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Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands

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Abstract. CO_2 and CH_4 fluxes during the winter were measured at natural and drained bog and fen sites in eastern Finland using both the closed chamber method and calculations of gas diffusion along a concentration gradient through the snowpack. The snow diffusion results were compared with those obtained by chamber, but the winter flux estimates were derived from chamber data only. CH_4 emissions from a poor bog were lower than those from an oligotrophic fen, while both CO_2 and CH_4 fluxes were higher in the *Carex rostrata*-occupied marginal (lagg) area of the fen than in the slightly less fertile centre. Average estimated winter CO_2-C losses from virgin and drained forested peatlands were 41 and 68 g CO_2-C m^{-2}, respectively, accounting for 23 and 21% of the annual total CO_2 release from the peat. The mean release of CH_4-C was 1.0 g in natural bogs and 3.4 g m^{-2} in fens, giving rise to winter emissions averaging to 22% of the annual emission from the bogs and 10% of that from the fens. These wintertime carbon gas losses in Finnish natural peatlands were even greater than reported average long-term annual C accumulation values (less than 25 g C m^{-2}). The narrow range of 10–30% of the proportion of winter CO_2 and CH_4 emissions from annual emissions found in Finnish peatlands suggest that a wider generalization in the boreal zone is possible. Drained forested bogs emitted 0.3 g CH_4-C m^{-2} on the average, while the effectively drained fens consumed an average of 0.01 g CH_4-C m^{-2}. Reason for the low CH_4 efflux or net oxidation in drained peatlands probably lies in low substrate supply and thus low CH_4 production in the anoxic deep peat layers. N_2O release from a fertilized grassland site in November–May was 0.7 g N_2O m^{-2}, accounting for 38% of the total annual emission, while a forested bog released none and two efficiently drained forested fens 0.09 (28% of annual release) and 0.04 g N_2O m^{-2} (27%) during the winter, respectively.

Introduction

Carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) are important atmospheric trace gases which are closely interconnected as components of the biological carbon and nitrogen cycles. The heat-absorbing properties of these gases increase the warming potential of the atmosphere (IPCC 1994). CO_2 efflux from peat is a combination of root-associated respiration and the results of aerobic and anaerobic decomposition processes, while the source of the wetland CH_4 emissions is the decomposition of organic material in water-saturated, anaerobic peat (Clymo 1984). N_2O emissions are enhanced by artifical or natural drawdown of the water table, which increases nitrification activity in nitrogen-rich peatlands (Martikainen et al. 1993; Lång et al. 1994; Regina et al. 1996a). Nitrogen load by fertilization (Nykänen et al. 1995) or atmospheric deposition may also promote this effect (Regina et al. 1996b).

The present paper deals with wintertime trace gas fluxes. The snow-free season fluxes of radiatively important trace gases in northern peatlands are becoming well established, but there is much uncertainty about the over-winter fluxes. Winter CO_2, CH_4 and N_2O fluxes have been monitored systematically only in a few studies (Dise 1992; Zimov et al. 1993; Melloh & Crill 1995, 1996), and the estimates are largely missing from the gas balance calculations. If the projected climate warming (IPCC 1995) raises the winter temperatures in the boreal zone and the distribution and amount of snowfall and wetland hydrology are altered, more information will be needed on the responses of decay processes in order to predict annual trace gas balances in northern wetlands.

Exchange of trace gases between peatland ecosystem and the atmosphere gives information on the matter balance. High rates of both carbon binding and decomposition occur during the growing season, but photosynthesis largely ceases below the snowpack due to declining temperature, senescence or dormancy of above-ground parts of the vegetation and the exclusion of light by the snow layer. Respiration and decomposition reduce the organic input in peat. Thus the quantity and nature of the new substrates entering the peat for the winter is largely determined by the residual of summertime gas exchange. Emissions of CO_2 and CH_4 from natural Finnish wetlands reach their peak from July to August, at least partly following the seasonal peat temperature cycle (Martikainen et al. 1995; Nykänen et al. 1995; Silvola et al. 1996; Nykänen et al. 1996; Kettunen et al. 1996). Thus, most of the gas exchange between peatlands and the atmosphere occurs during summertime, but some of the CO_2, CH_4 and N_2O formed in peat is stored in the pore water (e.g. Dise 1992) and the mineralization of organic matter may also continue in the peat, producing CO_2, CH_4 and N_2O.

Gas exchange between peat and the atmosphere can occur even through the frozen soil and snowpack (Dise 1992; Sommerfeld et al. 1993; Melloh & Crill 1995), the rates of the various mineralization processes being dependent, among other factors, on peat temperature and the availability of free water and substrates, so that they slow down in the frozen peat, but are not entirely exhausted (Coxson & Parkinson 1987; Zimov et al. 1993; Clein & Schimel 1995). In any case, the frost layer on boreal peatlands can be thin and the water-saturated anoxic peat below the frozen surface layer can maintain above-zero temperatures, and thus, anaerobic microbial activity in subpeat throughout the winter season. Drained peatlands may consume CH_4 throughout the year (Martikainen et al. 1995), but may also act as weak CH_4 sources at times of high water saturation (Nykänen et al. 1995). The seasonality of N_2O emissions in peatlands drained for forestry or agriculture seems to depend on changes in peat moisture conditions, nitrification activity and the availability of ammonium and nitrate in the peat (Davidson 1993; Martikainen et al. 1993; Nykänen et al. 1995). The spring thaw liberates the gaseous decomposition products if they have not already escaped during the winter.

The necromass harboured in the northern wetland ecosystems under waterlogged conditions comprises a globally important pool of carbon and nitrogen, the gas balances (CO_2, CH_4 and N_2O) associated with which can be disturbed by direct (e.g. drainage, eutrophication by atmospheric deposition or through enriched groundwater) or indirect (climate change) anthropogenic actions (Laine et al. 1996). The release of CO_2 from soil in winter has in some cases been reported to comprise as much as 22–37% of the annual decomposition in boreal mineral soils (Havas & Mäenpää 1972; Pajari 1995) and 10–34% in tundra and boreal peatlands (Clein & Schimel 1995). Similarly 2–20% of the total annual CH_4 release is reported to occur during the winter both in virgin temperate peatlands (Melloh & Crill 1996) and in boreal ones (Dise 1992; Nykänen et al. 1995).

Here we present winter trace gas fluxes in two intensive and eight extensive sites. Fluxes of CO_2 and CH_4 were monitored over one winter season in an ombrotrophic treeless bog and a minerotrophic nutrient-poor boreal fen in eastern Finland, in addition to which a few measurements of CO_2, CH_4 and N_2O were made at various fen and bog sites with different fertility in southern Finland. Some peatlands drained for forestry or agriculture were also studied. The intensive measurements are used as a "baseline" of wintertime gas release in order to construct winter fluxes also for the extensive sites. Surface gas fluxes determined by closed chamber techniques are compared with results obtained by the easier procedure of gas sampling and calculation of gas diffusion along the concentration gradient through the snowpack. However, only chamber results are used in the reconstruction of whole winter emissions.

Material and methods

Sites

Gas fluxes during winter 1994/95 were investigated in detail at two intensive sites, an ombrotrophic bog at Ahvensalo, Ilomantsi (65°51′N, 30°53′E, 150 m a.s.l) and a minerotrophic fen Salmisuo (62°47′N, 30°56′E, 145 m a.s.l). These sites were sampled during the winter from November to May about once a month. The bog site had also been visited once in February 1992 and the fen site once in March 1992. The mean January temperature in the area in January is −11.9 °C (1961–1990) and the mean July temperature +15.8 °C. The annual mean temperature is +2.0 °C and annual precipitation 600 mm. Mean snow depth is 63 cm and the average duration of the snow cover 183 days. The length of the winter of 1994/95 in Ilomantsi was about 180 days and the permanent snow cover formed in the latter half of November. The effective temperature sum in the Ilomantsi area is 1150 dd (Long-term average 1961–1990, data supplied by the Finnish Meteorological Institute).

The intensive bog site is an ombrotrophic, treeless c. 1 ha *Sphagnum fuscum* bog. The peat depth at the deepest point is 3.9 m. The vegetation of the bog consists of *S. balticum–S. angustifolium* lawns with some *Scheuzeria palustris* in the moist depressions, *Sphagnum fuscum* lawns and hummocks of varying height. The lower *S. fuscum* lawns were sparsely occupied by sedges (*Eriophorum angustifolium, Carex pauciflora*), herbs (*Rubus chamaedaphne*) and low shrubs (*Empetrum nigrum, Andromeda polifolia*), while the higher hummocks were characterized by larger shrubs (*Betula nana, Chamaedaphne calyculata* and *Vaccinium uliginosum*). The bog represents the nutrient-poor end of the scale of Finnish boreal mire site types (cf. Ruuhijärvi 1983) with low CH_4 emissions, while the CH_4 emissions from the oligotrophic fen are among the largest observed in southern Finland (cf. Nykänen et al. 1998), higher than those measured in Canada (Roulet et al. 1994) or norther Ontario (Bubier & Moore 1994) and at the high end of the fluxes reported in Minnesota, USA (Dise et al. 1993; Crill et al. 1992; Shanon & White 1994).

The intensive fen site was an oligotrophic short sedge *Sphagnum papillosum* pine fen within the Salmisuo peatland complex, consisting of a subsite in a narrow *Carex rostrata* lagg fen next to mineral soil, and another subsite of *Eriophorum vaginatum* lawn with scattered, mostly treeless *Sphagnum fuscum* hummocks. Peat depth in the area was c. 2 m. The vegetation, summer CH_4 emissions and annual carbon accumulation at the site are described in detail by Saarnio et al. (1997) and Alm et al. (1997). The history of the peatland complex of Salmisuo is described by Tolonen (1967).

Eight other extensive sites (Table 1) in central and eastern Finland were sampled 2–5 times during the snow-covered period in 1991/92, including 4

Table 1. Characteristics of the mire sites in southern Finland used for winter CO_2, CH_4 and N_2O measurements. Site codes are those employed by Silvola et al. 1996. The prefix "I" denotes the Ilomantsi area, eastern Finland and "L" the Lakkasuo area in central Finland. Mire site types and their Finnish abbreviations are also indicated. D_{WT} is the average depth of the water table during the growing season. "**Bog**" and "**Fen**" refer to the sites with monthly winter data. Nitrogen (N%) and pH were determined in samples from the 0–20 cm surface layer of the peat

Site code	Mire site type	Peat depth, cm	D_{WT}, cm	N (%)	pH
Bogs					
Ahvensalo I1	*Sphagnum fuscum* bog (RaN)	180–390	17	n.d.[a]	4.6
I6	*Sphagnum fuscum pine* bog (RaR)	200	16	1.4	4.3
I7	As above, drained –20 yr (RaRmu)	340	21	1.2	4.3
L8	Cottongrass pine bog with *S. fuscum* hummocks (RaTR)	230	15	0.5	3.8
L9	As above, drained –30 yr (RaTRmu)	230–250	20	0.5	3.8
Fens					
Salmisuo	Short sedge *Sphagnum papillosum* pine fen (LkR)				
	– *Carex rostrata* lagg	180–200	5	1.0	4.1
	– *Mire centre*	180–200	10	0.5	4.1
L19	Tall sedge fen (VSN)	160	2	1.9	5.6
L20	As above, drained –30 yr (VSNmu)	150	30	2.1	4.5
I23	Herb-rich sedge birch-pine fen, drained -40 yr (RhRSmu)	200	38	1.5	4.5
Grassland	Former wet flark fen, drained –60 yr	140	40	2.6	5.3

[a]Not determined.

sites, a bog and a fen with natural and drained counterparts within the Lakkasuo mire complex (61°48′N, 24°19′E, c. 150 m a.s.l.), a bog with natural and drained counterparts in Ilomantsi (62°49′N, 30°57′E, 148 m a.s.l), an effectively drained oligotrophic fen (62°49′N, 30°59′E, c. 150 m a.s.l) and a fen drained for grassland (62°49′N, 30°59′E). The characteristics of these peatland sites are described in more detail by Laine et al. (1986), Martikainen et al. (1995) and Silvola et al. (1996), and the grassland site by Nykänen et al. (1995).

Chamber measurements

The gas fluxes were determined using a closed chamber method (Crill 1991) and a snowpack diffusion method (Sommerfeld et al. 1993). In the first technique the chambers (54 dm^3, 60 × 60 cm) were placed on the peat surface after clearing it of snow and the type of microsite (hollow, lawn, hummock) was recorded prior to gas measurement. The snow was removed to prevent gas escape from the headspace of the chambers, as was observed when testing the procedure. The gaps between the edges of the chamber and the peat surface were first packed with moist snow, then the chamber was covered with plastic foil reaching c. 80 cm outwards and the edging was finally packed with snow. The aim of the last operation was also insulation: to prevent cool ambient air from lowering the temperature of the peat surface. Even so, some leakage of the headspace gas sometimes occurred, leading to unexpected downward shifts towards the ambient gas concentration. Samples disturbed in this way were identified during the gas analysis from unexpectable drops in headspace gas accumulation and were omitted from the flux calculations. Four evenly timed 40 ml samples were drawn from the chamber headspace with polypropylene syringes equipped with three-way stopcocks during a 60 min incubation period. No compensation air other than could have leaked through the snow packing into the chamber was provided. Drawing air into the syringes could thus have lowered the pressure in the chamber headspace slightly. The gas concentrations were determined in a laboratory within 6 hours using infrared gas analysis for CO_2 (HB Uras 3E) and gas chromatography for CH_4 and N_2O. Most of the CH_4 samples were analyzed using a Shimadzu GC-14-A apparatus (1.8 m Haye Sep Q 80/100 mesh packed metal column) and the remainder using two HP 5890 Series II gas chromatographs running parallel with a TC and FI detector in one and an EC detector in the other (Nykänen et al. 1995). The gas fluxes were calculated from the linear change in gas concentration in the chamber headspace. No tailing or flattening in the concentration curves was observed in a normal measurement. The intensive bog and fen sites were visited about once a month from November 1994 to May 1995, but not in March 1995. Chamber measurements were not made in the intensive bog site in May. During each sampling session 8 chamber measurements were made at different spots and the microsite type uncovered from snow was recognized. Wintertime gas fluxes were summed from chamber results averaged for and weighted by the number of days in the corresponding winter period (early winter; months XI–XII, midwinter; I–

IV and late winter; V). Flux rates from hummock and lawn microsites in the intensive fen site were compared with t-test.

Gradient measurements

Polypropylene syringes, calibrated volume 50 ml, and a 3 mm diameter metal pipe were used to draw pore space gas samples from different depths in the snowpack and the peat soil. The minimum procedure included taking 4–6 replicate 40 ml samples of ambient air from above the snowpack and an equal amount of 20 ml samples from close to the peat surface beneath the snow by inserting the pipe vertically through the snowpack. Additional samples from 2–4 depths in snow profile were taken to examine the gas concentration gradient within the snow. The concentrations of CO_2 and CH_4 were determined using the IR analyzer and gas chromatograph within 2–6 hours. Total snowpack depth and snow porosity were measured from 2–6 volumetric snow samples taken through the snowpack from top to the bottom with a 103 mm (inner) diameter PVC tube. The snow samples were weighed in the laboratory to calculate the average porosity using the density of pure ice = 0.9168 g cm^{-3}. The flux rate was then calculated using Fick's first law of diffusion through porous media (Eqn. 1).

$$J_g = D_g(dC_g/dz)f, \tag{1}$$

where J_g is the diffusive flux for a gas (g) along a concentration difference (dC_g) below z cm of snowpack with an air-filled snow porosity (f). The flux rates were calculated through the whole snowpack (z = snow depth), and for simplicity, assuming that all CH_4 released from peat would eventually be liberated to the atmosphere. N_2O fluxes were not calculated by the snow gradient method. Diffusion coefficients (D_g) for CO_2 (0.139 cm^2 s^{-1}) and CH_4 (0.22 cm^2 s^{-1}) were taken from Sommerfeld et al. (1993).

K-type CrNi–AlNi thermocouple sensors (K24-2-505 Watlow-Gordon, USA) were installed at depths of 10, 30, 50, 80 and 120 cm in the peat at the bog and fen sites in November 1994 to enable a peat temperature profile to be measured through the frozen soil. Temperature in peat layer 5–30 cm below the surface was measured on sites without buried probes if peat surface could be penetrated with a steel pin probe.

Nitrogen contents were measured on a Leco CHN 600 analyzer from 20 cm thick peat cores collected from the rooting zone below the photosynthetic moss layer. Pore water pH was determined in laboratory from the same cores.

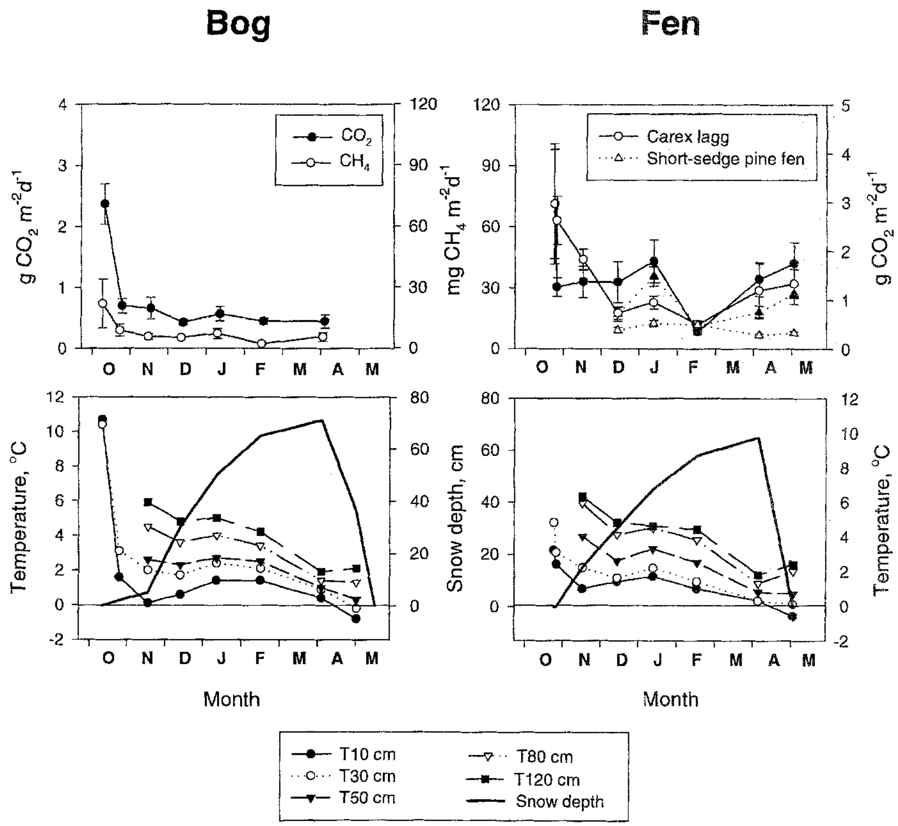


Figure 1. Average fluxes ± one standard error of the mean (S.E.M.) of CO_2 (solid markers) and CH_4 (open markers) of the Bog and Fen sites (upper figures). Fluxes from the *Carex rostrata*-occupied marginal area (*Carex* lagg, circles) and the central short-sedge pine fen area (triangles) are displayed separately. Temperatures at depths of 10, 30, 50, 80 and 120 cm below the peat surface and snow depths also shown (lower figures).

Results and discussion

Comparison of fluxes with gas gradients and chambers

The maximum snow depth reached during the winter was 60–75 cm, in March (Figure 1). The snowpack was almost homogeneous but not entirely, due to a few c. 0.5 cm layers of melted and refrozen surface snow that had formed on mild days. The average snow porosity decreased from 80% to 60% towards the spring. Subnivean CO_2 concentrations varied from 350 to 900 ppm in the bog and from 620 to 1100 ppm in the virgin fen. Simultaneous CH_4 concentrations were 4–12 ppm (bog) and 8–15 ppm (fen), respectively (Figure 2). The changes in gas concentration in the snow profile proceeded smoothly

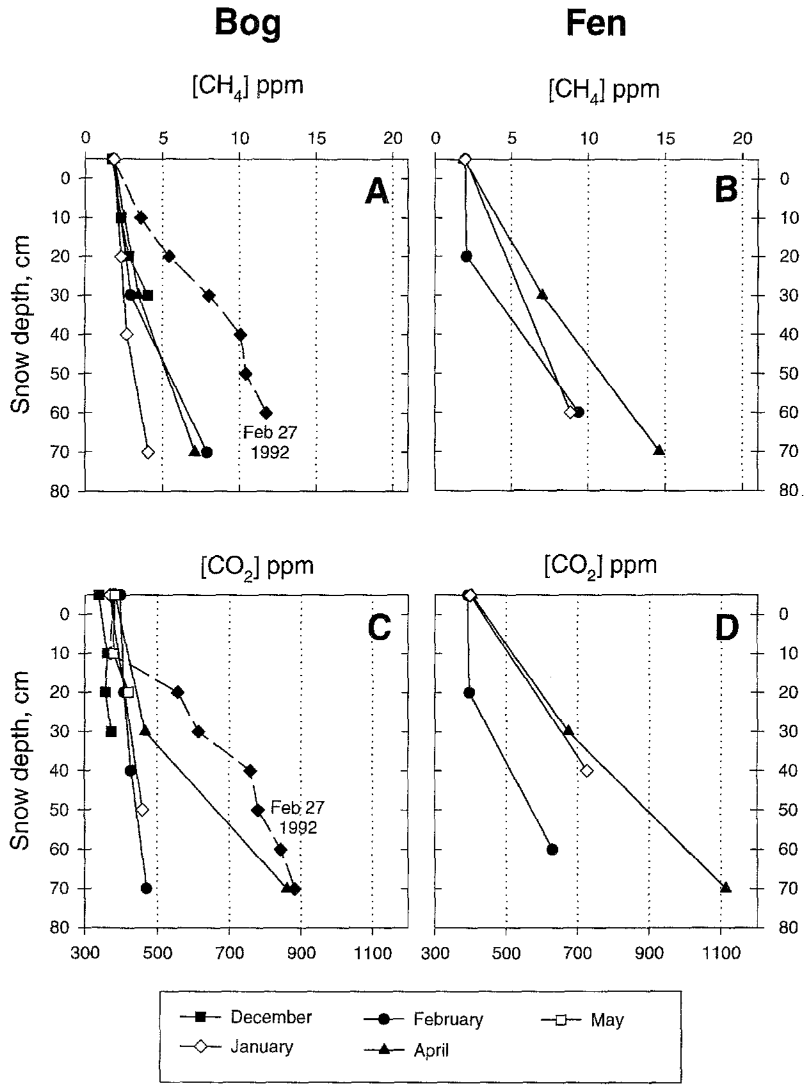


Figure 2. Profiles of CH_4 and CO_2 concentrations at the Bog (A,C) and Fen (B,D) sites from December 1994 to May 1995, when the snowpack was loose and homogeneous, compared with results for a sampling session on Feb 27, 1992, with icy layers in the snowpack.

during the winter of 1994/95, when the porosity of the snow was high and it was relatively homogeneously packed, resulting in linear or slightly concave concentration curves. Linearity (concentration decreasing more rapidly deeper in the snowpit than in the surface layers) in the emission curves in Figure 2. indicates free upward diffusion through the snow, concavity may be caused by mixing of ambient air or gas consumption in the upper pore

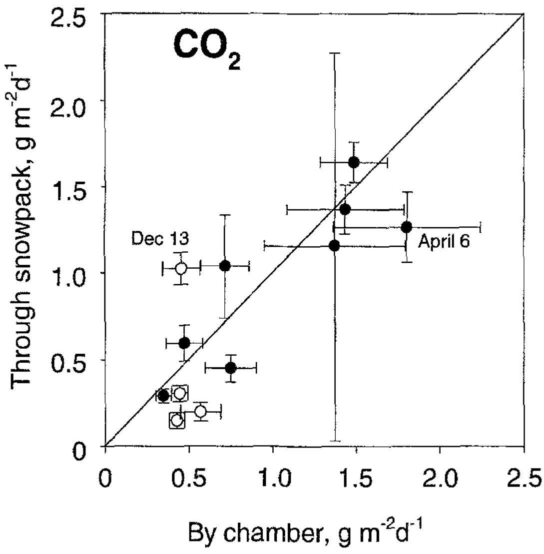
Table 2. Comparison of average CO_2 and CH_4 flux rates (±S.E.M and n = number of cases in parenthesis) in the Ahvensalo bog and the Salmisuo fen sites, measured from December 1994 to April 1995 both by chamber and gradient methods

	Chamber		**Snow gradient**	
Site	CO_2 **g m^{-2}d^{-1}**	CH_4 **mg m^{-2}d^{-1}**	CO_2 **g m^{-2}d^{-1}**	CH_4 **mg m^{-2}d^{-1}**
Bog	0.48 (±0.05, n = 28)	4.95 (±0.89, n = 29)	0.48 (±0.09, n = 19)	3.75 (±0.57, n = 19)
Fen, lagg	1.32 (±0.19, n = 19)	22.73 (±3.38, n = 19)	1.03 (±0.20, n = 12)	17.77 (±1.91, n = 12)
Fen, centre	0.89 (±0.13, n = 14)	9.99 (±0.83, n = 15)	1.11 (±0.15, n = 15)	14.24 (±0.99, n = 15)

spaces of the snowpit, while convexity in the curve indicates gas production (see Sommerfeld 1993) or the presense of one or more dense layers within the snow. The snow was more clearly layered in February 1992, which caused some accumulation of the gases below the icy layers at the bog I1 and drained fen I23 (Figures 2a,c and 7). Less permeable ice layers in snow would result in overestimated flux rates if Fick's formula (Eqn. 1) is applied with z = depth of the whole snowpack as was done in the present work.

Chamber and gradient methods yielded in some cases clearly different flux estimates for CO_2 and CH_4. The average CO_2 flux on the bog gave quite similar average values estimated by Fick's diffusion or by chamber (Table 2), but the same was not true for methane. For CH_4 the flux rates measured in the bog by chamber were even 30% higher than those by the gradient method. There were, however, considerable variation within the both methods (Figure 3). On the fen, where the overall CO_2 flux rates were higher, the two methods gave more comparable results, the difference between the gradient and the chamber CO_2 fluxes being about 20% (Table 2). Methane release rates in the fen showed large average differences between the methods and the subsites. The larger difference in CH_4 release rate, 43%, was obtained for the data from mire centre and the smaller, 28%, those from the lagg (fen margin adjacent to mineral soil) subsite (Table 2).

The highest subnivean concentrations of both CO_2 and CH_4 at the intensive bog and fen sites (winter 1994/95) were measured either in December or late winter (April). The peat surface fluxes measured by the chamber method



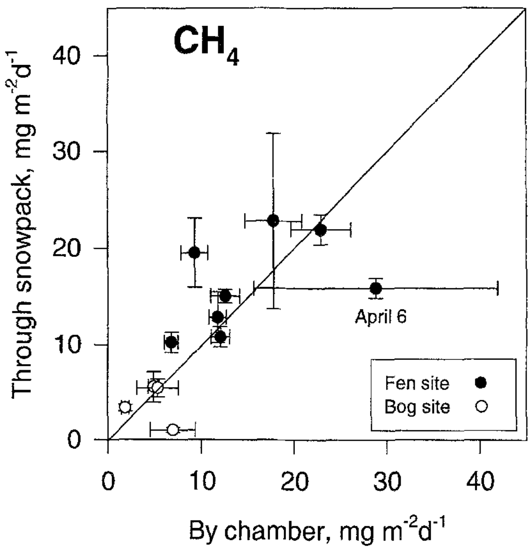


Figure 3. Comparison of average fluxes ±S.E.M of CO_2 and CH_4 obtained by the snowpack diffusion method with peat surface fluxes measured by closed chamber techniques at same sampling sessions during winter 1994/95. Number of snow gradient samples taken at the fen site was 2 in December, 7 in January and 6 for all other sessions, in the bog site 3 gradient samples were taken in December, 5 in Jan–Feb, and 6 in April. Bog (open symbols) and Fen (closed) data are plotted on the same graphs.

were much higher at April than those measured by the gradient method through the snowpack in the lagg subsite of the fen (Figure 3). It can be assumed that all the CH_4 already within the snowpack will eventually reach the atmosphere, but inhomogeneities such as icy layers in the melting snow, could have affected the diffusivity of CO_2 and CH_4 and thus the snow gradient flux calculations (see above, also Melloh & Crill 1995). Large variations in gas fluxes were encountered both in the gradient and the chamber measurements (Figure 3), partly because the methods may have picked out any spatial microvariation from a different footprint area, or because the snowpack had been ventilated by the wind to some extent prior to subnivean gas sampling. The probably more sensitive concentration gradient method could have resulted in overestimation or underestimation if flux rates obtained for one point in time were extrapolated over longer periods.

As diffusion is directly proportional to f in Fick's formula (Eqn. 1), the results are sensitive to the porosity values of the medium. For example, the decrease in porosity from 80% to 60%, observed over the winter, reduced the diffusivity by 25%. Snow porosity should be determined separately for the conditions prevailing at all the measurement sessions, as an average estimate for the whole winter can lead to large errors in individual flux rates. Subnivean gas sampling by drawing air from the pores in the snow is easy compared with peat surface flux determination using chambers, and makes it possible to collect larger amounts of data. Under conditions of homogeneous snowpack, Fick's formula can be applied, especially for the determination of CH_4 flux (Figures 2 and 3). It is, however, important to take gas samples throughout the snowpack to observe accumulation of gases below any less permeable layers in snow, which would affect the calculations. As peat surface fluxes tend to increase towards the spring thaw, probably due to gas build-up in the peat, the chamber method seems to be more reliable, but the results may be confused by spatial variability in gas release from the peat.

Spatial variability of CO_2 and CH_4 fluxes

The rates of CO_2 and CH_4 release from peat at the bog and the fen sites had already decreased from their high July–August values from hummocks to hollows, 101–410 mg CH_4 $m^{-2}d^{-1}$ in the fen (Saarnio et al. 1997) and 1–17 mg in the bog (Alm et al. in press), by the first half of October. The CO_2 and CH_4 emissions on the oligotrophic fen were higher than those on the poor bog during the growing season and also remained so through the 180 days of snow cover from mid-October to mid-May (Figure 1). The loss of CO_2-C over that period was 30 g m^{-2} from the bog and 55–76 g m^{-2} from the fen, the CH_4-C effluxes in the same period being 1 g m^{-2} and 2-6 g m^{-2}, respectively (Table 2).

There was clear spatial variation in surface CO_2 and CH_4 effluxes between the *Carex rostrata* lagg fen and the *Eriophorum vaginatum* lawns of the central part of the low-sedge *Sphagnum papillosum* pine fen (Figure 1) for example, the lagg releasing 76 g m^{-2} CO_2-C and the *Eriophorum* lawn 55 g m^{-2}. This difference is of significance for the annual C accumulation at these microsites, 34 and 73 g C m^{-2} in 1993, respectively (Alm et al. 1997). Moreover, three times more methane, 6 g m^{-2}, was emitted over the winter season from the *Carex rostrata*-occupied lagg than from the *Eriophorum* lawn (see also Table 2).

Freezing of the hollows with a solid ice layer in November almost cut off the gas fluxes from these microsites, but hollows and flarks occupied a negligible proportion at both the bog and fen sites, and the gas fluxes from the hollows were not systematically monitored later in the winter. The chamber data did not reveal any statistically significant differences between the hummock and lawn microsites, probably due to the small number of cases, but CH_4 emissions were 10–30% lower at the hummocks in the few cases where comparison was possible (Figure 4). The results are presented here as average emissions with no separation to hollow, lawn or hummock microsites.

Dependence of winter fluxes on peat temperature

The temperature of the surface layer of the peat controls CO_2 release in summer (e.g. Silvola et al. 1996), but summer CH_4 emission in Finnish peatlands is more closely linked to temperature in the deeper peat layers, 20–50 cm below the surface (Kettunen et al. 1996; Saarnio et al. 1997; Nykänen et al. 1998). The winter fluxes of both CO_2 and CH_4 seem to be connected to some extent with the dynamics of peat temperature, but not exclusively. The depth of the snowpack had reached about 80 cm in eastern Finland by February, but the snow was loose, with a porosity greater than 70%. Peat temperature increased temporarily from December to January (Figure 1), followed by a clear increase in the CO_2 and CH_4 fluxes, probably due to the insulating properties of the thick snowpack and relatively high air temperatures during January (air temperatures not shown). The main source of heat was evidently in the peat layers at depths greater than 1.2 m, which was the deepest position used for the thermocouple sensors.

There was an apparent relation between the low flux rates for CH_4 and CO_2 and the slight changes in peat temperature, although not over the whole winter. The relation between peat temperature and both CO_2 and CH_4 release from October to February (Figures 1 and 5) was obscured by an increase in gas emission during March–May following the February minimum, and leading up to the spring thaw, while the temperature in the peat was still decreasing (Figure 1). Similar results were obtained for CH_4 by Melloh

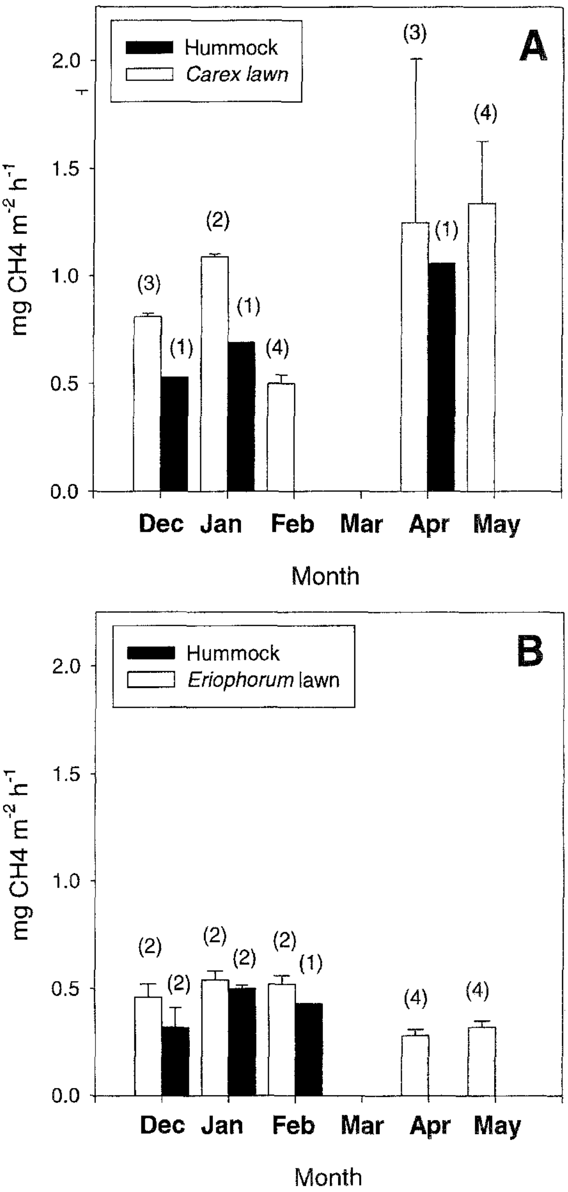


Figure 4. Comparison of mean CH_4 surface emissions (+S.E.M.) obtained with a chamber at hummock and lawn microsites during certain visits to the fen site in 1994/95. Margin lagg (A) and mire centre subsites (B). Number of observations (n, in parenthesis) is shown above the bars. All the measuring spots were cleared of snow at different locations in the mire.

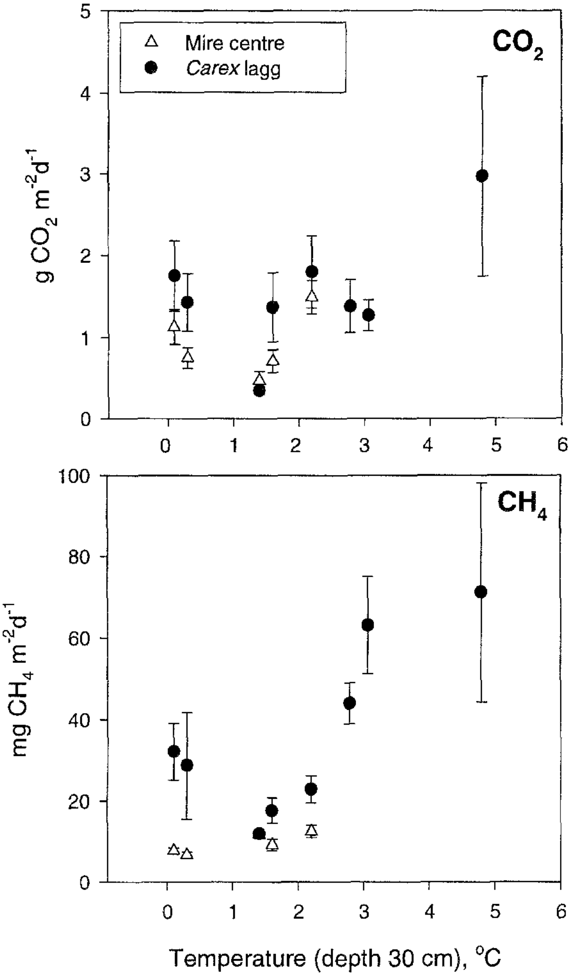


Figure 5. Mean CO_2 and CH_4 peat surface fluxes by chamber (±S.E.M.) at the Fen site plotted against peat temperature at depth 30 cm. Short sedge fen (Mire centre) and *Carex* lagg subsites are shown separately.

and Crill (1995), who reason that the CH_4 production slows down due to decreasing temperature, but also that gas transport may be restricted through ice layers forming in peat in the course of winter. Nevertheless, the relation of surface CH_4 flux to the autumn decrease in peat temperature was clear. The relationship between late autumn–early spring fluxes from the various peatlands are depicted in Figure 6. After spring thaw both CO_2 and CH_4 emissions increased following the rise in peat temperature (e.g. temperatures above +6 °C in Figure 6). There is an obvious curvilinear relationship between peat temperature, CO_2 and CH_4 (Figure 6), but no clear effect of

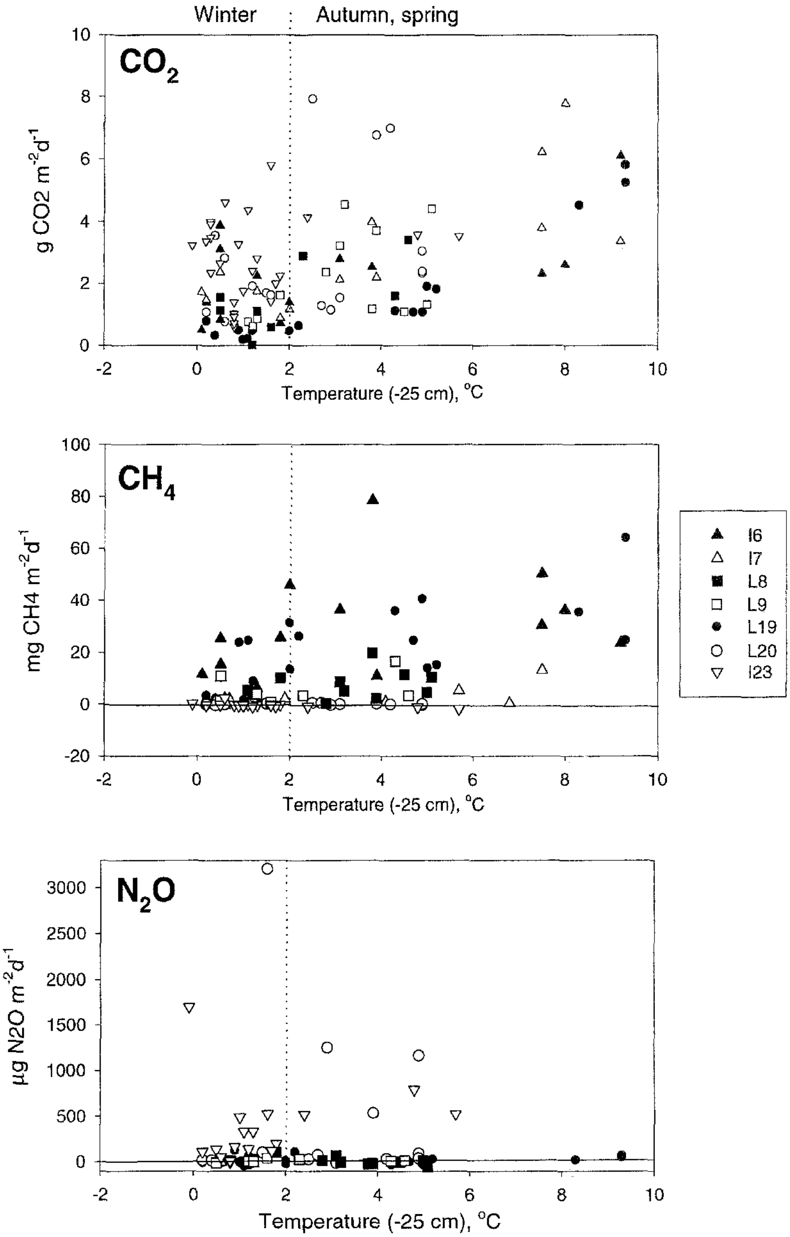


Figure 6. Fluxes of CO_2, CH_4 and N_2O measured by chamber at sites I6–I23 (see Table 1) during periods November–May in winter 1991/92 and November–December in 1992. Solid symbols denote fluxes from natural mires, open symbols from drained sites. The data consists of values representing winter, but also autumn and spring values prior and after the permanent snow cover. Dotted vertical lines indicate the threshold value (+2 °C) in peat temperature at depth of –25 cm, below which the corresponding flux data in May and November were accepted in wintertime calculations.

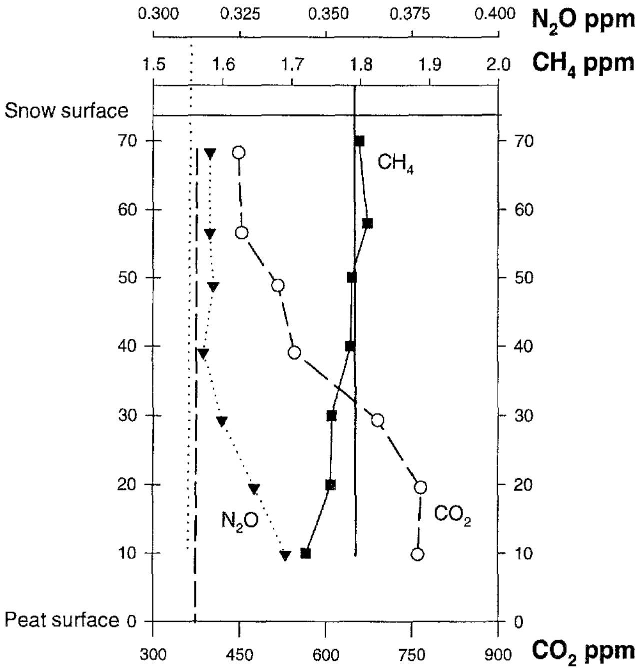


Figure 7. Examples of snow pore air gas concentration profiles for CO_2 (circles, connected with dashed line), CH_4 (squares, solid line) and N_2O (triangles, dotted line) at a drained and forested mesotrophic fen site on Feb 27, 1992. Ambient air CO_2, CH_4 and N_2O concentrations are indicated with vertical lines similar to the snow gas marker connectors.

temperature could be noticed in case of N_2O. A good predictor of early winter CH_4 release in the fen seems to be the temperature 25–30 cm below the peat surface (Figures 1, 5 and 6), in the same active layer as during the summer season (Saarnio et al. 1997). The warming of peat in January–February was most clearly reflected in the gas emissions at the fen site, but was also visible in the bog (Figure 1), indicating a positive correlation at least in the period from autumn to mid-winter.

Effect of drainage on the gas fluxes

Drained peatlands show higher CO_2 emissions than the natural ones, but the case is opposite for CH_4. Soil respiration at the drained forested sites was 0.2–0.5 g CO_2-C $m^{-2}d^{-1}$, and that at the grassland site even higher, 0.8 g (Table 3). Low CH_4 emissions, 1.3 and 1.4 mg CH_4-C $m^{-2}d^{-1}$, occurred at the two drained bog sites, I7 and L9, while the most effectively drained fen I23 appeared to consume CH_4 at rate –0.1 mg CH_4-C $m^{-2}d^{-1}$. Reason for the low CH_4 efflux or net oxidation in drained peatlands probably lies in a low substrate supply and thus low CH_4 production in the anoxic deep peat layers.

Table 3. Daily chamber fluxes of CO_2 and CH_4 in natural and drained (dr) peatlands as means weighted by number of days in the month or period (EW = early winter; months XI–XII, MW = midwinter; I–IV, LW = late winter; V) of the measurements with N of measurements indicated for each period. Some supplementary measurements made by dynamic chamber (Silvola et al. 1996) are included (N in parenthesis). Estimated winter and seasonal (May 15–November 15) emissions on bog (I1–L9), fen (Salmisuo–I23) and a grassland site. Winter fluxes are calculated using a period of 180 days. See Table 1 for site codes

Site	N			CO_2			CH_4		
	EW	MW	LW	Daily flux in winter $g\,C\,m^{-2}d^{-1}$	Winter flux $g\,C\,m^{-2}$	Summer flux[a] $g\,C\,m^{-2}$	Daily flux in winter $mg\,C\,m^{-2}d^{-1}$	Winter flux $g\,C\,m^{-2}$	Summer flux[b] $g\,C\,m^{-2}$
Bogs									
Ahvensalo (I1)	25	21	11	0.16	30	121	4.20	1.0	2.9[e]
									0.6–1.0
I6	4	7	4	0.30	53	110	5.10	1.7	3.4
	(12)								
I7, dr	4	2	4	0.49	86	140	1.28	0.2	1.0
	(12)								
L8	(18)	3	5	0.25	50	164	2.40	0.3	4.8
L9, dr	(18)	3	4	0.19	48	238	1.35	0.3	2.7
Fens									
Salmisuo, lagg	12	11	4	0.35	76	n.d.	24.40	6.0	29.8[c]
Salmisuo, centre	4	11	4	0.25	55	n.d.	7.65	2.0	22.0[c]
L19	5	5	2	0.14	30	188	8.18	2.1	31.0
L20, dr	6	6	2	0.25	57	356	0.08	0.01	–0.01
I23, dr	9	9	5	0.46	81	428	–0.08	–0.02	–0.16
Grassland, dr				0.79	143	592[d]	0.69	0.12	0.03[d]

[a] Silvola et al. (1996). [b] Nykänen et al. (1996).
[c] Saarnio et al. (submitted). [d] Nykänen et al. (1995). [e] Alm et al. (submitted, b).

Table 4. Chamber fluxes of N_2O in peatlands drained for forestry and agriculture. Estimates of winter emission (180 days) are calculated using daily average flux rates weighted by number of days during periods EW, MW and LW, and displayed with summer emissions from Regina et al. 1996. See Tables 1 and 2 for explanations on the codes

Site	EW	MW	LW	Daily flux in winter $\mu g\ N_2O\ m^{-2}d^{-1}$	Total winter flux $g\ N_2O\ m^{-2}$	Summer flux[a] $g\ N_2O\ m^{-2}$
L9	3	3	6	< 100	< 0.01	0.00
L20	3	2	2	517	0.09	0.15
I23	6	5	7	211	0.04	0.11
Grassland	2	3	6	4121	0.74	1.19[b]

[a] Regina et al. (1996).
[b] Nykänen et al. (1995).

Virgin sites and nitrogen poor bogs (see Table 1) showed no winter N_2O emissions (Figure 6). However, considerable N_2O emissions were measured at a farmed peatland, comprising a release of 0.7 g N_2O m^{-2} during the winter season (Table 4). N_2O release from drained forested bogs and fens were much lower, 0–0.09 g N_2O m^{-2} (Table 4, Figure 6, Figure 7), but demonstrated a similar tendency of higher autumn and spring emissions. Availability of nitrate, either due to fertilization or increased decomposition, seems to favour the N_2O formation in drained peatlands (Martikainen et al. 1993; Nykänen et al. 1995).

Drainage had increased winter soil respiration markedly at sites I7, L9 and L20 as compared with the natural reference sites I6, L8 and L19, respectively (Figure 6, Table 3). The mean increase in CO_2 release from the bog sites was 24%, but comparison of the natural and drained fen sites was problematic due to uncertainties in the flux estimates for site L19. The reason for the low CO_2 fluxes in L19 (Table 3) could be in the freezing of the wet surface of L19 into solid ice. CH_4 emissions from the drained sites had decreased to 14–86% of those in the natural state at the less effectively drained sites with summer average water tables below 40 cm (Silvola et al. 1996), but had practically ceased or turned to net consumption in the effectively drained sites L20 and I23. The differences caused by drainage in summertime peat CO_2 release (Silvola et al. 1985; Silvola et al. 1996), and those in summer CH_4 emission (Nykänen et al. 1996), thus also prevailed during winter. The vertical concentration gradients measured from the snowpack supported the chamber results, e.g. the consumption of CH_4 at site I23 was indicated by a decrease in gas concentration in the snow (Figure 7).

Winter fluxes compared with total annual release

Winter CO_2, CH_4 and N_2O release from the peatland sites sampled occasionally was estimated from the average daily fluxes and the duration of snow cover, 180 days. These figures are presented together with the growing-season fluxes (May 15–November 15) estimated for the sites in Table 3 and 4. The winter CO_2 and CH_4 fluxes calculated in this way were between 30 and 76 g CO_2-C m^{-2}, 0.2 and 6.0 g CH_4-C m^{-2} for the virgin mires, while the range for CO_2-C was from 48 to 86 g m^{-2} and for CH_4-C from –0.02 to 0.3 g m^{-2} in the drained peatlands, respectively. The winter CO_2 emissions estimated average 25% of the total annual peat CO_2-C release from the virgin bog sites, while the proportion in a minerotrophic virgin fen was 14%.

Proportion of winter CO_2 emissions from the annual total were surprisingly large, 33% the *Sphagnum fuscum* pine bog I6 and 38% at its drained counterpart I7, but this can perhaps be explained by a short ombrotrophic history of the bog. According to microscopic peat analysis, the present bog peat reaches only 10–20 cm deep (Kimmo Tolonen, personal communication), below which the peat contains *S. papillosum* and *Scheuchzeria palustris* that indicate minerotrophy in Finland. Thus the basic level of peat decomposition could be high, supporting CO_2 release similar to that at site I23 (Figure 6), while the low summertime efflux (Table 3, Silvola et al. 1996) was sustained by an ombrotrophic surface layer with sparse vascular vegetation. Unexpectedly low CO_2 and CH_4 emissions were measured at a fen with constantly high water table, site L19, where solid ice cover may have retarded the gas emissions and, on the other hand, caused oxygen deficiency for the aerobic decomposers.

The CO_2 emissions estimated here (Table 3) are of similar magnitude to that quoted for a poor heath pine forest in eastern Finland by Pajari (1995), 43 g C m^{-2}, and those for subalpine sites in North America, 35–174 g C m^{-2} over a longer period of 235 days (Sommerfeld et al. 1993). Tundra soil was estimated to release 30 g C m^{-2} (Zimov et al. 1993), while a fertile *Hylocomium–Myrtillus* spruce forest floor in Finland was reported to release very much more CO_2 during the period of snow cover, about 160 g C m^{-2} (Havas & Mäenpää 1972).

The CH_4-C winter efflux in our data for undisturbed natural peatlands amounted to 5–33% of the annual methane efflux, figures similar to those reported by Dise (1992) for northern Minnesota, with a climate resembling that in Finland. The highest proportions were encountered at ombrotrophic bogs, where low production and lower summertime water tables keep the annual CH_4 emissions low. On the other hand, our proportions were somewhat larger than reported for the annual total methane release from a temperate fen, 2–9%, in New Hampshire, where the winter season is much shorter (Melloh & Crill 1996). The proportion of winter effluxes of annual net CO_2 and CH_4 release from natural peatlands seems to increase towards the high latitudes due to a longer winter period. The larger winter (and summer) CO_2 and CH_4 release in fens than in bogs can probably be explained by differences in the vegetation, summertime hydrology and litter quality. The peat dominated by sedge remains in fens is perhaps more easily degradable during the winter than the peat formed from hummock-forming *Sphagnum* species growing in the bogs (Johnson & Damman 1991). In bogs aerobic decay processes turn the litter into a less degradable form (Hogg 1993). More substrates may also be introduced into anoxic layers in fens with higher summer water table by deep-rooted sedges than in bogs with generally lower summer water tables and shrubs having more superficial root systems.

Winter C losses, concerning mainly CO_2-C but also CH_4-C, have a marked influence on the C balance of virgin mires. At the different microsites in the intensive fen site, the winter CO_2 release was 34–51% of the summertime net ecosystem production, while 8–17% of the annual CH_4 release occurred during the snow-covered period (Alm et al. 1997). Carbon losses from our virgin study sites were even larger than long-term average C accumulation as estimated by Tolonen & Turunen (1996), 24.0 g C $m^{-2}a^{-1}$ for Finnish bogs, and 15 g C $m^{-2}a^{-1}$ for fens, respectively.

Winter N_2O fluxes were negligible at all virgin sites and drained bogs, but the emissions on efficiently drained fens L20 and I23 were 28% and 27% of their annual emission, respectively (Table 4). N_2O emissions peaked on the grassland during the onset of winter and during spring thaw, probably enhanced by fertilization (Nykänen et al. 1995), and no less than 38% of the annual N_2O was released from peat between November 15 and May 15.

Conclusions

The snowpack concentration gradient method can give especially CH_4 flux estimates that are similar to surface fluxes obtained using the tedious chamber techniques under conditions of thick, homogeneous snow, provided that gas concentrations within the snowpack are not recently disturbed by e.g. wind. CO_2 and probably also N_2O as water soluble gases seem to be more difficult to measure using the snow gradient method.

Winter CO_2-C and CH_4-C release cannot be ignored in annual C balance calculations for peatlands. CO_2 losses are greatest at efficiently drained grasslands and forested, minerotrophic peatlands, whereas consumption of

CH_4 may continue there even below the snowpack. Low CH_4 fluxes occur on drained bogs throughout the winter and even on drained fens in times when the surface peat is water-saturated. The narrow range of 10–30% in the proportion of winter CO_2 and CH_4 effluxes from annual gas release found in Finnish peatlands suggest that a wider generalization in the boreal zone is possible. Effective agricultural drainage, combined with fertilization, will induce the liberation of N_2O in winter, with maxima during periods of elevated water tables in early spring and late autumn.

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References

Alm J, Talanov A, Saarnio S, Silvola J, Ikkonen E, Aaltonen H, Nykänen H & Martikainen PJ (1997) Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. Oecologia 110: 423–431

Alm J, Schulman L, Walden J, Nykänen H, Martikainen PJ & Silvola J (submitted) Fluxes of CO_2, CH_4 and the carbon balance of a boreal bog with exceptionally low water table. Ecology, in press

Bubier J & Moore TR (1994) An ecological perspective on methane emissions from northern wetlands. TREE 9: 460–464

Clein JS & Schimel JP (1995) Microbial activity of tundra and taiga soils at sub-zero temperatures. Soil Biol. Biochem. 27(9): 1231–1234

Clymo RS (1984) The limits to peat bog growth. Phil. Trans. R. Soc. Lond. B 303: 605–654

Coxson DS & Parkinson D (1987) Winter respiratory activity in Aspen woodland forest floor litter and soils. Soil Biol. Biochem. 19(1): 49–59

Crill PM (1991) Seasonal pattern of methane uptake and carbon dioxide release by temperate woodland soil. Global Biogeochem. Cycles 5(4): 319–334

Crill PM, Bartlett KB & Roulet NT (1992) Methane fluxes from boreal peatlands, Suo 43: 173–182 (1993)

Davidson EA (1993) Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil. In: Oremland RS (Ed) Biogeochemistry and Global Change, Radiatively Active Trace Gases (pp 369–386). Chapman & Hall, NewYork

Dise NB (1992) Winter fluxes of methane from Minnesota peatlands. Biogeochemistry 17: 71–83

Dise NB, Gorham E & Verry ES (1993) Environmental factors controlling methane emissions from peatlands in northern Minnesota. J. Geophys. Res. 98: 10583–10594

Havas P & Mäenpää E (1972) Evolution of carbon dioxide at the floor of a Hylocomium myrtillus type spruce forest. Aquilo Ser. Bot. 11: 40–22

Hogg EH (1993) Decay potential of hummock and hollow Sphagnum peats at different depths in a Swedish raised bog. Oikos 66: 269–278

IPCC (1994) Radiative forcing of climatye change. The 1994 Report of the Scientific Assessment Working Group of IPCC, summary for policymakers (WMO, UNEP)

IPCC (1995) Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York

Johnson LC & Damman AWH (1991) Species-controlled Spahgnum decay on a South Swedish raised bog. Oikos 61: 234–242

Kettunen A, Kaitala V, Alm J, Silvola J, Nykänen H & Martikainen PJ (1996) Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland. Global Biogeochem. Cycles 10(3): 457–471

Laine J, Silvola J, Tolonen K, Alm J, Nykänen H, Vasander H, Sallantaus T, Savolainen I, Sinisalo J & Martikainen PJ (1996) Effect of water-level drawdown on global climatic warming: northern peatlands. Ambio 25(3): 179–184

Laine J, Päivänen J, Schneider H & Vasander H (1986) Site types at Lakkasuo mire complex. Field guide, 35 p. Publications from the Department of Peatland Forestry, University of Helsinki 8. Yliopistopaino, Helsinki 1986.

Lång K, Lehtonen M & Martikainen PJ (1994) Nitrification potentials at different pH values in peat samples from various layers of a drained mire. Geomicrobiol. J. 11: 141–147

Martikainen PJ, Nykänen H, Crill P & Silvola J (1993) Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. Nature 366: 51–53

Martikainen PJ, Nykänen H, Alm J & Silvola J (1995) Change in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophy. Plant Soil 168–169: 571–577

Melloh RA & Crill P (1995) Winter methane dynamics beneath ice and in snow in a temperate poor fen. Hydrological Processes 9: 947–956

Melloh RA & Crill P (1996) Winter methane dynamics in a temperate peatland. Global Biogeochem. Cycles 10(2): 247–254

Nykänen H, Alm J, Lång K, Silvola J & Martikainen PJ (1995) Emissions of CH_4, N_2O and CO_2 from a virgin fen and a fen drained for grassland in Finland. J. Biogeography 22: 351–357

Nykänen H, Alm J, Silvola J & Martikainen PJ (1996) Fluxes of methane on boreal mires with different hydrology and fertility in Finland. In: Laiho R, Laine J & Vasander H (Eds) Northern Peatlands in Global Climatic Change. Proceedings of the International Workshop held in Hyytiälä, Finland, 8–12 October 1995 (pp 127–135). Publ. Academy of Finland 1/96, Edita, Helsinki

Nykänen H, Alm J, Silvola J, Tolonen K & Martikainen PJ (1998) Methane fluxes on peatlands with different hydrology and fertility in southern and middle boreal zone in Finland. Global Biogeochem. Cycles 12(1): 53–69

Pajari B (1995) Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperatures and atmospheric carbon concentration. Plant Soil 168–169: 563–570

Regina K, Nykänen H, Silvola J & Martikainen PJ (1996a) Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity of the peat. Biogeochemistry 25: 401–418

Regina K, Nykänen H, Silvola J & Martikainen PJ (1996b) Fluxes of nitrous oxide and nitrification on a drained and forested boreal peatland treated with different nitrogen compounds. In: Laiho R, Laine J & Vasander H (Eds) Northern Peatlands in Global Climatic Change. Proceedings of the International Workshop held in Hyytiälä, Finland, 8–12 October 1995 (pp 154–157). Publ. Academy of Finland 1/96, Edita, Helsinki

Roulet NT, Ash R & Moore TR (1992) Low boreal wetlands as a source of atmospheric methane. J. Geophys. Res. 97: 3739–3749

Ruuhijärvi R (1983) The Finnish mire types and their regional distribution. In: Gore AJP (Ed) Ecosystems of the World, Vol. 4B Mires: Swamp, Bog, Fen and Moor (pp 47–65). Regional Studies. Elsevier, Amsterdam

Saarnio S, Alm J, Silvola J, Nykänen H & Martikainen PJ (1996) Seasonal and spatial variation of CH_4 emission in an oligotrophic pine fen. In: Laiho R, Laine J & Vasander H (Eds) Northern Peatlands in Global Climatic Change. Proceedings of the International Workshop held in Hyytiälä, Finland, 8–12 October 1995 (pp 171–177). Publ. Academy of Finland 1/96, Edita, Helsinki

Saarnio S, Alm J, Silvola J, Lohila A, Nykänen H & Martikainen PJ (1997) Seasonal variation in CH_4 emission and production and oxidation potentials at microsites on an oligotrophic pine fen. Oecologia 110: 414–422

Shanon RD & White JR (1994) A three-year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry 27: 35–60

Silvola J, Välijoki J & Aaltonen H (1985) Effect of draining and fertilization on soil respiration at three ameliorated peatland sites. Acta For. Fennica 191:1–32

Silvola J, Alm J, Ahlholm U, Nykänen H & Martikainen PJ (1996) CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol. 84: 219–228

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

Tolonen K (1967) Über die Entwicklung die Moore im finnischen Nordkarelien. Ann. Bot. Fenn. 4: 219–416

Tolonen K & Turunen J (1996) Accumulation rates of carbon in mires in Finland and implications for climate change. The Holocene 6(2): 171–178

Zimov SA, Semiletov IP, Daviodov SP, Voropaev YuV, Prosyannikov SF, Wong CS & Chan Y-H (1993) Wintertime CO_2 emission from soils of northeastern Siberia. Arctic 46(3): 197–204