Global Change Biology (2002) **8,** 885–894

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

SOFIE SJÖGERSTEN and PHILIP A. WOOKEY
Department of Earth Sciences, Physical Geography, Uppsala University, Villavägen 16, S-752 36 Uppsala, Sweden

Abstract

We report on temporal and spatial variability in net methane (CH_4) 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 CH_4 uptake at mesic sites spanning the forest-tundra ecotone: on average 0.031 and 0.0065 mg $CH_4\,m^{-2}\,h^{-1}$ during the 1999 and 2000 thaw periods, respectively, in Abisko (Sweden), and 0.019 and 0.032 mg $CH_4\,m^{-2}\,h^{-1}$ 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 CH_4 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 CH_4 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 CH_4 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 CH_4 fluxes even in predominantly methanotrophic environments. We conclude that net CH_4 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

Received 6 November 2001; revised version received 26 February 2002 and accepted 5 March 2002

Introduction

Atmospheric methane (CH_4) 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 CH_4 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 CH_4 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 CH_4 through the process of

Correspondence: Sofie Sjögersten, tel. +46 (0)18 471 25 13, fax + 46 (0)18 55 59 20, e-mail: sofie.sjogersten@geo.uu.se

biological CH_4 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 CH_4 fluxes is necessary for modelling the climate system (Christensen & Cox, 1995; Houghton *et al*., 1995). Changes in climate and atmospheric chemistry will influence CH_4 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 CH_4 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 CH_4 fluxes.

The objectives of the present study were, therefore, (i) to quantify natural spatial (latitude and altitude) and temporal variability in CH_4 fluxes in subarctic/alpine ecotone regions between mountain birch forest and tundra heath and (ii) to evaluate the sensitivity of CH_4 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-Tröndelag, 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 northwesterly 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.

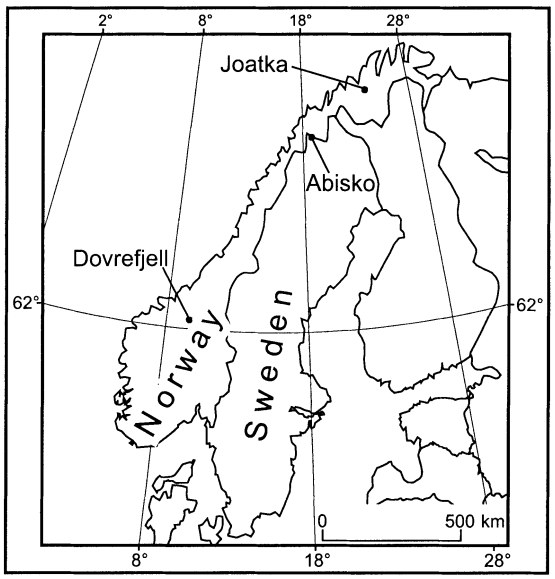

Fig. 1 Map of Scandinavia showing the locations of the main research areas, Dovrefjell (Norway), Abisko (Sweden) and Joatka (Norway).

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 CH_4 sampling.

Methane flux, temperature and soil-water measurements

We measured CH_4 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 cm^2. 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 cm^2 gave comparable results for net CH_4 fluxes in a study in Denmark. Larger chambers (51.2–70.8 L in headspace volume and covering 2463 cm^2 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 CH_4 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 CH_4 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 CH_4. 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 CH_4 were assigned a flux value of 0 mg $CH_4\,m^{-2}\,h^{-1}$. Average values presented subsequently, however, are based upon unmodified data. Initial ('Time 0') samples (atmosphere) ranged typically from 1.8 to 2.4 ppm CH_4.

At Abisko, CH_4 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 CH_4 sampling using a hand-held digital thermometer. In Abisko, volumetric soil-water content (5–10 cm depth) was also measured during CH_4 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 CH_4 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 CH_4 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 $CH_4\,m^{-2}\,h^{-1}$, 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 $CH_4\,m^{-2}\,h^{-1}$, respectively). For this reason,

Table 1 Summary output of multifactorial repeated-measures analysis of variance (ANOVA) for methane (CH_4) 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′	*0.15*
	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 CH_4 fluxes in the control plots at Abisko during the 1999 and 2000 thaw season were −0.031 and −0.0065 mg $CH_4\,m^{-2}\,h^{-1}$, respectively (where negative values indicate CH_4 uptake from the atmosphere by the soil). Methane uptake was also noted at the Dovrefjell and Joatka sites (−0.019 and −0.032 mg $CH_4\,m^{-2}\,h^{-1}$, respectively, in 2000). Methane uptake was recorded on the majority of measurement occasions over each season (Table 2). No significant differences in CH_4 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 CH_4 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 $CH_4\,m^{-2}\,h^{-1}$) 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

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

[a]Results 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 mg $CH_4\,m^{-2}\,h^{-1}$ compared with -0.031 mg $CH_4\,m^{-2}\,h^{-1}$ 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 mg $CH_4\,m^{-2}\,h^{-1}$; -0.0065 vs. -0.020 mg $CH_4\,m^{-2}\,h^{-1}$ and -0.032 vs. -0.052 mg $CH_4\,m^{-2}\,h^{-1}$ 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 $m^3\,m^{-3}$ 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

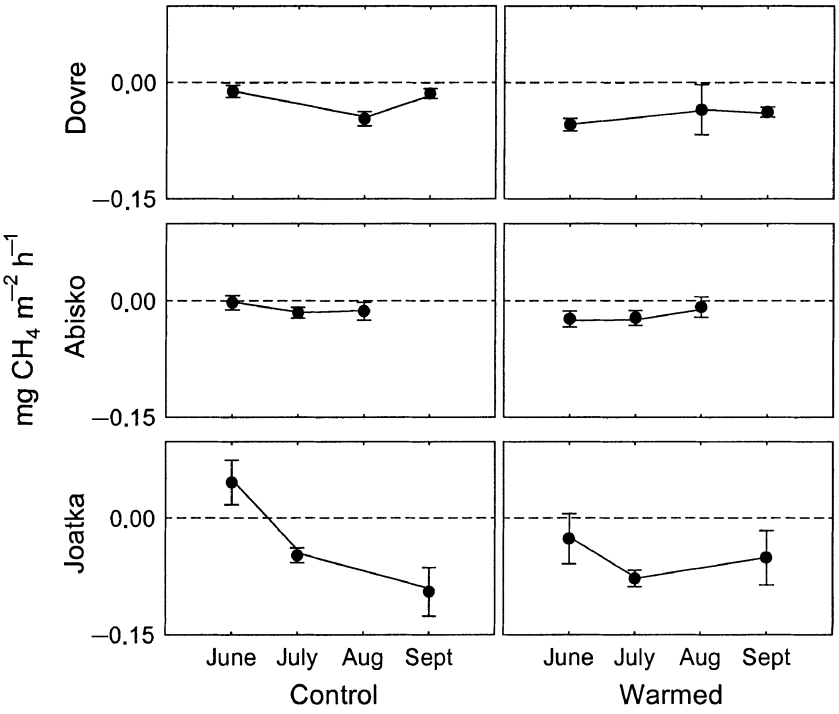

Fig. 2 Seasonal variation and impact of experimental warming on methane fluxes measured at three areas in the Fennoscandian mountain range during the thaw season of 2000. Mean values (± 1 SE) are shown in the diagram (negative values indicate CH_4 uptake). The full seasonal data set for Abisko is not 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 CH_4 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 CH_4 sinks (-0.021 mg $CH_4\,m^{-2}\,h^{-1}$ on average over all sites and locations during 2000; equivalent to $-0.50\,mg\,m^{-2}\,day^{-1}$, 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 mg $CH_4\,m^{-2}\,day^{-1}$ (Christensen *et al*., 1995; Torn & Harte, 1996; Reeburgh *et al*., 1998). The occurrence of CH_4 emission at the sites is sporadic, but suggests that microsites with suitable conditions for CH_4 production exist within the soils. The significant CH_4 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 CH_4 oxidation rates in the area do not reflect the aboveground vegetation communities. This compares well with the general pattern found in other biomes. Rates of CH_4 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 CH_4 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 CH_4 fluxes at Abisko (Table 2) also has no ready explanation based upon differences in soil temperature or moisture status. These data suggest that CH_4 uptake in these environments is a process rather insensitive to changes in soil temperature and moisture within the thaw period. Low Q_{10} values (e.g. 1.2 and 1.5) for CH_4 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 CH_4 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 CH_4 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 CH_4. That is to say the soils were neither so wet as to cause diffusional limitations to CH_4 or O_2 transport, nor were they sufficiently dry to result in physiological stress for the methanotrophs (Mancinelli, 1995).

The warming treatment generally increased CH_4 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 tranpiration 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 CH_4 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 CH_4 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 CH_4 uptake rates (Groffman *et al*., 1999). Furthermore, the OTC effect on early season CH_4 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 NH_4^+ concentrations in soil solution, with potential impacts on CH_4 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 CH_4 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 CH_4, and they should be incorporated as such into regional and global models of the CH_4 budget; (2) there are no clear systematic differences in CH_4 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 CH_4 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 CH_4 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 CH_4 fluxes.

Acknowledgements

We thank the European Commission (Project No. ENV4-CT97-0586), the Swedish Royal Academy of Sciences, Svenska Sällskapet för Antropologi och Geografi, Uppsala University Linné Fonden, and Sernanders Resestipendium for funding this work. We are especially grateful for the help and support from ANS and our field assistants (Pär Eriksson, Magnus Karlsson, Karin Luthbom, Marie Nilsson, Katrin Sjögersten and Per Thermaenius), and to Dr Robert Baxter (University of Durham) and Linda Dalen (University of Trondheim) for contributing to the microclimatic and soil-moisture data sets. We thank Professor Else Kolstrup for commenting on an earlier draft of this article and Markus Gustavsson for help with the map-drawing. We are also grateful to Docent Ingvar Sundh (Swedish University of Agricultural Sciences, Uppsala) for use of laboratory equipment.

References

Alexandersson H, Karlstöm C, Larsson-McCann S (1991) Temperaturen och Nederbörden i Sverige: *1961–90 Referensnormaler. SMHI Meteorologi Report no. 81, SMHI (Sveriges meteorologiska och hydrologiska institut).* Norrköping.

Arft AM, Walker MD, Gurevitch J *et al.* (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs*, **69** (4), 491–511.

Born M, Dörr H, Levin I (1990) Methane consumption in aerated soils of the temperate zone. *Tellus*, **42B**, 2–8.

Bowden RD, Newkirk KM, Rullo GM (1998) Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biology and Biochemistry*, **30**, 1591–1597.

Bradford MA, Wookey PA, Ineson P *et al.* (2001) Controlling factors and effects of chronic nitrogen and sulphur deposition on methane oxidation in temperate forest soil. *Soil Biology and Biochemistry*, **33**, 93–102.

Castro MS, Steudler PA, Melillo JM, Aber JD, Bowden RD, (1995) Factors controlling atmospheric methane consumption by temperate forest soils. *Global Biogeochemical Cycles*, **9**, 1–10.

Christensen TR (1993) Methane emission from Arctic tundra. *Biogeochemistry*, **21**, 117–139.

Christensen TR, Cox P (1995) Response of methane emission from arctic tundra to climatic change: results from a model simulation. *Tellus*, **47B**, 301–309.

Christensen TR, Jonasson S, Callaghan TV *et al.* (1995) Spatial variation in high-latitude methane flux along a transect across Siberian and European tundra environments. *Journal of Geophysical Research*, **100**, 21,035–21,045.

Christensen TR, Michelsen A, Jonasson S (1999) Exchange of CH_4 and N_2O in a subarctic heath soil: effects of inorganic N and P and amino acid addition. *Soil Biology and Biochemistry*, **31**, 637–641.

Crill PM (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles*, **5**, 319–334.

Dlugokencky EJ, Masarie KA, Lang PM *et al.* (1994) A dramatic decrease in the growth rate of atmospheric methane in the northern hemisphere during 1992. *Geophysical Research Letters*, **21**, 45–48.

Groffman PM, Hardy JP, Nolan S *et al.* (1999) Snow depth, soil frost and nutrient loss in a northern hardwood forest. *Hydrological Processes*, **13**, 2275–2286.

Gulledge J, Doyle AP, Schimel JP (1997) Different NH_4^+-inhibition patterns of soil CH_4 consumption: a result of distinct CH_4-oxidizer populations across sites? *Soil Biology and Biochemistry*, **29**, 13–21.

Gulledge J, Schimel JP (1998) Low-concentration kinetics of atmospheric CH_4 oxidation in soil and mechanism of NH_4^+ inhibition. *Applied and Environmental Microbiology*, **64**, 4291–4298.

Hollister RD, Webber PJ (2000) Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, **6**, 835–842.

Houghton JT, Meira Filho LG, Callender BA *et al.* (1995) The Science of Climate Change. *Contribution of Working Group I to the Second Assessment of the Intergovernmental Panel on Climate Change*. Cambridge University Press, UK.

Khalil MAK, Rasmussen RA, Shearer MJ (1998) Effects of production and oxidation processes on methane emission from rice fields. *Journal of Geophysical Research*, **103**, 25,233–25,239.

King GM (1997) Responses of atmospheric methane consumption by soils to global climate change. *Global Change Biology*, **3**, 351–362.

King GM, Adamsen APS (1992) Effects of temperature on methane comsumption in a forest soil and in pure cultures of the methanotroph *Methylomonas rubra*. *Applied and Environmental Microbiology*, **58**, 2758–2763.

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, **115**, 445–459.

Koschorreck M, Conrad R (1993) Oxidation of atmospheric methane in soil: Measurements in the field, in soil cores and in soil samples. *Global Biogeochemical Cycles*, **7**, 109–121.

Mancinelli RL (1995) The regulation of methane oxidation in soil. *Annual Reviews of Microbiology*, **49**, 581–605.

Marion GM, Henry GHR, Freckman DW *et al.* (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20–32.

Moore T, Roulet N, Knowles R (1990) Spatial and temporal variations of methane flux from subarctic/northern boreal fens. *Global Biogeochemical Cycles*, **4**, 29–46.

Morrissey LA, Livingston GP (1992) Methane emissions from Alaska arctic tundra: An assessment of local spatial variability. *Journal of Geophysical Research*, **97**, 16,661–16, 670.

Priemé A, Christensen S, Galle B *et al*. (1996) Spatial variability of CH_4 uptake in Danish forest soil and its relation to different measurement techniques. *Atmospheric Environment*, **30**, 1375–1379.

Reeburgh WS, King JY, Regli SK *et al*. (1998) A CH_4 emission estimate for the Kuparuk River Basin, Alaska. *Journal of Geophysical Research*, **103**, 29,005–29,013.

Rustad LE, Fernandez IJ (1998) Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology*, **4**, 597–605.

Sebacher DI, Harriss RC, Bartlett KB *et al*. (1986) Atmospheric methane sources: Alaskan tundra bogs, an alpine fen, and a subarctic boreal marsh. *Tellus*, **38B**, 1–10.

Sommerfeld RA, Mosier AR, Musselman RC (1993) CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. *Nature*, **361**, 140–142.

StatSoft (1995) *STATISTICA*, **Vol. 1**. – *General Conventions and Statistics I*, 2nd edn. StatSoft, Tulsa.

Svensson BH, Rosswall T (1984) *In situ* methane production from acid peat in plant communities with different moisture regimes in a subarctic mire. *Oikos*, **43**, 341–350.

Torn MS, Chapin FS III (1993) Environmental and biotic controls over methane flux from Arctic tundra. *Chemosphere*, **26**, 357–368.

Torn MS, Harte J (1996) Methane consumption by montane soils: implications for positive and negative feedback with climatic change. *Biogeochemistry*, **32**, 53–67.

West AE, Schmidt SK (1998) Wetting stimulates atmospheric CH_4 oxidation by alpine soil. *FEMS Microbiology Ecology*, **25**, 349–353.

Whalen SC (2000) Influence of N and non-N salts on atmospheric methane oxidation by upland boreal forest and tundra soils. *Biology and Fertility of Soils*, **31**, 279–287.

Whalen SC, Reeburgh WS (1990) Consumption of atmospheric methane by tundra soils. *Nature*, **346**, 160–162.

Appendix A

Soil profile descriptions

Dovrefjell

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	Gravely 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	Gravely sand	5.09	1.14			5.99
	Spodic	11–21	7.5 YR 5/6	Gravely 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					