tundra heath soils compared with the forest might be linked to ammonium inhibition in the forest soils: The latter have higher ammonium mineralization rates than tundra soils (Schnell and King, 1994; Saari et al., 2004; Sjögersten and Wookey, 2005), and in a nearby tundra heath CH<sub>4</sub> oxidation was also strongly reduced in response to ammonium additions (Christensen et al., 1999), suggesting that this is a likely mechanism by which the nutrient cycling is tightly linked to CH<sub>4</sub> oxidation rates even in these strongly nitrogen-limited ecosystems (Press et al., 1998; Hobbie et al., 2002).

Although mountain birch forest and adjacent tundra heath soils differ in the depth distribution of net CH<sub>4</sub> oxidation, and in their response to removal of the upper soil, our results nonetheless provide evidence of a physical diffusion barrier to the movement of CH<sub>4</sub> from the atmosphere to sites of active methanotrophy. In order to improve the mechanistic understanding of the abiotic and biotic controls on CH<sub>4</sub> fluxes between soils and the atmosphere, it will be important to understand the depth distribution of the processes of CH<sub>4</sub> oxidation and production (in methanogenic systems). The implications for net CH<sub>4</sub> fluxes of environmental changes which result in alterations in the physicochemical properties (or extent) of contrasting soil horizons, and the biological processes occurring there, can also be more accurately predicted.

## Acknowledgments

We thank the European Commission IVth Environment and Climate Framework Programme, and the Swedish Royal Academy of Sciences, for funding this work. We are grateful for the assistance of the staff at the Abisko Scientific Research Station.

## References Cited

- Born, M., Dörr, H., and Levin, I., 1990: Methane consumption in aerated soils of the temperate zone. *Tellus*, 42B: 2–8.
- Christensen, T. R., Michelsen, A., and Jonasson, S., 1999: Exchange of CH<sub>4</sub> and N<sub>2</sub>O in a subarctic heath soil: effects of inorganic N and P and amino acid addition. *Soil Biology & Biochemistry*, 31: 637–641.
- Crill, P. M., 1991: Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles*, 5: 319–334.

- Dong, Y., Scharffe, D., Crutzen, P. J., and Sanhueza, E., 1998: Fluxes of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O from a temperate forest soil: the effects of leaves and humus layers. *Tellus*, 50B: 243–252.
- Dörr, H., Katruff, L., and Levin, I., 1993: Soil texture parameterization of the methane uptake in aerated soils. *Chemosphere*, 26: 697–713.
- Ehhalt, D., Prather, M. J., Dentener, E., Derwent, R., Dlogokenky, E., Holland, E., Isaksen, I., Katima, J., Kirchhoff, V., Matson, P., Midgley, P., and Wang, M., 2001: Atmospheric chemistry and Greenhouse Gases. In Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., and Johnson, C. A. (eds.), *Climate Change 2001*. Cambridge: Cambridge University Press, 243–278.
- Hobbie, S. E., Nadelhoffer, K. J., and Hogberg, P., 2002: A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil*, 242: 163–170.
- IPCC, 1990, *Radiative Forcing of Climate Change*. Intergovernmental Panel on Climate Change. Meteorological Office, Bracknell, U.K.
- IPCC, 2001, *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- King, G. M., 1997: Responses of atmospheric methane consumption by soils to global climate change. *Global Change Biology*, 3: 351–362.
- Koschorreck, M., and Conrad, R., 1993: Oxidation of atmospheric methane in soil: measurements in the field, in soil cores and soil samples. *Global Biogeochemical Cycles*, 7: 109–121.
- Littell, R. C., Milliken, G. A., Stroup, W. W., and Wolfinger, R. D., 1996: *SAS systems for mixed models*. Cary, North Carolina: SAS.
- Mancinelli, R. L., 1995: The regulation of methane oxidation in soil. *Annual Reviews of Microbiology*, 49: 581–605.
- Press, M. C., Potter, J. A., Burke, M. J. W., Callaghan, T. V., and Lee, J. A., 1998: Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, 86: 315–327.
- Saari, A., Heiskanen, J., and Martikainen, P. J., 1998: Effect of the organic horizon on methane oxidation and uptake in soil of a boreal Scots pine forest. *FEMS Microbiology Ecology*, 26: 245–255.
- Saari, A., Rinnan, R., and Martikainen, P. J., 2004: Methane oxidation in boreal forest soils: kinetics and sensitivity to pH and ammonium. *Soil Biology & Biochemistry*, 36: 1037–1046.
- Schlesinger, W. H., 1997: *Biogeochemical cycles: an analysis of global change*. Academic Press.
- Schnell, S., and King, G. M., 1994: Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils. *Applied Environmental Microbiology*, 60: 3514–3521.
- Shrestha, B. M., Sitaula, B. K., Singh, B. R., and Bajracharya, R. M., 2004: Fluxes of CO<sub>2</sub> and CH<sub>4</sub> in soil profiles of a mountainous watershed of Nepal as influenced by land use, temperature, moisture and substrate addition. *Nutrient Cycling in Agroecosystems*, 68: 155–164.
- Sitaula, B. K., Bakken, L. R., and Abrahamsen, G., 1995: N-fertilization and soil acidification effects on N<sub>2</sub>O and CO<sub>2</sub> emission from temperate pine forest soil. *Soil Biology & Biochemistry*, 27: 1401–1408.
- Sjögersten, S., and Wookey, P. A., 2002: Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biology*, 8: 885–894.
- Sjögersten, S., and Wookey, P. A., 2005: The role of soil organic matter quality and physical environment for nitrogen mineralization at the forest-tundra ecotone in Fennoscandia. *Arctic, Antarctic, and Alpine Research*, 37: 118–126.
- Sjögersten, S., Turner, B. L., and Mahieu, N., et al., 2003. Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biology*, 9: 759–772.
- Torn, M. S., and Chapin, F. S., III, 1993: Environmental and biotic controls over methane flux from arctic tundra. *Chemosphere*, 26: 357–368. [add citation for this reference]
- Torn, M. S., and Harte, J., 2006: Methane consumption by montane soils: implications for positive and negative feedback with climatic change. *Biogeochemistry*, 32: 53–67.
- Whalen, S. C., and Reeburgh, W. S., 1990: Consumption of atmospheric methane by tundra soils. *Nature*, 346: 160–162.

*Ms accepted September 2006*