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Source: Arctic, Antarctic, and Alpine Research, 39(3) : 438-448

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

URL: https://doi.org/10.1657/1523-0430(06-020)[KOCH]2.0.CO;2

Arctic, Antarctic and Alpine Research, Vol. 39, No. 3, 2007, pp. 438–448

Seasonal and Diurnal Net Methane Emissions from Organic Soils of the Eastern Alps, Austria: Effects of Soil Temperature, Water Balance, and Plant Biomass

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Abstract

Although the contribution of methane emission to global change is well recognized, analyses of net methane emissions derived from alpine regions are rare. Therefore, three fen sites differing in water balance and plant community, as well as one dry meadow site, were used to study the importance of soil temperature, water table, and plant biomass as controlling factors for net methane emission in the Eastern Alps, Europe, during a period of 24 months. Average methane emissions during snow-free periods in the fen ranged between 19 and 116 mg CH_4 m^{-2} d^{-1}. Mean wintertime emissions were much lower and accounted for 18 to 59% of annual flux. The alpine dry meadow functions as a methane sink during snow-free periods, with mean flux of -2.1 mg CH_4 m^{-2} d^{-1} (2003) and -1.0 mg CH_4 m^{-2} d^{-1} (2004). Seasonal methane emissions of the fen were related to soil temperature and groundwater table. During the snow-free periods the water table was the main control for seasonal methane emission. The net methane flux related to water table was much higher for the distinctly drier year 2003 than for the wetter year 2004. Methane emissions differed diurnally at sites where the water table position was high or very low. The influence of total above-ground plant biomass on methane emission was apparent only for those sites with high water table positions. Seasonal and diurnal methane uptake of the dry meadow was related to soil temperature and water-filled pore space, whereas plant biomass did not significantly influence methane fluxes. Our studies gave evidence that fens in the Eastern Alps act as a source of methane throughout the whole year and that a dry meadow site acts as a net methane sink during snow-free periods.

DOI: 10.1657/1523-0430(06-020)[KOCH]2.0.CO;2

Introduction

Methane is an important greenhouse gas and the atmospheric concentration has increased (0.8% y^{-1}) during the past few decades more than CO_2 (0.5% y^{-1}) (Mosier et al., 1998). Methane emission from wetlands accounts for roughly 70% of natural CH_4 sources (Khalil, 2000). Recent studies of methane sources have focused on high-latitude wetlands because they store about 30% of the global carbon pool in the soil (Gorham, 1991). Methane emissions from alpine tundra regions are often compared with northern tundra ecosystems. Our knowledge of net CH_4 emissions from alpine environments, however, is only limited to North America (Chimner and Cooper, 2003; Mast et al., 1998; West et al., 1999; Wickland et al., 2001) and to recent investigations in the Tibetan Plateau (Hirota et al., 2004). Model estimations from ecosystems across the entire pan-arctic region (area north of 45°N) revealed a net methane flux of 51.0 Tg CH_4 y^{-1}, including a small net gain for Austria of 0 to -1 g CH_4 m^{-2} y^{-1} (Zhuang et al., 2004). A wide range of mean daily net methane fluxes from various alpine dry or wet tundra (-0.77 mg CH_4 m^{-2} d^{-1} to 8.45 mg CH_4 m^{-2} d^{-1}) and alpine wetlands (33 CH_4 m^{-2} d^{-1} to 251 CH_4 m^{-2} d^{-1}) have been reported. However, there are no available data for net methane flux from alpine environments of the European Alps. Since alpine tundra covers an area of roughly 10.5 million km^2 globally (Archibold, 1995) and the variability of net methane fluxes from alpine ecosystems is high, more precise investigations are necessary to estimate the role of alpine environments for the global CH_4 budget.

In general, methane flux rates from wetlands are the net result of CH_4 production (anaerobic), CH_4 oxidation (aerobic), and CH_4 transport from below-ground to the atmosphere (Bubier and Moore, 1994; Conrad, 1996). The main controls for various methane-emitting environments are water table, temperature (Bubier et al., 2005; Rask et al., 2002), but also peat chemistry (Yavitt et al., 2005). In addition, plant community and plant biomass have been found to influence net methane emissions considerably (Bellisario et al., 1999; Schimel, 1995).

Methane is released from soils either from ebullition of biogenic gas bubbles, diffusion, or plant-mediated transport (e.g. Bubier and Moore, 1994). The diffusion of methane is only important for aerated soil pores because diffusion in air is 10^4 times higher than in water (Schachtschabel et al., 1998). The role of plant communities may be important, since diffusion of methane via plants may account for 37 to 100% of total net methane flux in various moist tundra regions and wetlands (Schimel, 1995; Kelker and Chanton, 1997; Hirota et al., 2004). Diurnal variations of net methane emission have been investigated for various methane-emitting environments (Mikkelä et al., 1995; Thomas et al., 1998). Diurnal emission patterns have been related to radiation, plant biomass, soil temperature or redox potential. So far, only a few plant species or plant communities have been investigated. Hence, the overall daily variation of methane emission remains poorly understood, but it often differs considerably between vegetation types and depends on total plant biomass and soil water conditions.

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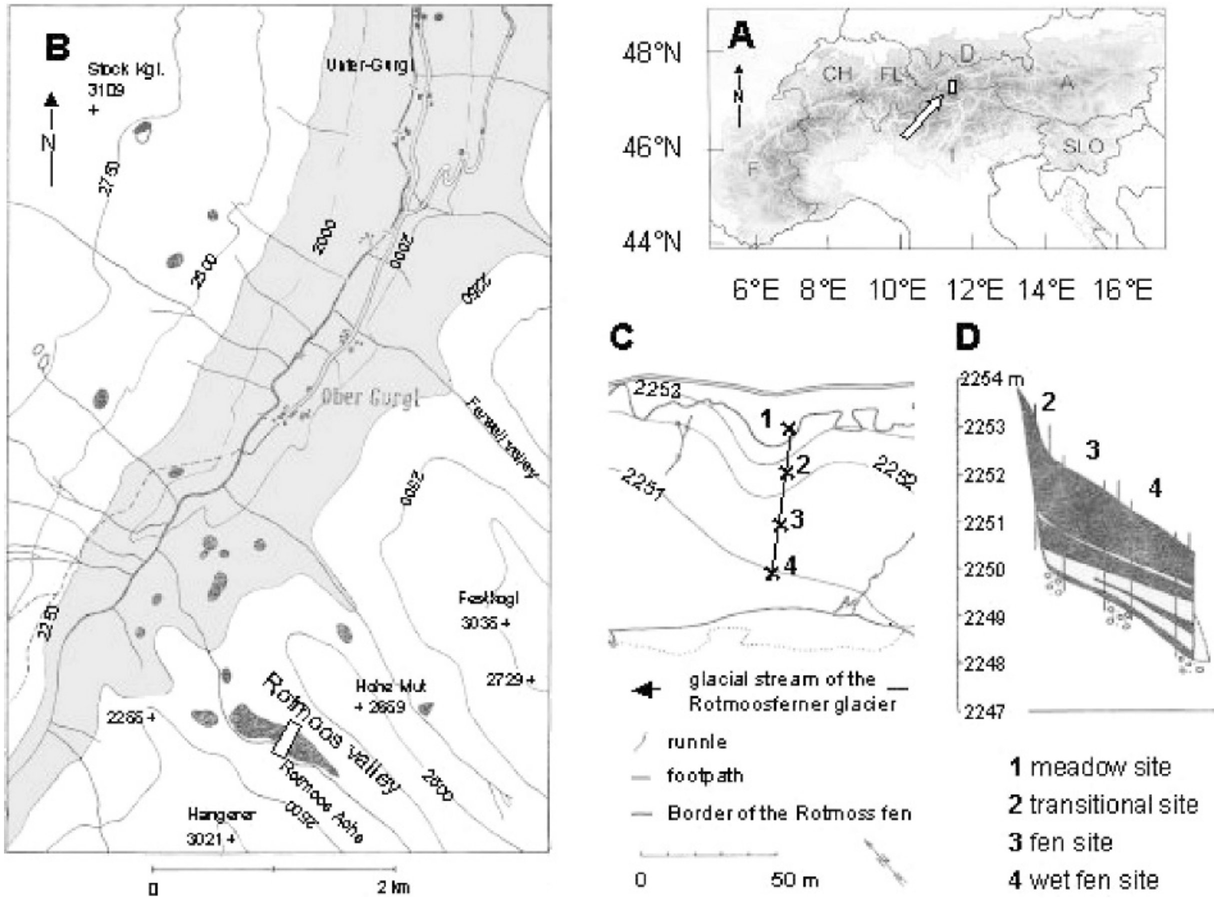

FIGURE 1. (A) Geographical position of the study area in the European Alps (A = Austria, CH = Switzerland, D = Germany, F = France, I = Italy, SLO = Slovenia). (B) Distribution of alpine fens in the study area (black locations); the gray area in the map represents the potential tree area below 2250 m a. s. l. (C) Position of the study sites outside and within the Rotmoos fen. (D) Peat profile of the Rotmoos fen (only major sediment layers are illustrated) (Figs. 1B–1D modified from Rybníček and Rybníčková, 1977).

In well-drained soils, methanotrophs can utilize atmospheric CH_4 (1.7 ppmv) for biomass production. These adapted "high affinity" methanotrophs are related, but not identical, to type II methanotrophs and are different from those ("low affinity" methanotrophs) of wetlands (Conrad, 1996). Hence, unsaturated soils represent the only biological net sink for atmospheric methane, in contrast to wetlands (Conrad, 1996). Alpine tundra ecosystems have been found to act as net sinks and sources for atmospheric methane depending on the moisture conditions and soil temperature (Mast et al., 1998; Wickland et al., 1999; West et al., 1999).

The objectives of this study were to (1) quantify the seasonal variation of net methane emission and (2) determine key factors controlling the diurnal and seasonal patterns of net methane emission derived from soils of the alpine zone in the European Alps. Four study sites (dry meadow and three sites in a fen) differing in vegetation type and water balance were selected and monitored over a period of two years.

Material and Methods

STUDY AREA

This research was conducted in the Ötztal range (46°50′N, 11°03′E) in Tyrol, Austria, at an altitude of 2250 m a.s.l. The research area lies in the Rotmoos valley above the present treeline (Fig. 1B). The valley is flanked by the mountain Hohe Mut (2659 m a.s.l.) and the mountain Hangerer (3021 m a.s.l.) and is exposed south to northwest. According to Hoinkes and Thöni (1993), the principal basic material consists mainly of mica slate and silicate. The climate has a continental character with cool summers and cold, snowy winters. The snow-free period is about 4.5 months (June to mid-October) (M. Strobel, personal communication) with a mean annual precipitation of 820 mm (1970–1996). The mean annual air temperature for 1997–1998 was −1.3 °C (Kaufmann, 2001). The study sites are located in the Rotmoos fen (Fig. 1C). The Rotmoos measures 8.5 ha, with an average peat depth of 1.5 m (range 0.5–2.9 m) (Rybníček and Rybníčková, 1977) (Fig. 1D). It is fed mainly by the water flowing down the hill slopes of the flanking mountains. The peat water drains into the glacial stream of the Rotmoosferner glacier. The oldest organic layer at the bottom of the peat is around 5200 years old (Bortenschlager, 1970). During peat formation the Rotmoos was periodically overwhelmed with 15 layers (1–27 cm) of silt or sand sediments (or both). The deepest and oldest layer is eolian while the others were glacial or colluvial (Rybníček and Rybníčková, 1977). Nearly all sediment layers are located 2 m below the peat surface.

STUDY SITES

Four study sites were chosen (alpine dry meadow and three sites in the Rotmoos fen). They differ in water balance and vegetation community. All sites have a southwest exposure and

1–4° slope. The study sites are traditionally used as a pasture for sheep and horses. At the dry meadow site, these domestic animals were more frequent compared to the fen sites. The first site is an alpine meadow (meadow), which was classified as a *Curvulo-Nardetum* (G.-H. Zeltner, personal communication) and is relative rich in herbs. The soil (maximum depth 50 cm) is a Cambisol out of loamy sand over scree. The meadow is well-drained over the snow-free period, and 90% (10% small boulders) of the soil surface is covered by vegetation. The herbs here are *Alchemilla vulgaris* L., *Anthoxanthum odoratum* L., *Anthyllis vulneraria* L., *Campanula cochlearifolia* Lamk., *Campanula scheuchzeri* Vill., *Dianthus carthusianorum* L., *Euphrasia alpina* Lamk., *Euphrasia minima* Jacq. Ex. DC., *Gentiana ramosa* L., *Geum montanum* L., *Hippocrepis comosa* L., *Leonthodon helveticus* Mérat, *Ligusticum mutellina* (L.) Crantz, *Phyteuma hemisphaericum* L., *Potentilla aurea* L., *Rhinantus angustifolius* C.C. Gmelin, and *Silene vulgaris* (Moench.) Garcke. Grass species are *Carex curvula* All., *Carex flava* L., *Carex sempervirens* Vill., *Deschampsia cespitosa* (L.) P.B., *Luzula campestris* (L.) DC., *Nardus stricta* L., and *Poa alpina* L. The shrubs are *Calluna vulgaris* (L.) Hull, *Salix herbacea* L., *Rhododendron ferrugineum* L., and *Vaccinium myrtillus* L. The surface cover of each species was less than 5%, except for *Nardus stricta* (10%).

The second study site (transitional site) is located in the transition area between the alpine meadow and the Rotmoos fen. The vegetation is described as a *Carici echinatae–Trichophoretum caespitosi* community (Rybníček and Rybníčková, 1977). Additionally, a relative high cover of plant species belonging to *Curvulo-Nardetum* was observed. The surface of the transitional site is completely covered by vegetation, with the dominant species (and their cover) being: herbs: *Bartsia alpina* L. (<5%), *Homogyne alpina* (L.) Cass. (<5%), *Leonthodon hispidus* L. (<5%), *Ligusticum mutellina* (5%), *Potentilla aurea* (10%); grass species: *Carex echinata* Murray (5%), *Eriophorum angustifolium* Honck. (20%), *Nardus stricta* (20%), *Trichophorum caespitosum* (L.) Hartman (30%); and shrubs: *Calluna vulgaris* (<5%). The third site (fen) is located in the Rotmoos fen and is characterized by a typical *Carici echinatae–Trichophoretum caespitosi* plant community. The fen site has a lower species richness than the transitional site. Dominant species and their cover (in parentheses) are *Carex echinata* (5%), *Carex nigra* (L.) Reichard (<5%), *Eriophorum angustifolium* (40%), and *Trichophorum caespitosum* (60%). The fourth study site (wet fen) is located in the center of the fen and consists solely of *Carex nigra*, which covers 30% of the soil. This site can be temporarily flooded by groundwater. All soils of the Rotmoos fen (transitional, fen, and wet fen) were classified as Rheic Histosols, with observed soil depths deeper than one meter (Fig. 1D).

METHANE MEASUREMENTS

The CH_4 flux rates were measured using the static closed chamber method. During the snow-free period we used chambers consisting of a quadratic frame (40 cm × 40 cm × 30 cm) and a lid with an inserted septum. The chambers were equipped with a small battery-driven fan that allowed circulation of the enclosed air. The material was acrylic glass, highly porous for photosynthetic active radiation (89%). Three chambers per site were carefully inserted 3 cm into the soil at least 15 h before each measurement started. Because of moderate grazing (sheep and horses) the frames had to be removed between the sampling days, but the exact location of each chamber was discernible throughout the snow-free periods. On each site, one chamber was provided with a common resistance thermometer 5 cm above ground level for estimating the temperature difference inside and outside the chamber. Three stainless steel pots (diameter 15.5 cm; 25.0 cm height) per site were used for gas measurements during the snow periods. After the snow was removed from an area of about 2 m × 2 m at each study site, the steel pots were placed gently on the soil surface and sealed with wet snow. After the gas sampling, the area was covered with snow again. Gas samples were collected using evacuated flasks (22.5 mL) with butyl-rubber septum. Prior to sampling, the flasks were evacuated five times and flushed with nitrogen in the laboratory. Gas samples were collected approximately every 3 weeks within the snow-free season in 2003 (n = 7) and once a month during the snow-free season in 2004 (n = 4). One tip of a double needle was inserted through the septum of the chamber lid and the other tip of the needle was inserted through a butyl-rubber septum of an evacuated flask. One sample drawing consists of four gas sub-samples, which were drawn at 0, 6, 20, and 30 min after the chamber was closed. During the snow-free period, gas samples were taken every 3 h to account for diurnal changes, yielding eight independent samples per day. The sampling procedures (n = 10 for each site) always started at noon and ended at 9:00 the following day. During the snow periods, one sample drawing (time intervals 0, 30, 60, and 90 min) at about noon was done in intervals of 1 to 3 months (n = 11 for each site).

Methane concentrations were measured using a flame ionization detector in a Perkin Elmer (PE Auto system and PE Headspace Sampler HS 40XL) gas chromatograph. Chromatographic separations were made using a 6 ft (1.8 m) stainless steel column packed with Poropak Q (100/120 mesh). The oven of the column and the detector was maintained at 40 °C (oven temperature) and the detector was operated at 350 °C. The oven had to be heated to 120 °C for 10 min after each gas sample to prevent water accumulation in the column. Nitrogen was used as carrier gas, with a gas flow rate of 45 mL min^{-1}. Gas standards (1.0, 5.0, and 10.0 ppm CH_4) were used for calibration. All single values were corrected for air temperature and air pressure using the ideal gas law. This procedure allowed an analytical precision of 40 nL L^{-1}.

The flux rates were calculated from the linear slope of the increase (or decrease) of the methane concentration versus the accumulation time in the chamber. Non-significant regressions were rejected. This occurred in 4% of the cases (almost exclusively during winter sampling) and was probably due to sporadic events like ebullition.

HYDROLOGY

Groundwater tables were measured at every fen site (transitional, fen, wet fen) with horizontally slotted (width 0.3 mm) PVC wells (total length 100 cm). One tube was installed on each fen site with a standard bucket auger. The space between the tubes and the peat soil was filled with silica sand (grain size 1.2–1.7 mm) to avoid accumulation of mud. The top was sealed with a PVC cap to prevent the direct contact of the groundwater with precipitation. Water tables were determined at every gas sampling date (n = 22). Soil moisture on the alpine meadow site was measured hourly with a soil moisture sensor SMS3 (Cylobios, Austria) at 5 cm below the soil surface. For calibrating the soil moisture sensor, three undisturbed soil cores (100 cm^3) were taken from 0–5 cm soil depth at every sampling date during the snow-free periods. The volumetric water content (θ) was determined gravimetrically after drying at 105 °C for 48 h. For the conversion of the volumetric water content to water-filled pore space (wfps), the maximum saturation water content (g cm^{-3}) for the soil depth was determined in the laboratory. Briefly, undisturbed soil cores (100 cm^3; n = 5) were slowly saturated with degassed water over a

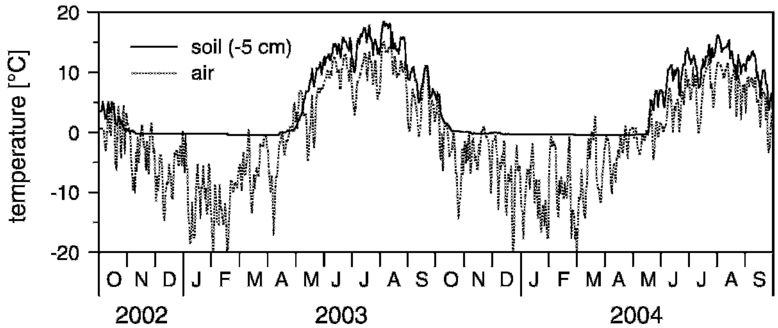

FIGURE 2. Time course of air temperature and soil temperature (5 cm depth) at the transitional site.

4-day period and weighed before and after drying at 105 °C for 48 h. A density for water of 1 g cm^{-3} was assumed and wfps (%) was calculated by the proportion of water content to the maximum saturation water content. Moisture data for the winter period were not used because values were not reliable due to frozen water.

Groundwater samples for chemical analysis and for the determination of dissolved methane were taken from the PVC tubes at 20 cm below the water table. One sample per site was taken at each sampling date. Before sampling, the water in the tubes was pumped out and the soil solution that drained into the tubes was sampled after reaching the prior water level. Groundwater samples were collected with a syringe to determine dissolved methane. Evacuated flasks (22.5 mL) were immediately filled one-third and the remaining vacuum was balanced later with pure N_2 in the laboratory. The methane concentration in the headspace was measured by the same GC procedure as described above and was related to the sampled water. The amount of water and the corresponding headspace volume was determined gravimetrically. Dissolved methane concentrations were corrected by the Bunsen solubility coefficient for methane. All water samples for chemical analysis were filtered (PET 45/25; Macherey-Nagel, Düren, Germany) and kept frozen until analysis. DOC was determined with a DIMA-TOC 100 (Dimatec, Essen, Germany), and ammonium and nitrate were photometrically determined. The pH was measured potentiometrically.

PLANT BIOMASS

Above-ground plant biomass was determined for every sampling date during the snow-free periods in 2003 and 2004. The plant biomass was calculated from 25 cm × 25 cm soil surface areas. Five replicates for each site were collected (randomly positioned on the soil surface). After sampling, the plant material was stored in plastic bags and frozen at −20 °C until analysis. The live (green) and dead biomass was separated and oven dried at 60 °C for 72 h before weighing. Only the live above-ground standing biomass was considered for above-ground biomass.

CLIMATE DATA

The climate data used in this study were provided by R. Kaufmann (personal communication). The weather station (2270 m a.s.l.) is located 2 km away from the study sites, with an altitude difference of about 20 m. Air temperature, global radiation, precipitation, and relative humidity were recorded every 15 min. The soil temperature at every study site was recorded hourly at 5 cm below the soil surface using temperature loggers (UTL-1, Geotest AG, Switzerland). Since June 2003, temperature was additionally recorded at 15 cm, as well as at 35 cm below the soil surface at all fen sites (transitional, fen, wet fen).

STATISTICS

In the snow-free periods, the net methane flux values per day (mg CH_4 m^{-2} d^{-1}) were obtained by summarizing the diurnal measurements (mg CH_4 m^{-2} h^{-1}) of one day ($n = 8$ per day). For the snow periods, the single measurement per day was assumed to be constant during the day. The cumulative annual flux was roughly estimated by linear interpolation between the sampling dates during the snow-free season and the mean flux during the snow periods (which was not statistically different between sampling dates). The length of the snow-free periods was defined as the time-frame between an abrupt increase and decrease of soil temperature (5 cm soil depth). Water tables were linearly interpolated. All given errors are standard errors.

The methane flux values were logarithmically transformed to obtain homogeneity of variance (Levene' test). Differences in the methane flux of the dry meadow (meadow) between the sampling dates were tested by univariate analysis of variance. For the fen sites (transitional, fen, wet fen), a simple two-factorial analysis of variance (time and site) was applied to quantify variations in methane emissions according to sampling time and study site. The ANOVA was calculated separately for each snow and snow-free period. Additionally, the effect of season and study site on the plant biomass was quantified using simple two-factorial analysis of variance (time and site). Stepwise multiple linear regression analyses were applied to evaluate the relationship between methane flux rates and environmental properties. The data of the seasonal and diurnal measurements were separated. The water table (transitional, fen, wet fen), water-filled pore space (meadow), soil temperature (5 cm soil depth), and dissolved methane concentration in the groundwater were used in the regression model to explain seasonal net methane flux. For the diurnal net methane flux, water table (transitional, fen, wet fen), water-filled pore space (meadow), soil temperature (5, 15, 35 cm soil depth), global radiation, and plant biomass were included in the model. Partial correlation analysis was applied to measure the contribution of each environmental factor to the variation of methane emission, while holding the other remaining factors in the regression equation constant. All calculations were carried out using Statistica 6.0 (StatSoft. Inc., Tulsa, Oklahoma, U.S.A.).

Results

CLIMATIC PROPERTIES

The annual mean air temperature was −0.4 °C (2003) and −1.3 °C (2004). The mean annual soil temperature (5 cm) ranged between 3.5 °C (wet fen, 2004) and 4.6 °C (wet fen, 2003) (Fig. 2). The average snow-free period was 149 days (May 9 to October 5) and 123 days (May 27 to October 4) for 2003 and 2004, respectively. Temperature and precipitation differed considerably for both snow-free periods. The mean air temperature was 8.9 °C

TABLE 1

Mean values and interpolated values (interpol.) of water table (wt[a]) (cm) at the transitional site (trans), the fen site (fen), and the wet fen site (wet fen). Water-filled pore space (wfps[b]) (5 cm soil depth) at the alpine meadow site (meadow). The range of live above-ground standing biomass (pla. bio.) for the entire study period and the snow-free periods 2003 and 2004.

	Hydrology and plant biomass										
	Entire study period (731 days)			Snow-free period 2003 (149 days)				Snow-free period 2004 (123 days)			
	trans[a]	fen[a]	wet fen[a]	trans[a]	fen[a]	wet fen[a]	meadow[b]	trans[a]	fen[a]	wet fen[a]	meadow[b]
wt[a], wfps[b]											
mean	−34	−12	−2	−53	−33	−19	47	−27	−8	−1	66
interpol.	−32	−9	+1	−51	−31	−16		−19	−5	+3	
pla. bio. (g m^{-2})											
min				81	33	19	54	65	7	4	96
max				239	204	64	242	290	222	71	237

(2003) and 6.4 °C (2004). Precipitation during snow-free period was 276 mm (2003) and 326 mm (2004). In contrast, the mean global radiation was more balanced, being 218 W m^{-2} and 207 W m^{-2} for 2003 and 2004, respectively. The mean soil temperature ranged from 10.4 °C (wet fen; −35 cm) to 13.0 °C (transitional; −5 cm) and 8.4 °C (wet fen; −35 cm) to 10.9 °C (transitional; −5 cm) for the snow-free periods of 2003 and 2004, respectively. Soil temperature showed large diurnal differences during the snow-free periods. The maximum temperature in 5 cm soil depth occurred at about 14:00–15:00 (Central European Time) and minimum temperature at about 5:00–6:00. The maximum and minimum temperatures in 15 cm soil depth were roughly four to six hours later than at 5 cm, and the amplitudes between diurnal minimum and maximum temperature were much more dampened with increasing soil depth. During the snow periods, mean soil temperature was almost constant and ranged between 0.1 °C (meadow, fen, wet fen) and 0.2 °C (transitional) (Fig. 2). Due to the insulation of the deep snow cover (maximum 235 cm), the absolute minimum soil temperature (hourly recordings) reached −0.5 °C in the topsoil. Neither diurnal differences nor differences between study sites were observed during snow periods.

HYDROLOGY

The interpolated average water table position for the entire study period increased in the order transitional (−32 cm) > fen (−9 cm) > wet fen (+1 cm) (Table 1). The water table position for all fen sites remained almost constant during the winter (Fig. 3A). During the snow-free periods, the water tables of all fen sites decreased, reaching minimum values in August and then increasing again and remaining constant for the following winter period. The decline was much more pronounced during the snow-free period of 2003 than for 2004. At the alpine meadow site, the mean water-filled pore space (wfps) was much lower in 2003 (47%) than in 2004 (66%) throughout the snow-free season (Table 1). Four distinctive desiccation periods were observed in 2003, whereas wfps was much more balanced in 2004 (Fig. 3B).

GROUNDWATER CHEMISTRY OF THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

The dissolved methane concentration in the groundwater was much higher during snow-free periods than in the winter (Fig. 4). The increase of methane concentration at the onset of both snow-free periods was more delayed for the transitional site than for the fen site and the wet fen site. The ranges of dissolved methane for the entire study period were 1.6 to 1295.2 µg CH_4 L^{-1} (transitional), 4.9 to 1325.2 µg CH_4 L^{-1} (fen), and 4.3 to 1395.1 µg CH_4 L^{-1} (wet fen). The ammonium concentration ranged from 0 to 1.3 mg L^{-1}, DOC from 7.8 to 34.8 mg C L^{-1}, and pH from 4.3 to 6.1 for all fen sites. Nitrate was not detectable (detection limit <0.2 mg L^{-1}) at any site. Except for the dissolved methane concentration, no clear effect of site or sampling date was found for any dissolved component.

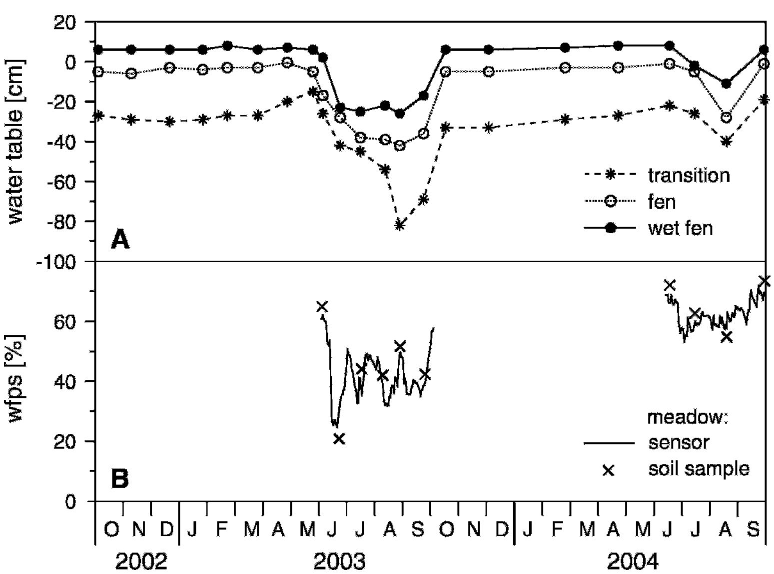

FIGURE 3. Time course of water table at the transitional, fen, and wet fen sites (A) and water-filled pore space (wfps) at the meadow site during the snow-free periods (B).

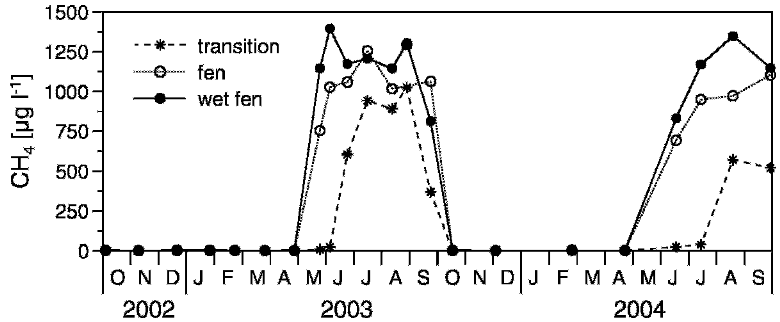

FIGURE 4. Time course of dissolved methane concentrations in groundwater (to maximum 1 m soil depth) at the transitional, fen, and wet fen sites.

PLANT BIOMASS

The total above-ground plant biomass was determined for the snow-free periods. Peak biomass was reached during 2003 in mid-July on the meadow site, the transitional site, and the fen site and in late August on the wet fen site. The snow-free period in 2004 started about three weeks later and maximum biomass was reached in August at all study sites. Plant biomass at the wet fen site was much lower than at the other sites (Table 1). Significant differences for sampling date and study site for both snow-free periods were found (2003: $F_{(site)} = 83.55$, $P < 0.001$; $F_{(sampling\ date)} = 49.25$, $P < 0.001$; $F_{(site\ x\ sampling\ date)} = 34.9$, $P < 0.001$; and 2004: $F_{(site)} = 74.55$, $P < 0.001$; $F_{(sampling\ date)} = 34.05$, $P < 0.001$; $F_{(site\ x\ sampling\ date)} = 8.9$, $P < 0.001$).

SEASONAL METHANE FLUX OF THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

Seasonal methane emission was higher and more variable during the snow-free periods than during winter (Fig. 5A). For the snow periods the net methane flux was two orders of magnitude lower than during the snow-free periods. In winter, the mean methane emission was 14 ± 11 mg CH_4 m^{-2} d^{-1} for the transitional site, 15 ± 11 mg CH_4 m^{-2} d^{-1} for the fen site, and 13 ± 11 mg CH_4 m^{-2} d^{-1} for the wet fen site. No significant differences between study sites and sampling dates were found [$F_{(site)} = 0.42$, $P = 0.659$; $F_{(sampling\ date)} = 0.45$, $P = 0.897$; $F_{(site\ x\ sampling\ date)} = 0.39$, $P = 0.984$]. In the snow-free periods, the transitional site had the lowest emission rate, followed by the fen and wet fen site (Table 2, Fig. 5A). Significant differences between sampling dates and study sites were found for the snow-free period of 2003 [$F_{(site)} = 130.02$, $P < 0.001$; $F_{(sampling\ date)} = 18.61$, $P < 0.001$; $F_{(site\ x\ sampling\ date)} = 10.05$, $P < 0.001$], whereas only significant differences between study sites were detected in 2004 [$F_{(site)} = 8.24$, $P = 0.002$; $F_{(sampling\ date)} = 0.39$, $P = 0.765$; $F_{(site\ x\ sampling\ date)} = 0.05$, $P = 0.999$]. The cumulative annual methane flux for 2003 at the transitional site was 7 g CH_4 m^{-2} y^{-1} (snow period 47%), followed by 14 g CH_4 m^{-2} y^{-1} (snow period 31%) for the fen site, and 15 g CH_4 m^{-2} y^{-1} (snow period 27%) for the wet fen site. For 2004 the cumulative annual methane emission was 6 g CH_4 m^{-2} y^{-1} (snow period 59%) for the transitional site, 13 g CH_4 m^{-2} y^{-1} (snow period 29%) for the fen site, and 17 g CH_4 m^{-2} y^{-1} (snow period 18%) for the wet fen site.

SEASONAL METHANE FLUX OF THE DRY ALPINE MEADOW (MEADOW)

The alpine meadow was a net sink for atmospheric methane during the snow-free periods, whereas no detectable methane emission or consumption was found for the snow periods (Fig. 5B). The net methane consumption during the two snow-free periods differed considerably, being higher in 2003 than in 2004 (Table 2). The net methane flux differed significantly between sampling dates in 2003 ($F = 6.28$; $P = 0.004$), but not in 2004 ($F = 1.24$, $P = 0.38$).

CONTROLS OF SEASONAL METHANE EMISSION OF THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

Multiple linear regression analysis identified water table and soil temperature as major controls of methane emission in alpine

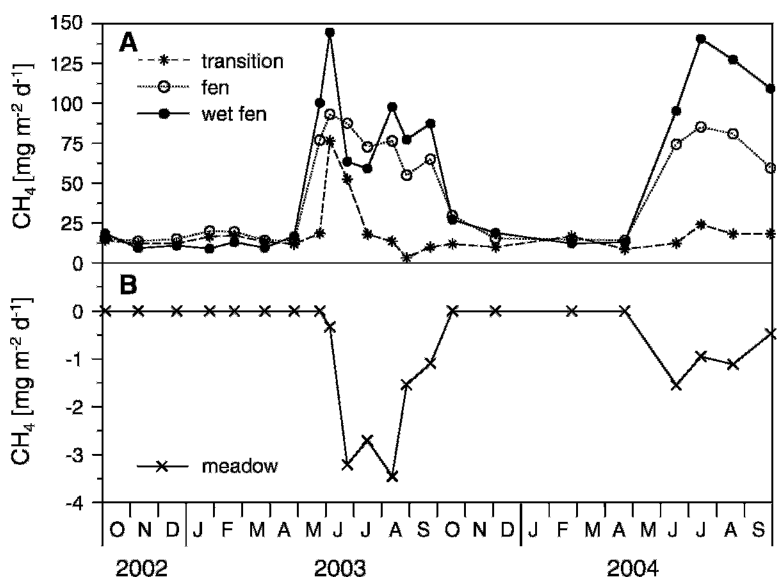

FIGURE 5. Time course of net methane emissions at the transitional, fen, and wet fen sites (A) and the meadow site (B).

TABLE 2

Mean net CH_4 flux and standard error (SE), mean of interpolated values (interpol.), and cumulative CH_4 flux (cum. flux) of the entire study period and the snow-free periods 2003 and 2004.

	Seasonal net CH_4 flux										
	Entire study period (731 days)			Snow-free period 2003 (149 days)				Snow-free period 2004 (123 days)			
	trans	fen	wet fen	trans	fen	wet fen	meadow	trans	fen	wet fen	meadow
net CH_4 flux (mg m^{-2} d^{-1})											
mean	19	46	57	28	76	89	−2.1	19	83	116	−1.0
SE	5	13	10	4	18	18	0.5	2	18	20	0.2
interpol.	17	36	43	24	67	78	−1.9	19	71	112	−0.8
cum. flux (g m^{-2})											
	12	26	32	4	10	11	−0.3	2	9	14	−0.1

fen sites (Table 3B). The derived models explained 38% (transitional) to 76% (wet fen) of the seasonal variance. Seasonal methane emissions during the entire study period tended to be positively related to soil temperature and water table (Table 3A). The dissolved methane concentration had no influence on methane emission at any study site.

For the snow-free periods, the water table was the most important environmental control for within- and among-site variability of the seasonal net methane emission (Fig. 6). However, this relationship differed considerably, being much higher for the dryer snow-free period of 2003 than for 2004.

CONTROLS OF SEASONAL METHANE EMISSION AT THE ALPINE DRY MEADOW (MEADOW)

Partial regression analysis showed that seasonal net methane emissions were positively related to wfps and negatively related to soil temperature (Table 3A). The derived multiple regression model explained 74% of the seasonal variance (Table 3B). Nonetheless, the partial correlation coefficients were not significant for both variables.

DIURNAL METHANE EMISSION OF THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

Diurnal changes in methane flux tended to be highest if the water table position was very high or very low. No clear changes were found at intermediate water table positions. For water-saturated conditions, methane flux was highest in the afternoon, whereas at low groundwater level the methane flux was highest at night (Fig. 7). The biggest difference between daily maximum and minimum methane emissions was found at water-saturated conditions at the wet fen site, with methane emissions twice as high in the afternoon as at night. For all study sites the average difference between the diurnal maximum and minimum methane flux was 155%.

The water table was the most powerful control of diurnal methane flux, followed by soil temperature (Table 4A). At the transitional site, methane emission was positively correlated with the temperature in 35 cm soil depth, whereas at the fen site and the wet fen site the influence of temperature was most significant in 15 cm soil depth. The above-ground plant biomass positively influenced the fen site and the wet fen, but not the transitional site. Global radiation was not important for any study site. The empirical linear multiple regression model explained 61% (fen site) to 69% (transitional site) of the variance (Table 4B).

DIURNAL METHANE EMISSION OF THE DRY MEADOW (MEADOW)

Net methane emission at the alpine meadow site showed no distinct diurnal pattern (data not shown). Multiple linear regression analysis identified temperature at 15 cm soil depth and wfps to be most important, explaining 52% of the methane uptake at the meadow site (Tables 4A and 4B). The influence of soil temperature at 5 cm depth, global radiation, and plant biomass was weak.

TABLE 3

Partial regression coefficients (A) and multiple linear models (B) for daily net methane emission of the entire study period [n = 22 for the transitional site (trans), the fen site (fen), and the wet fen site (wet fen); n = 10 for the alpine meadow site (meadow)]. Dependent variable: ln transformed methane flux (mg CH_4 m^{-2} h^{-1}) (ln flux) for trans, fen and wet fen and methane uptake (mg CH_4 m^{-2} h^{-1}) (flux) for meadow. Independent variables: water table (wt^a) (cm) and ln-transformed dissolved methane concentration (µg CH_4 L^{-1}) (CH_{4aq}), water-filled pore space ($wfps^b$) (%), and soil temperature (°C) at 5 cm soil depth (st_5). Level of significance: $P \leq 0.05$ (*$P < 0.001$, **$P < 0.01$, *$P < 0.05$).**

	Partial regression coefficients (R) of the daily net methane flux				
A	trans[a]	fen[a]	wet fen[a]	trans[a], fen[a], wet fen[a]	meadow[b]
wt[a] wfps[b]	0.59**	0.37	0.33	0.54*	0.57
st_5	0.52*	0.61**	0.53*	0.50*	−0.58
CH_{4aq}	−0.19	−0.17	0.20	−0.10	

B	Multiple linear models of the daily net methane flux	
trans:	ln flux = 0.023 wt + 0.048 st_5 + 3.209	R = 0.61*
fen:	ln flux = 0.007 wt + 0.117 st_5 + 2.912	R = 0.87***
wet fen:	ln flux = 0.008 wt + 0.091 st_5 + 1.952	R = 0.82***
trans, fen, wet fen:	ln flux = 0.022 wt + 0.107 st_5 + 2.624	R = 0.74**
meadow:	flux = 0.038 wfps − 0.167 st_5 − 1.658	R = 0.86**

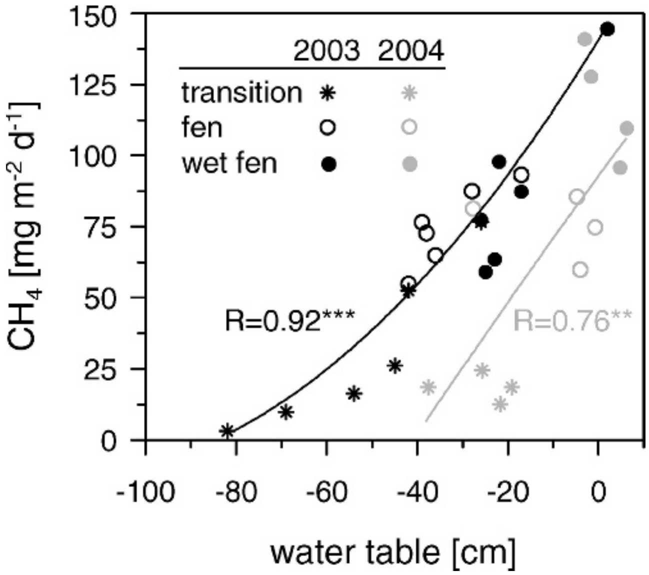

FIGURE 6. Relation between water table and daily net methane flux at the transitional, fen, and wet fen sites for the snow-free period of 2003 (n = 18) and 2004 (n = 12). Second polynomial function was used for both regressions (*$P \leq 0.5$, **$P < 0.01$ ***$P < 0.001$).

Discussion

ENVIRONMENTAL CONTROLS OF SEASONAL METHANE EMISSION AT THE FEN SITES (TRANSITIONAL; FEN; WET FEN)

Seasonal methane flux was positively related to soil temperature and water table position. Several studies confirm the importance of water table and soil temperature. However, the influence for environmental properties can change seasonally or between study years (Bubier et al., 2005; Shannon and White, 1994). Q_{10} values derived from the multiple linear regression models in this study were 1.6 (transitional), 3.1 (fen), and 2.6 (wet fen), or 2.9 if all plots were pooled. These values fit to the lower range (1.6 to 11) of *in situ* data calculated by simple Arrhenius equations from various water-saturated environments (Chapman and Thurlow, 1996). The water table was the main driver for net methane emissions during snow-free periods. The water table fluctuation during 2003 was much more pronounced than during 2004 and resulted in much higher net CH_4 emission related to the water table depth in 2003. Net methane flux was even observed at a water table position of −82 cm at the transitional site. Chimner and Cooper (2003) found a similar pattern on a drained alpine fen exposed to a large water table drop. A mean annual water table position of about −15 cm as a critical threshold factor for zero net flux was found for temperate soils (Fiedler and Sommer, 2000) and for several boreal ecosystems (Rask et al., 2002). However, the history of water table fluctuations may be crucial, leading to long- and short-term effects for the microbial community composition and function (Moore and Dalva 1993; Shannon and White, 1994). During a three-year study, Shannon and White (1994) found long-term effects after a desiccation period during the summer: methane flux was influenced even for the subsequent snow-free period. Large fluctuations in the water table may cause long-term effects by disturbing the location of an effective methanotroph population. This is because the highest methanotrophic activity in wetland soils is often found around the mean standing water table (Conrad, 1996). In contrast, the spatial distribution of strictly anaerobic methanogens may be limited to deeper soil layers (Chimner and Cooper, 2003). Besides the altering of the microbial community, temporarily aerated soils may also favor the formation of alternative electron acceptors (sulfate, nitrate, ferric iron), which play a greater role in overall anaerobic respiration than methanogenesis (Moore and Dalva, 1993; Conrad, 1996). On the other hand, the water table may also imply short-term effects for flooded soils. Enhanced methane flux from a Canadian wetland ecosystem could be observed after the water table dropped below the soil surface, probably due to the reduced resistance of methane transfer in air (Bellisario et al., 1999). Furthermore, a dropping water table from submerged soils uncovers plant parts responsible for plant-mediated CH_4 emissions (Kelker and Chanton, 1997). In our study, methane fluxes

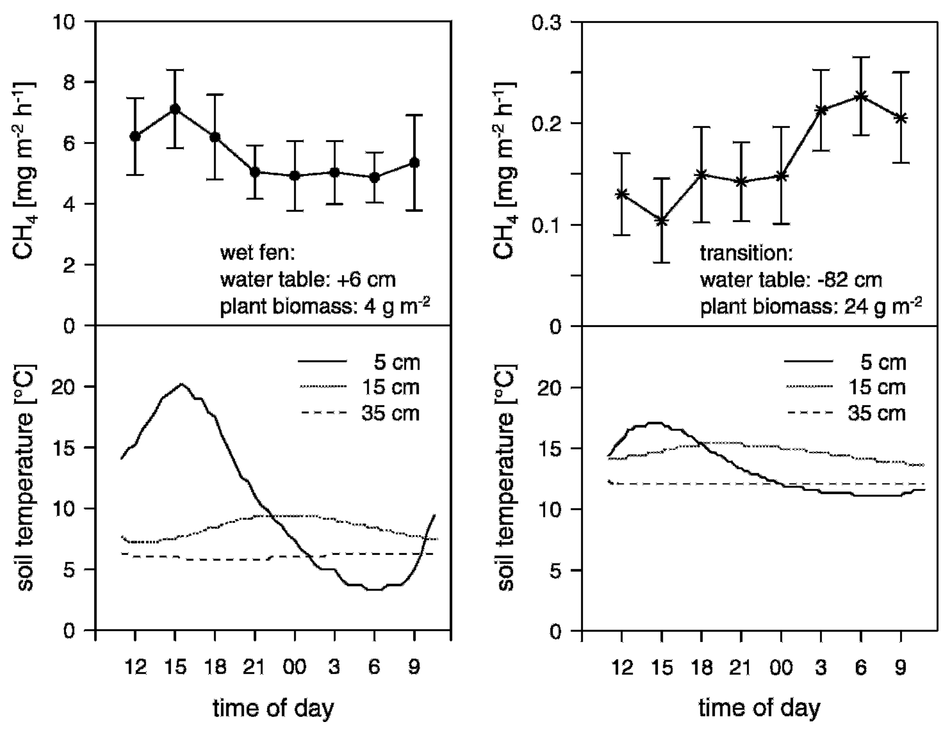

FIGURE 7. Time course of diurnal net methane emissions and soil temperature (5, 15, and 35 cm soil depth) at the wet fen site (17 June 2004) (A) and at the transitional site (28 August 2003) (B).

TABLE 4

Partial regression coefficients (A) and multiple linear models (B) for all diurnal measurements during the snow-free periods (n = 73–80 for each site). Dependent variable: ln transformed net methane flux (mg CH_4 m^{-2} h^{-1}) (ln flux) for transitional site (trans), fen site (fen), and wet fen site (wet fen), and methane uptake (mg CH_4 m^{-2} h^{-1}) (flux) for alpine meadow (meadow). Independent variables: water table (wt[a]) (cm), water-filled pore space (wfps[b]) (5 cm soil depth) (%), soil temperature (°C) [soil depth: 5 cm (st_5), 15 cm (st_{15}), 35 cm (st_{35})], global radiation (globl. rad.) (W m^{-2}), and live above-ground plant biomass (pla. bio.) (g m^{-2}). Level of significance: $P \leq 0.05$ (*$P < 0.001$, **$P < 0.01$, *$P < 0.05$).**

A	Partial regression coefficient (R) of the diurnal net methane flux				
	trans[a]	fen[a]	wet fen[a]	trans[a], fen[a], wet fen[a]	meadow[b]
wt[a] wfps[b]	0.72***	0.73***	0.80***	0.87***	0.21
st_5	0.01	−0.24*	0.30*	0.02	−0.13
st_{15}	0.06	0.61**	0.40*	0.01	−0.22
st_{35}	0.54**	−0.16	0.01	0.62***	
globl. rad.	−0.07	0.06	0.12	−0.06	−0.14
pla. bio.	0.19	0.28*	0.54**	−0.03	−0.10

B	Multiple linear models of the diurnal net methane flux	
trans:	ln flux = 0.046 wt + 0.250 st_{35} + 0.425	R = 0.83***
fen:	ln flux = 0.015 wt − 0.012 st_5 + 0.074 st_{15} + 0.001 pla. bio. + 0.619	R = 0.78***
wet fen:	ln flux = 0.033 wt + 0.017 st_5 + 0.052 st_{15} + 0.008 pla. bio. + 0.618	R = 0.81***
trans, fen, wet fen:	ln flux = 0.053 wt + 0.191 st_{35} + 0.014	R = 0.87***
meadow:	flux = 0.004 wfps − 0.234 st_{15} − 0.342	R = 0.72***

related to the water table position were lower for the snow-free period of 2004 than for 2003, indicating more long-term effects caused by the severe desiccation in 2003.

ENVIRONMENTAL CONTROLS OF DIURNAL METHANE EMISSION AT THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

Diurnal differences of CH_4 emission were only apparent for low or high water tables. Low water tables increased methane flux during the night, whereas at high water tables methane flux peaked together with the temperature of the topsoil in the afternoon. Similar results were obtained for boreal wetlands in north Sweden, with higher nighttime flux for drained sites but smaller differences at high water tables (Mikkelä et al., 1995). The influence of temperature on diurnal methane emission differed with soil depth. The net flux at the driest fen site (transitional) was controlled more by temperature in deeper soil layers, whereas the fen site and the wet fen site, with higher water tables, were controlled more by temperature in shallower soil depths. The importance of soil temperature may be influenced by standing water table, because anaerobic methane production is linked to water-saturated soil conditions. According to Rask et al. (2002), stronger positive correlations of net methane flux with temperature at certain soil depths indicate the main location of CH_4 formation; this agrees with our results. The negative relationship between net methane flux and the topsoil temperature at the fen study site can be explained by the highest methane oxidation potential just above the standing water table (Conrad, 1996).

Total above-ground plant biomass had no significant influence on diurnal methane emission for the driest fen site (transitional), but the influence increased with higher mean water table of the fen and wet fen sites. The lack of influence for the transitional site may be attributed to the deeply aerated upper soil layer. Hence, the proportion of plant-mediated methane flux should be low and less important than at wetter ecosystems (Kutzbach et al., 2004). The partial influence of total plant biomass was eight times higher for the wet fen than for the fen site. This leads to the assumption that the *Carex nigra*–dominated wet fen site has a more pronounced effect on plant-derived methane flux than the *Trichophorum caespitosum*–dominated fen site. *Trichophorum caespitosum* has a relative shallow root system with no root aerenchyma and tolerates saturated but not flooded soil conditions (Bragazza and Gerdol, 1996). In contrast, the *Carex* species and *Eriophorum angustifolia* have distinctive root aerenchyma down to about 80 cm and may be therefore more important for methane transport via plants in the fen and wet fen sites. Evidence for species-specific methane transport is given by Schimel (1995), who showed that the plant-mediated methane transport of *Eriophorum angustifolia* was higher than that of *Carex aquatilis*. The greater influence of plant biomass on methane flux at the wet fen site compared to the fen site might also be attributed to passive methane transport by diffusion, as reported for different *Carex* species and several sedges (Hirota et al., 2004; Kelker and Chanton, 1997; Kutzbach et al., 2004).

Global radiation was not correlated to diurnal methane flux. Accordingly, methane flux seems not to be controlled by stomata conductivity. Field studies have shown different results in relation to radiation. Hirota et al. (2004) found no response of *Carex allivescers* V. Krez to radiation, in contrast to the response of different sedges. In a laboratory experiment, Thomas et al. (1998) reported that plant-mediated methane transport from *Carex* species and *Eriophorum* species largely responded to light under constant temperature due to higher stomata conductance. The authors concluded that the diurnal temperature course may mask the stomata effect for *in situ* measurements. Since many alpine plants have their maximum diurnal stomatal conductivity in the afternoon (Körner and Mayr, 1981) together with the maximum diurnal soil temperature, this effect could explain the lack of a relationship between global radiation and net methane flux in our study.

ENVIRONMENTAL CONTROLS OF METHANE OXIDATION AT THE ALPINE MEADOW SITE

The alpine meadow functions as a net sink for methane during snow-free periods. Diurnal and seasonal net methane emission was negatively correlated with temperature and positively with water-filled pore space. Moreover, for diurnal net methane emissions, soil temperature in 15 cm soil depth was more important than in 5 cm. Similar results were reported by West et al. (1999) for alpine meadows in the Colorado Front Range. These results lead to the assumption that atmospheric methane oxidation in alpine environments is located in deeper soil layers as found for many other environments (Conrad, 1996). The maximum atmospheric methane oxidation in the deeper soil layer can be explained by the higher inorganic nitrogen concentrations usually found in the topsoil, since ammonium is known to be a competitive inhibitor for methane oxidation (de Visscher and van Cleemput, 2003).

MAGNITUDE OF METHANE FLUX AT THE FEN SITES (TRANSITIONAL, FEN, WET FEN)

The range of the mean seasonal net CH_4 flux during the snow-free periods was 19 mg CH_4 m^{-2} d^{-1} (transitional, 2004) to 116 mg CH_4 m^{-2} d^{-1} (wet fen, 2003), with a maximum value of 145 mg CH_4 m^{-2} d^{-1} at waterlogged soil conditions at the wet fen site. Mean net methane emissions of the study sites in the Rotmoos fen were in the order wet fen > fen > transitional, with mean water table levels having the same order. The estimated annual flux rates corresponded to the lower range of flux values reported from alpine wetlands in the Rocky Mountains (Chimner and Cooper, 2003; Mast et al., 1998; Wickland et al., 1999) and in the Tibetan Plateau (Hirota et al., 2004). The relatively low methane flux at the wet fen site may be partly due to the low plant productivity, because 4% of the daily net CO_2 assimilation is emitted as methane as found for Canadian submerged wetlands (Bellisario et al., 1999).

The range of the mean net CH_4 flux during the snow periods was remarkably similar, being 13 mg CH_4 m^{-2} d^{-1} (wet fen) to 15 mg CH_4 m^{-2} d^{-1} (fen) with no obtained seasonal differences. During the snow periods 2003/2004 the relatively constant soil temperature at all fen sites in 15 cm and in 35 cm depth (0.3 °C and 1.0 °C, respectively) and the high and constant water table levels may be responsible for similar net methane flux between study sites and the lack of seasonal differences. In contrast, Mast et al. (1998) found differences in methane flux rates for moist alpine (4.4 mg CH_4 m^{-2} d^{-1}) and water saturated soils (45.9 mg CH_4 m^{-2} d^{-1}) in the Rocky Mountains. Much lower net CH_4 flux (minimum 1.6 mg CH_4 m^{-2} d^{-1}) was obtained for an alpine wetland by Wickland et al. (1999). These differences of reported net methane flux during snow periods may be partly attributed to the different gas measurement methods. A comparison of the chamber method with the snow-gradient method resulted in higher net methane flux values if chambers were used (Alm et al., 1999).

The contribution of wintertime emission to annual methane flux ranged from 18% (wet fen) to 59% (transitional fen site). These values fit to the broad range observed for alpine wetland ecosystems in the Rocky Mountains having similar length of snow periods compared to our study site (Mast et al., 1998; Wickland et al., 1999).

MAGNITUDE OF METHANE OXIDATION AT THE ALPINE MEADOW SITE

The average net methane uptake at the alpine meadow site differed considerably for the two investigated snow-free periods, with much higher methane consumption for 2003 (−2.1 mg m^{-2} d^{-1}) than 2004 (−1.0 mg m^{-2} d^{-1}). In contrast to Sommerfeld et al. (1993), we found no methane flux at snow-covered soil conditions. Methane consumption during the snow-free periods was higher than mean values reported for several alpine tundra ecosystems (+8.5 to −0.8 mg CH_4 m^{-2} d^{-1}) (West et al., 1999; Neff et al., 1994; Whalen and Reeburgh, 1990). However, the net oxidation rates in this study were comparable with the range observed from arctic tundra ecosystems (Whalen and Reeburgh, 1992; Christensen, 1993). The higher rates found in our study may be also caused by higher soil fertility due to the traditional use of the study sites as pasture (Kruse and Iversen; 1995).

GLOBAL ASPECTS OF ALPINE METHANE FLUX

In the alpine zone of Austria (2000–3800 m a.s.l.), wetlands cover about 0.14% (5.5 km^2), alpine grassland (meadow) about 78.3% (3150 km^2), and forested land about 21.7% (875 km^2) of the vegetation area (Steiner, 1992). Within the Rotmoos fen, the transitional, fen, and wet fen sites represent roughly 10%, 85%, and 5%, respectively. If we extrapolate our data to the total alpine area in Austria, we would expect that alpine regions are a small net sink for methane (−0.14 g CH_4 m^{-2} y^{-1}) in areas with no forest sites. So far, there are no data from other alpine regions in Europe. This rough estimation agrees with findings from Niwot Ridge, Colorado Rocky Mountains, acting as a small net CH_4 sink (West et al., 1999). West et al., (1999) estimated that the global alpine area (10.5 million km^2) may be responsible for −1 to +10 Tg CH_4 y^{-1}. Based on a model dealing with the entire pan-arctic region, the entire European Alps may act as a small net sink of methane (0 to −1 g CH_4 m^{-2} y^{-1}) (Zhuang et al., 2004). There are still high uncertainties about net methane fluxes from alpine regions and more investigations are necessary to estimate the role of alpine areas in the global methane budget.

Conclusions

Abiotic environmental properties were mainly responsible for regulating seasonal and diurnal net methane emissions of an alpine ecosystem. The influence of the water table was found to be most important for seasonal within- and among-site variability. The effect of temperature on methane emission rates varied in the different soil depths, presumably due to differences in the vertical distribution of methanogenes and methane oxidizers. Our results indicate that plant-mediated methane transport is only important for water-saturated soil conditions, whereas at drier soil conditions diffusion through the soil matrix becomes more important. Methane fluxes during the winter period substantially contributed to the methane flux rate of a year and should be considered in future studies. We conclude that alpine wetlands act as a methane source, while well-drained alpine grassland could function as a net sink of methane in the Eastern Alps of Europe. More investigations of methane fluxes from alpine landscapes are necessary to evaluate the role of alpine areas in the global methane budget.

Acknowledgments

This research was financed by the DFG project 768. Support was also received from R. Kaufmann, University of Innsbruck, who provided the climate data from the weather station used in this study and from I. Oberleitner, Federal Environmental Agency of Austria, who provided data of the distribution of wetlands in Austria. Additionally, we thank M. Stachowitsch for editing the text and M. Strobel from the alpine research station Obergurgl (University of Innsbruck, Austria) for technical support and hospitality during field measurements.

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Ms accepted August 2006