

Spatio-temporal variability and environmental controls of methane fluxes at the forest–tundra ecotone in the Fennoscandian mountains

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Abstract

We report on temporal and spatial variability in net methane (CH₄) fluxes measured during the thaw period of 1999 and 2000 at three study sites along a c. 8° latitudinal gradient in the Fennoscandian mountain range and across the mountain birch-tundra ecotone. All of the sites studied here were underlain by well-drained mesic soils. In addition, we conducted warming experiments in the field to simulate future climate change. Our results show significant CH₄ uptake at mesic sites spanning the forest-tundra ecotone: on average 0.031 and 0.0065 mg CH₄ m⁻² h⁻¹ during the 1999 and 2000 thaw periods, respectively, in Abisko (Sweden), and 0.019 and 0.032 mg CH₄ m⁻² h⁻¹ during 2000 in Dovrefjell and Joatka (Norway), respectively. These values were both temporally and spatially highly variable, and multiple regression analysis of data from Abisko showed no consistent relationship with soil-moisture status and temperature. Also, there was no consistent difference in CH₄ fluxes between forest and tundra plots; our data, therefore, provide no support for the hypothesis that conversion of tundra to mountain birch forest, or *vice versa*, would result in a systematic change in the magnitude or direction of net CH₄ fluxes in this region. Experimental warming treatments were associated with a 2.4 °C increase in soil temperatures (5 cm depth) in 1999 in Abisko, but no consistent soil warming was noted at any of the three field locations during 2000. In spite of this, there were significant treatment effects, principally early during the thaw period, with increased CH₄ uptake compared with control (ambient) plots. These results suggest that direct effects of air warming on vegetation processes (e.g. transpiration, root exudation and nutrient assimilation) can influence CH₄ fluxes even in predominantly methanotrophic environments. We conclude that net CH₄ oxidation is significant in these cold, mesic soils and could be strengthened in an environmental change scenario involving a combination of (i) an increase in the length of the thaw period and (ii) increased mean temperatures during this period in combination with decreased soil-moisture content.

Keywords: climate, ecotone, Fennoscandia, landscape, methane, tundra

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Introduction

Atmospheric methane (CH₄) is an important radiatively active trace gas for which the global budget of sources and sinks is currently out of balance (Dlugokencky *et al.*, 1994; Houghton *et al.*, 1995). Biogenic sources and sinks of atmospheric CH₄ vary greatly in strength, both

temporally and spatially, and can be expected to respond to environmental and land-use changes. In arctic and subarctic environments, wetland and waterlogged soils are globally significant as CH₄ sources (Svensson & Rosswall, 1984; Sebacher *et al.*, 1986; Moore *et al.*, 1990; Morrissey & Livingston, 1992; Christensen, 1993; Torn & Chapin, 1993; Christensen *et al.*, 1995; Reeburgh *et al.*, 1998). There is, however, a growing awareness that high latitude and montane ecosystems with well-drained aerobic soils are net sinks for CH₄ through the process of

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biological CH₄ oxidation (methanotrophy) by soil bacteria (Whalen & Reeburgh, 1990; Sommerfeld *et al.*, 1993; Torn & Harte, 1996; Reeburgh *et al.*, 1998; West & Schmidt, 1998; Christensen *et al.*, 1999).

Improved understanding of how environmental change affects biogenic CH₄ fluxes is necessary for modelling the climate system (Christensen & Cox, 1995; Houghton *et al.*, 1995). Changes in climate and atmospheric chemistry will influence CH₄ fluxes directly through changes in the rates of methanogenesis and methanotrophy (King, 1997), but also indirectly through alterations in the structure and function of the broader ecosystem. It can be hypothesized that indirect mediators of CH₄ fluxes may be expressed most strongly where an ecotone shifts in response to environmental change. A shift from tundra to forest, or *vice versa*, will influence microclimate (e.g. through differential shading effects, and/or alterations in snow-pack characteristics), soil water regime (through differential interception by the canopy and contrasting evapotranspirative demand), litter inputs and thus soil chemistry (see Körner (1998) for a review). Each of these factors, singly or in combination, could influence net system CH₄ fluxes.

The objectives of the present study were, therefore, (i) to quantify natural spatial (latitude and altitude) and temporal variability in CH₄ fluxes in subarctic/alpine ecotone regions between mountain birch forest and tundra heath and (ii) to evaluate the sensitivity of CH₄ fluxes to experimental warming in the same regions. The work forms an integral component of a broader-based European Union-funded project on tree-line dynamics in the Scandes mountains, entitled 'Dynamic Response of the Forest-Tundra Ecotone to Environmental Change' (acronym: DART).

Materials and methods

Study area

The study sites are situated at the mountain birch (*B. pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti) – tundra ecotone in the Fennoscandian mountain range. The three study areas are: Dovrefjell (Sør-Trøndelag, Norway), Abisko (Norrbotten, Sweden) and Joatka (Finnmark, Norway) (Fig. 1). The three areas form a gradient in both latitude and continentality, with Dovrefjell being the most southerly and maritime and Joatka being the most northerly and continental. The main species in the heath areas are: *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *V. vitis-idea* and *Betula nana*, lichens and bryophytes (and additionally in Dovrefjell, *Arctostaphylos uva-ursi*). Mesic areas within the mountain birch forest have comparable understorey vegetation, although tending toward greater cover of *V. myrtillus*.

Dovrefjell The sites in Dovrefjell 62°18'N, 9°37'E are situated between 1000 and 1100 m a.s.l. across an alpine tree line positioned on a moderately steep (10°), northwest-facing slope. The transition zone from mountain birch forest to tundra is quite sharp, covering *c.* 50 m. The mean January and June temperatures at Kongsvoll field-station (972 m a.s.l.) are –7.9 and 10.2 °C, respectively, and the annual precipitation is 473 mm. The bedrock in the area is composed of gneisses.

Abisko The study sites in Abisko are located across the subarctic/alpine tree line 68°21'N, 18°49'E between 520 and 620 m a.s.l. on an undulating gentle slope of north-westerly aspect. The ecotone here is composed of a patchwork of tundra and isolated extensions of mountain birch forest up to 700–800 m a.s.l. The bedrock is mainly hard-shale and the small-scale topography is dominated by hummocky till deposits. At Abisko research station (365 m a.s.l.), the mean January and July temperatures are –11.9 and 11 °C, respectively, and the annual precipitation 304 mm (Alexandersson *et al.*, 1991).

Joatka The field sites in Joatka are located on an undulating plateau lying between 420 and 500 m a.s.l. at 69°45'N, 23°59'E. Large parts of the area are dominated by tundra vegetation which begins to prevail above 400 m a.s.l., and the mountain birch forest has the nature of discontinuous woodlands. The annual precipitation at Joatka is 354 mm, and the mean February and July temperatures are –14 and 11 °C, respectively.

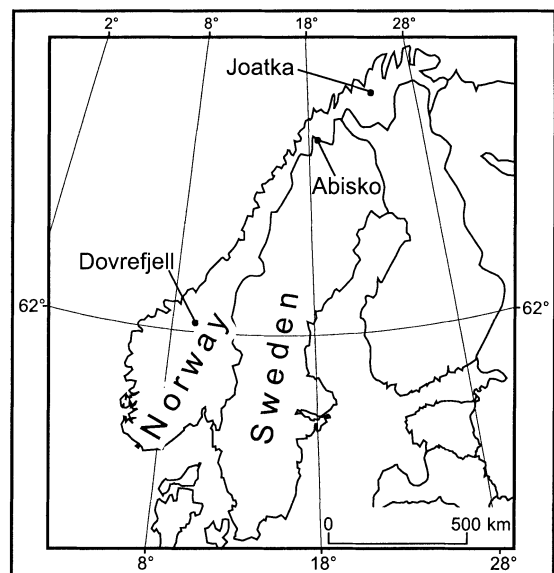


Fig. 1 Map of Scandinavia showing the locations of the main research areas, Dovrefjell (Norway), Abisko (Sweden) and Joatka (Norway).

Experimental design

In June 1998, we established four experimental sites at each main study area, spanning the mountain birch-tundra ecotone. Two of these sites have a mountain birch canopy (one at lower altitude and one at higher altitude, denoted 'Lower Forest' and 'Upper Forest', respectively) and two sites represent open tundra at different altitudes (subsequently denoted 'Lower Tundra' and 'Upper Tundra'). The sites are mesic and the soils are predominantly thin spodosols (principally orthods) developed within medium to coarse-grained till deposits (soil profile descriptions are given in Appendix A). Ten experimental plots were established at each site with five 1 × 1 m control plots and five plots which were randomly assigned an experimental warming treatment using open top chambers (OTCs) of International Tundra Experiment (ITEX) design (Marion *et al.*, 1997; Hollister & Webber, 2000). At each plot, we emplaced polyvinyl chloride (PVC) pipe (10 cm diameter; 15 cm deep) into the soil surface to 5–10 cm depth to serve as permanent bases for headspace CH₄ sampling.

Methane flux, temperature and soil-water measurements

We measured CH₄ fluxes by using the closed-chamber technique. The headspace volumes ranged from 1.1 to 1.5 L and the ground surface area was 78.5 cm². Small headspace samplers were a necessity because of space limitations within our OTCs. Priemé *et al.* (1996) noted, however, that chambers covering 78 and 4900 cm² gave comparable results for net CH₄ fluxes in a study in Denmark. Larger chambers (51.2–70.8 L in headspace volume and covering 2463 cm² ground surface) used in the vicinity of the field sites in Abisko showed comparable results to flux rates recorded from the smaller headspaces (S. Sjögersten *et al.*, personal observation). On each CH₄ sampling date the lids of headspace samplers were carefully applied and sealed. In Abisko, we took 2 mL air samples with syringes from all the headspaces initially and then after 1 h, and the samples were analysed the following day. From Dovrefjell and Joatka, however, 12 mL air samples were taken initially and after 1 h and stored in evacuated glass vials prior to analysis 2–3 weeks later. We used a Perkin Elmer AutoSystem XL Gas Chromatograph (GC) with flame ionization detector (FID) and 12' steel packed column containing 1/8" 5A molecular sieve. The injector temperature was set to 200°C, the detector to 150°C and the oven to 100°C. The GC was calibrated with a 4.92 ppmv CH₄ standard, and the analytical accuracy was 8% (based upon variability of a span control); this corresponds to a minimum detectable change in concentration (based upon the 90 percentile) of 0.39 ppm CH₄. With respect to the analytical

constraints we therefore performed statistical analyses on (i) the full data set, with no modifications, and (ii) on a modified data set, where all headspace concentration changes (positive or negative) of ≤ 0.39 ppm CH₄ were assigned a flux value of 0 mg CH₄ m⁻² h⁻¹. Average values presented subsequently, however, are based upon unmodified data. Initial ('Time 0') samples (atmosphere) ranged typically from 1.8 to 2.4 ppm CH₄.

At Abisko, CH₄ samples were collected on 18 occasions from 10 June to 12 September 1999, with a more frequent sampling interval at the beginning of the series. During 2000, samples were collected on 9 occasions from 15 May to 25 September, at fortnightly intervals. Measurements at Dovrefjell and Joatka were conducted on three occasions; that is, in June, August and September during the 2000 thaw season only (logistic constraints precluded more frequent sampling at Dovrefjell and Joatka).

Soil temperature data were collected year-round at all three main sites on an hourly basis using TinyTag dataloggers (INTAB Interface-Teknik AB, Stenkullen, Sweden) with thermistor probes at 5 cm depth. In Abisko, soil-temperature data were complemented during 2000 with point measurements at each plot during CH₄ sampling using a hand-held digital thermometer. In Abisko, volumetric soil-water content (5–10 cm depth) was also measured during CH₄ sampling at three locations in each sampling plot using a ThetaProbe and hand-held ThetaMeter (Delta-T Devices, Burwell, UK). At Dovrefjell and Joatka, soil-moisture content was recorded in control and OTC plots occasionally, but these measurements did not coincide with the CH₄ sampling owing to logistical constraints.

Statistical analysis

We used repeated-measures analysis of variance (ANOVA) in order to test for effects of the various sites, warming treatment, and time. The unevenly distributed (in time) data points from Abisko in 1999 were transformed into an early and late month average in order to avoid weighting toward the months with more frequent sampling intervals. When comparing the three main areas with one another, three dates from the Abisko series were picked for the ANOVA which were comparable to the sampling dates for Dovrefjell and Joatka. This procedure was necessary in order to compensate for the lower sampling frequency at Dovrefjell and Joatka. Where significant effects were indicated, we used Tukey's Honest Significant Difference (HSD) for means separation. In order to test the effects of soil water and temperature on CH₄ fluxes, we used multiple regression analysis. Statistical analyses were performed using STATISTICA (StatSoft, 1995).

Results

Results from statistical analyses on (i) the unmodified data set and (ii) where all fluxes below the minimum detection limit were assigned a value of 0 mg

CH₄ m⁻² h⁻¹, have broadly similar features (Table 1). In addition, mean values for each data set (unmodified vs. corrected with respect to detection limit; including all sites, and all treatments) were comparable (−0.029 and −0.024 mg CH₄ m⁻² h⁻¹, respectively). For this reason,

Table 1 Summary output of multifactorial repeated-measures analysis of variance (ANOVA) for methane (CH₄) flux data. Main effects are shown, together with all factorial interactions. At Dovrefjell, owing to lack of data during August, two ANOVAs were performed – one on June and September data (Dovre a) and one when data from the lower forest and tundra was duplicated to also the upper tundra and forest site (Dovre b). Results from both the ANOVAs with all data (unmodified) as well as data corrected with respect to the detection limit (*in italics*) are shown. Statistical significance of comparisons are denoted by: ****P* < 0.001, **P* < 0.05, †*P* < 0.1

	Effect	df	F	P-level			
2000 Dovrefjell, Abisko and Joatka	Area	2*	2*	3.13*	2.95*	0.044*	0.054*
	Site	3	3	1.07	0.71	0.36	0.55
	Treatment	1'	1*	3.61'	4.04*	0.058'	0.045*
	Area × Site	6	6	0.18	0.19	0.98	0.98
	Area × Treatment	2	2	0.32	0.47	0.72	0.62
	Site × Treatment	3	3	0.39	0.59	0.75	0.62
	Area × Site × Treatment	6	6	0.29	0.33	0.94	0.92
	2000 Dovre a	Site	3'	3	2.44'	1.92	0.084'
Treatment		1***	1***	18.1***	15.9***	0.0002***	0.00036***
Time		1	1	0.94	0.89	0.34	0.35
Site × Treatment		3	3	0.044	0.43	0.99	0.73
Site × Time		3	3	1.51	1.65	0.23	0.20
Treatment × Time		1	1*	1.36	4.85	0.25	0.035*
Site × Treatment × Time		3	3	0.64	0.45	0.60	0.72
2000 Dovre b	Site	3	3	0.31	0.06	0.82	0.98
	Treatment	1'	1'	4.04'	3.98'	0.054'	0.055'
	Time	2	2	0.76	0.46	0.47	0.63
	Site × Treatment	3	3	0.98	1.02	0.41	0.40
	Site × Time	6	6	1.06	1.14	0.39	0.35
	Treatment × Time	2'	2'	2.64'	2.67'	0.080'	0.077'
	Site × Treatment × Time	6	6	1.02	1.42	0.42	0.22
1999 Abisko	Site	3***	3***	6.51***	7.18***	0.00025***	0.00081***
	Treatment	1	1	6.36	0.086	0.55	0.77
	Time	6***	6	2.03***	0.86	0.00047***	0.53
	Site × Treatment	3'	3	2.83'	2.01	0.070'	0.13
	Site × Time	18	18	0.80	0.52	0.81	0.95
	Treatment × Time	6	6	1.19	0.99	0.44	0.44
	Site × Treatment × Time	18	18	0.77	0.97	0.29	0.49
2000 Abisko	Site	3	3	1.30	0.48	0.29	0.70
	Treatment	1*	1*	5.62*	4.23*	0.025*	0.049*
	Time	5	5	0.80	0.55	0.55	0.74
	Site × Treatment	3	3	1.98	2.06	0.14	0.13
	Site × Time	15*	15*	1.78*	1.88*	0.044*	0.030*
	Treatment × Time	5	5	2.13	1.38	0.065'	0.24
	Site × Treatment × Time	15	15	1.23	0.91	0.26	0.55
2000 Joatka	Site	3	3	1.33	0.98	0.28	0.41
	Treatment	1*	1*	4.73*	5.36*	0.037*	0.027*
	Time	2*	2'	3.60*	3.01'	0.033*	0.056'
	Site × Treatment	3	3	1.93	1.59	0.14	0.21
	Site × Time	6	6	0.028	0.05	1.00	1.00
	Treatment × Time	2	2	1.52	1.48	0.23	0.24
	Site × Treatment × Time	6	6	0.49	0.38	0.81	0.89

we have decided to base our evaluation upon the unmodified data, although we note that some *P*-values around statistical thresholds shifted when the second data set was analysed (Table 1). This is especially the case at Abisko, where the fluxes were lowest (Table 2).

Average CH₄ fluxes in the control plots at Abisko during the 1999 and 2000 thaw season were -0.031 and -0.0065 mg CH₄ m⁻² h⁻¹, respectively (where negative values indicate CH₄ uptake from the atmosphere by the soil). Methane uptake was also noted at the Dovrefjell

and Joatka sites (-0.019 and -0.032 mg CH₄ m⁻² h⁻¹, respectively, in 2000). Methane uptake was recorded on the majority of measurement occasions over each season (Table 2). No significant differences in CH₄ fluxes between the tundra and the forest sites were found, but some variation between sites and locations was noted (Table 1); during 2000, the Joatka sites had significantly (*P* < 0.05) higher CH₄ uptake rates than the Abisko sites. The upper tundra and the lower forest sites in Abisko differed significantly (*P* < 0.05) from the upper forest and

Table 2 Summary table of methane flux data (mg CH₄ m⁻² h⁻¹) from the forest-tundra gradient (and warming/OTC experiment) at Dovrefjell, Abisko and Joatka. Monthly mean fluxes and Standard Error are given for all sites, and for OTC treatment and unmanipulated control plots

Year site	Month	Control				Mean	Treatment				Mean		
		Upper tundra	Upper forest	Lower tundra	Lower forest		Upper tundra	Upper forest	Lower tundra	Lower forest			
1999 Abisko	June	-0.020 (0.26)	-0.040 (0.019)	-0.046 (0.020)	0.00058 (0.023)	-0.026	-0.031 (0.020)	-0.047 (0.024)	-0.032 (0.023)	-0.019 (0.022)	-0.032		
	July	-0.021 (0.016)	-0.030 (0.014)	-0.017 (0.017)	-0.0061 (0.015)		-0.019	-0.022 (0.012)	-0.041 (0.019)	-0.045 (0.015)		-0.024 (0.018)	-0.033
	Aug	-0.011 (0.030)	-0.060 (0.037)	-0.052 (0.040)	0.0045 (0.039)		-0.030	-0.0018 (0.031)	-0.032 (0.039)	-0.032 (0.031)		-0.037 (0.026)	-0.026
	Sept	-0.013 (0.034)	-0.067 (0.040)	-0.016 (0.022)	-0.047 (0.058)		-0.036	-0.0062 (0.034)	-0.023 (0.067)	-0.044 (0.037)		-0.034 (0.031)	-0.027
	Mean	-0.016	-0.049	-0.033	-0.012			-0.015	-0.036	-0.039		-0.029	
2000 Abisko	May	-0.018 (0.023)		-0.026 (0.021)		-0.022^a	-0.0030 (0.010)		0.0070 (0.0050)		0.0020^a		
	June	-0.012 (0.019)	0.025 (0.011)	-0.013 (0.011)	-0.015 (0.011)		-0.0038	-0.037 (0.0046)	-0.035 (0.014)	-0.0096 (0.014)		-0.011 (0.020)	-0.023
	July	-0.0040 (0.015)	-0.0097 (0.012)	-0.015 (0.011)	0.021 (0.0091)		-0.0019	-0.015 (0.012)	-0.046 (0.012)	-0.016 (0.0094)		0.00022 (0.0018)	-0.019
	Aug	-0.011 (0.015)	-0.0068 (0.017)	-0.028 (0.0088)	-0.015 (0.015)		-0.015	0.0033 (0.016)	-0.0007 (0.015)	-0.037 (0.011)		0.00075 (0.017)	-0.0084
	Sept			-0.025 (0.026)	-0.048 (0.042)		-0.036			-0.0034 (0.042)		0.057 (0.047)	0.027
	Mean	-0.011	0.0028	-0.021	-0.014		-0.013	-0.027	-0.018	-0.017			
2000 Dovrefjell	June	0.0063 (0.022)	-0.015 (0.0052)	-0.015 (0.012)	-0.023 (0.014)	-0.012	-0.031 (0.012)	-0.074 (0.019)	-0.041 (0.013)	-0.068 (0.014)	-0.053		
	Aug			-0.040 (0.0033)	-0.058 (0.013)		-0.049			0.073 (0.017)		0.0035 (0.061)	-0.035
	Sept	-0.0019 (0.014)	0.036 (-0.0074)	-0.0074 (0.012)	-0.0060 (0.015)		-0.013	-0.036 (0.011)	-0.053 (0.013)	-0.040 (0.012)		-0.027 (0.018)	-0.039
	Mean	-0.0022	-0.026	-0.021	-0.029			-0.034	-0.064	-0.051		-0.031	
2000 Joatka	June	0.035 (0.055)	0.070 (0.098)	0.080 (0.042)	0.0012 (0.031)	0.046	0.017 (0.071)	-0.060 (0.090)	-0.062 (0.053)	-0.0020 (0.053)	-0.027		
	Aug	-0.040 (0.012)	-0.080 (0.018)	-0.020 (0.026)	-0.053 (0.010)		-0.048	-0.046 (0.013)	-0.082 (0.022)	-0.10 (0.013)		-0.080 (0.029)	-0.077
	Sept	-0.076 (0.050)	-0.15 (0.10)	-0.10 (0.051)	-0.055 (0.033)		-0.095	-0.063 (0.074)	-0.022 (0.098)	-0.042 (0.057)		-0.078 (0.069)	-0.051
	Mean	-0.027	-0.053	-0.013	-0.036			-0.031	-0.055	-0.068		-0.053	

^aResults from tundra sites only.

the lower tundra over the season of 1999, with generally higher CH_4 uptake rates at the upper forest and the lower tundra sites. Additionally, at Dovrefjell a near-significant ($P=0.056$) difference between the upper tundra and the upper forest sites was noted with higher CH_4 uptake rates at the upper forest.

There was substantial temporal variation in CH_4 fluxes during each season, and although the general trend was for CH_4 uptake, emission occurred on several occasions (Table 2). Only the Joatka sites had a clear seasonal pattern ($P<0.05$) with significant CH_4 production in June followed by increased CH_4 uptake rates toward the end of the thaw season (Fig. 2).

For the Abisko sites, we found no significant effect of the OTC treatment during 1999, with average CH_4 flux within the OTCs of $-0.033 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ compared with $-0.031 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at control plots. Conversely, the data from 2000 show significantly ($P<0.001, <0.05, <0.05$, at Dovrefjell, Abisko and Joatka, respectively) higher uptake rates in the OTCs at nearly all sites (11 of 12). Average uptake rates, comparing control to OTC plots, were: -0.019 vs. $-0.043 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$; -0.0065 vs. $-0.020 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ and -0.032 vs. $-0.052 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at Dovrefjell, Abisko and Joatka, respectively. The effect of the OTCs on the CH_4 uptake rates also varied temporally over the measuring periods. Because 'time' was found to be significant as a main effect (Table 1) and as an interaction with 'treatment' (OTC vs. control), we analysed data month by month. In Abisko, a significant

OTC effect ($P<0.05$) was thus noted in July 1999, and also in June 2000 ($P<0.05$). At this site, higher CH_4 uptake rates within OTCs were most marked during the early summer. At Joatka, the largest effect of the OTCs was noted in June ($P<0.05$), but the difference ceased in September. In Dovrefjell, the effect of the OTCs was largest at the beginning and at the end of the thaw period (June and September), apparently mainly because the CH_4 uptake rates in the control plots increased markedly in August ($P=0.079$).

The OTCs generally decreased soil-moisture content and increased surface temperature at all sites, but soil temperature (at 5 cm) was not significantly affected during 2000. The effect of the chambers, however, varied both temporarily and spatially. In Dovrefjell, Abisko and Joatka, the OTCs reduced soil-moisture content from 0.32 to 0.28 (seasonwide, 6 measurement dates); 0.33–0.30 (seasonwide, 25 measurement dates); and 0.20–0.17 $\text{m}^3 \text{ m}^{-3}$ soil (one end-of-season measurement), respectively ($P<0.05$). During the 1999 measuring period at Abisko, the summer average soil temperatures at 5 cm depth were significantly different ($P<0.001$) in control and OTC plots (6.1°C and 8.5°C , respectively), giving a 2.4°C increase in soil temperatures within the OTCs. However, in 2000 the OTC effect on soil temperatures had ceased in Abisko, and both control and OTC plots had seasonal mean soil temperatures of 7.6°C . No systematic temperature increase was recorded at 5 cm depth over the measuring period at Dovrefjell and Joatka (7.0°C

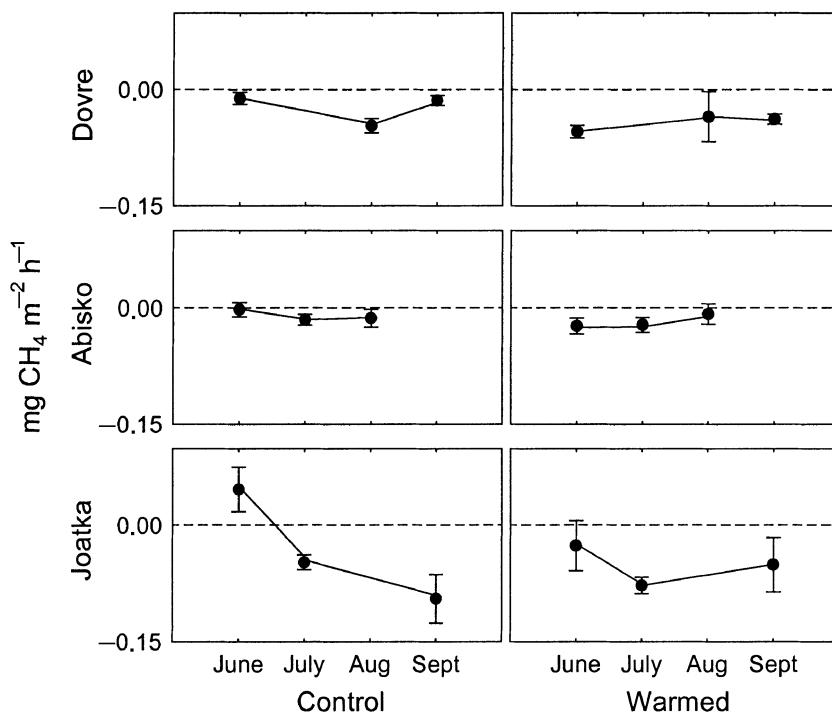


Fig. 2 Seasonal variation and impact of experimental warming on methane fluxes measured at three areas in the Fennoscandian mountain range during the thaw season of 2000. Mean values (± 1 SE) are shown in the diagram (negative values indicate CH_4 uptake). The full seasonal data set for Abisko is not shown here; only those data points used in the statistical analysis (multifactorial ANOVA: See Table 1) of intern-area comparisons are included. Sample collection in September 2000 in Abisko could not be undertaken owing to the sampling campaigns at Dovrefjell and Joatka.

and 6.0°C; and 7.7°C and 7.8°C in control and OTC plots, respectively). The OTCs, however, advanced the frost-free period on average 11 days.

Multiple regression analysis of CH₄ flux data from the four sites in Abisko revealed no significant relationship with either soil temperature or water status in either year.

Discussion

Mesic sites in the Fennoscandian mountain range spanning the forest-tundra ecotone were significant CH₄ sinks ($-0.021 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ on average over all sites and locations during 2000; equivalent to $-0.50 \text{ mg m}^{-2} \text{ day}^{-1}$, assuming diurnal variations do not occur) (Table 2). These flux rates compare well with data obtained in similar environments (mainly tundra ecosystems) both in North America and in Eurasia (c. -0.53 to $-1 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) (Christensen *et al.*, 1995; Torn & Harte, 1996; Reeburgh *et al.*, 1998). The occurrence of CH₄ emission at the sites is sporadic, but suggests that microsites with suitable conditions for CH₄ production exist within the soils. The significant CH₄ emissions noted in June in Joatka (Table 2, Fig. 2) are likely to be the result of waterlogging, as the measurements were made just after snowmelt and the surface water drainage was probably impeded by residual ground ice.

The absence of a significant difference overall between tundra and forest sites (Tables 1 and 2) suggests that CH₄ oxidation rates in the area do not reflect the above-ground vegetation communities. This compares well with the general pattern found in other biomes. Rates of CH₄ uptake similar to those reported here have been found in tropical rainforest soils, temperate forests and grasslands and boreal forests (King, 1997).

The large temporal and spatial variation in net CH₄ consumption at our sites is, however, difficult to explain on the basis of soil-water status and/or temperature differences, or indeed any physical treatment artefacts. The large interannual difference in CH₄ fluxes at Abisko (Table 2) also has no ready explanation based upon differences in soil temperature or moisture status. These data suggest that CH₄ uptake in these environments is a process rather insensitive to changes in soil temperature and moisture within the thaw period. Low Q₁₀ values (e.g. 1.2 and 1.5) for CH₄ uptake in temperate forests have been reported by Born *et al.* (1990), Crill (1991), King & Adamsen (1992), Bowden *et al.* (1998) and Rustad & Fernandez (1998). The lack of significant regression between either soil temperature or moisture and CH₄ uptake rate might be explained, in part, by the depth distribution of methanotrophs in the soil profile. Recent observations in Abisko (E. Melander and the authors) suggest that the methanotrophs are most active in the upper eluvial (albic) horizon; that is, at greater depth

than our soil temperature or moisture measurements, especially with mountain birch-forest soil.

Soil-moisture content often is a significant controlling factor for CH₄ uptake in soils (Koschorreck & Conrad, 1993; Castro *et al.*, 1995; Torn & Harte, 1996; Bowden *et al.*, 1998; Bradford *et al.*, 2001). The apparent insensitivity of the methanotroph community to soil moisture at our field sites may be related to the fact that the soil-moisture contents we measured were within a range in which modest variations may not affect CH₄. That is to say the soils were neither so wet as to cause diffusional limitations to CH₄ or O₂ transport, nor were they sufficiently dry to result in physiological stress for the methanotrophs (Mancinelli, 1995).

The warming treatment generally increased CH₄ uptake rates at most sites, especially early in the season, despite no temperature increase at 5 cm depth in response to the OTCs in 2000 (the third year of the warming treatment). The OTCs did, however, consistently reduce soil-water content in the upper 10 cm, likely via two mechanisms: (i) greater water loss by transpiration earlier in the season within OTCs, associated with accelerated vegetative phenology (Arft *et al.*, 1999) and (ii) physical shelter from precipitation inputs around the edges of the OTCs. The CH₄ flux data, therefore, possibly reflect a stronger response of the methanotrophic community to reduced soil-moisture content (i) at lower soil temperatures and/or (ii) when the methanotroph population/metabolism and CH₄ concentration gradients become established following the thaw. An additional mechanism by which the OTCs could have provided the methanotrophs with improved conditions is through protection from freezing events, which have been shown to have significant negative impacts on CH₄ uptake rates (Groffman *et al.*, 1999). Furthermore, the OTC effect on early season CH₄ fluxes could also be mediated by changes in soil/rhizosphere chemistry (e.g. in root exudates and extractable mineral nutrient content). Accelerated plant phenology and growth within OTCs could, for example, reduce NH₄⁺ concentrations in soil solution, with potential impacts on CH₄ fluxes (Gulledge *et al.*, 1997; Gulledge & Schimel, 1998; Whalen, 2000). We hypothesize, therefore, that the OTC effect is related to improved physical and chemical conditions for the methanotrophs. We cannot rule out the possibility, however, that the OTCs create an environment that is less favourable for methanogens, so that the net CH₄ flux may reflect effects on both populations (Khalil *et al.*, 1998).

Finally, in the context of global environmental change, the main implications of our results are (1) that mesic subarctic soils are currently net sinks for CH₄, and they should be incorporated as such into regional and global models of the CH₄ budget; (2) there are no clear systematic differences in CH₄ sink strength between mountain

birch forest and tundra heath soils in this region, but (3) the potential exists in both of these systems for increased CH₄ uptake in response to rather modest decreases in soil-water content early in the season and/or changes in the length of the thaw period. We hypothesize, in particular, that early summer warming in combination with earlier snow-melt and a longer thaw season will significantly strengthen CH₄ uptake in these mesic systems. More work is needed, however, on finer-scale landscape variability in these regions as topographic controls on soil-moisture status and texture produce a mosaic of mesic areas interspersed with wetter or drier landscape units that may have markedly contrasting net CH₄ fluxes.

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Appendix A

Soil profile descriptions

Dovre fjell

Site	Horizon	Depth (cm)	Colour	Texture	pH	Density (g cm ⁻³)	Tot C (mg g ⁻¹)	Tot N (mg g ⁻¹)	LO (%)
Tundra (i)	Organic	0–18		Dense, felty	6.18	0.16			88.2
	Oi	0–3					394.4	16.73	
	Oe	3–12	5 YR 2/3				352.2	17.43	
	Oa	12–18	5 YR 2/1			0.30			56.5
	Albic	18–32	7.5 YR 4/2	Sand	5.88	1.42			4.63
	Spodic	32–37	7.5 YR 3/3	Gravelly sand	6.08				2.88
	C	37–44	2.5 Y 4/3	Silty sand	6.16				
Forest (i)	Organic	0–10	5 YR 3/3	Fibrous/felty	4.46	0.15			68.4
	Oi	0–1					400.3	19.17	
	Oe	1–7					419.9	18.3	
	Oa	7–11							
	Albic	11–21	5 Y 5/2	Sandy silt	4.51	1.55			2.13

Abisko

Site	Horizon	Depth (cm)	Colour	Texture	pH	Density (g cm ⁻³)	Tot C (mg g ⁻¹)	Tot N (mg g ⁻¹)	LO (%)
Tundra (i)	Organic	0–8	5 YR 3/3	Felty	4.53	0.15			78.47
	Albic	8–11	10 YR 5/4	Gravelly sand	5.09	1.14			5.99
	Spodic	11–21	7.5 YR 5/6	Gravelly sand	5.55	0.74			19.54
Tundra (ii)	Organic	0–7	7.5 YR 2/3	Felty	3.86	0.14			96.19
	Oi	0–1					405.2	13.30	
	Oe	1–5					384.8	12.71	
	Oa	5–7							
	A	7–9	7.5 YR 4/3	Silt	4.35	0.34			50.44
	Albic	9–13	10 YR 5/2	Silt	5.14	0.84			5.62
	Spodic	13–16	10 YR 4/6	Sandy gravel	5.61	1.73			1.014
	C		7.5 YR 3/3	Sandy gravel	6.22	1.66			0.71

Abisko

Site	Horizon	Depth (cm)	Colour	Texture	pH	Density (g cm ⁻³)	Tot C (mg g ⁻¹)	Tot N (mg g ⁻¹)	LO (%)
Forest (i)	Organic	0-5	5 YR 2/4	Fibrous	5.22	0.066			94.18
	Oi	0-0.2							
	Oe	0.2-4.8					296.3	14.02	
	Oa	-							
	Albic	5-8	2.5 YR 5/2	Sandy silt	4.20	1.47			5.18
	C	8-33	2.5 YR 4/3	Silt	5.58	1.10			1.13
Forest (ii)	Organic	0-5	5 YR 2/3	Fibrous	4.07	0.11			96.43
	Oi	0-0.5							
	Oe	0.5-2.5							
	Oa	2.5-5							
	Albic	5-20	5 Y 6/2	Heterogenous silt	4.95	1.30			2.23
	C	20-29	5 Y 4/3	Sandy silt	5.91	1.68			1.25

Joatka

Site	Horizon	Depth (cm)	Colour	Texture	pH	Density (g cm ⁻³)	Tot C (mg g ⁻¹)	Tot N (mg g ⁻¹)	LO (%)
Tundra (i)	Organic	0-4	5 YR 2/2	Felty	4.03	0.15			79.8
	Oi	0-0.5							
	Oe	0.5-2					427.2	15.05	
	Oa	2-4							
	Albic	4-9	10 YR 7/3	Sand	4.85	1.58			0.82
	Spodic	9-22	7.5 YR 4/6	Silty gravely sand	5.13	1.39			2.47
	Iron crust	22-30	2.5 YR 3/3	Gravely sand iron-rich aggregate	5.32	1.44			3.97
	Spodic	30-39	7.5 YR 4/6	Gravely sand	5.89				1.74
	C	39-44		Gravely sand	5.55				
Tundra (ii)	Organic	0-4.5	5 YR 4/3	Felty	4.04				71.6
	Oi	0-0.5							
	Oe	0.5-3.5							
	Oa	3.5-4.5							
	Albic	4.5-14.5	2.5 Y 7/2	Sand	5.21				0.64
	Spodic (i)	14.4-23.5	7.5 YR 4/6	Sand, iron-rich aggregates	4.61				2.17
	Spodic (ii)	23.5-47.5	5 YR 3/4	Sand	5.43				6.08
Forest (i)	Organic	0-4	5 YR 2/2	Fibrous	4.07	0.18			78.9
	Oi	0-0.2							
	Oe	0.2-1.2						369.9	14.60
	Oa	1.2-4							
	Albic	4-8	10 YR 6/2	Sand	5.30	1.43			1.44
	Spodic	8-28	7.5 YR 5/8	Sand, iron-rich aggregate	5.49	1.62			1.03
	C	28-37	2.5 Y 5/4	Gravely sand	5.89	1.62			0.86
Forest (ii)	Organic	0-7.5	2.5 YR 2/2	Fibrous	4.00	0.11			95.6
	Oi	0-0.5							
	Oe	0.5-3.5							
	Oa	3.5-7.5							
	Albic	7.5-16.5	10 YR 7/2	Sand	5.12	1.50			0.77
	Spodic	16.5-33.5	7.5 YR 5/8	Sand	5.34	1.52			2.86
	C	33.5-36.5	10 YR 4/6	Sandy silt					