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Temporal and spatial variation in methane emissions from a flooded transgression shore of a boreal lake

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Abstract. Variation of CH_4 emissions over a three-year period was studied in a reed-dominated (*Phragmites australis*) littoral transect of a boreal lake undergoing shoreline displacement due to postglacial rebound. The seasonal variation in plant-mediated CH_4 emissions during open-water periods was significantly correlated with sediment temperature. The highest plant-mediated emission rates (up to 2050 mg CH_4 m^{-2} d^{-1}) were found in the outermost reed zone, where culms of the previous growing seasons had accumulated and free-floating plants grew on the decomposing culms. In reed zones closer to the shoreline as well as in mixed stands of reed and cattail, the maximum daily rates were usually > 500 mg CH_4 m^{-2} d^{-1}. The total plant-mediated CH_4 emission during the open-water period was significantly correlated with the seasonal maximum of green shoot biomass. This relationship was strongest in the continuously flooded (water depth > 25 cm) outermost zones. In this area, emissions through ebullition were of greatest importance and could exceed plant-mediated emissions. In general, total emissions of the open-water periods varied from ca. 20 to 50 g CH_4 m^{-2} a^{-1}, but in the outermost reed zone, the plant-mediated emissions could be as high as 123 g CH_4 m^{-2} a^{-1}; ebullition emissions from this zone reached > 100 g CH_4 m^{-2} a^{-1}. The proportion of CH_4 released in winter was usually < 10% of annual emissions. Emissions of CH_4 were higher in this flooded transgression shore the than those measured in boreal peatlands, but the role of ancient carbon stores as a substrate supply compared with recent anthropogenic eutrophication is unknown.

Introduction

Due to the high global warming potential of methane (23-fold compared with CO_2 over 100 years) and its increasing concentration in the atmosphere since pre-industrial times, the fluxes of methane from natural and anthropogenic sources have been intensively studied for the past two decades (reviewed by Khalil and Shearer 2000; Houghton et al. 2001). At present, about 40% of global emissions of methane to the atmosphere has been estimated to originate from natural and agricultural wetlands (Hein et al. 1997; Lelieveld et al. 1998). Methane is produced by methanogenic Archaea in anoxic conditions and transported to the atmosphere by diffusion, ebullition or aerenchymal plants growing in water-logged soils and sediments (e.g., Chanton and Dacey 1991; Kiene 1991). In northern areas, most studies are from peatlands, where the marked inter-annual, seasonal and spatial variation of methane emissions is often related to variation of soil temperature, plant growth and water level (reviewed e.g., by Crill et al. 1992; Bubier and Moore 1994; Nykänen et al. 1998; Joabsson and Christensen 1999). Much less attention has been paid to freshwater lakes. Globally, most freshwater bodies are quite shallow with extensive habitats for aquatic macrophytes, which form one of the most productive ecosystems on earth (Westlake 1982). Northern areas alone are estimated to contain millions of lakes that have a mean depth of less than three metres and a littoral zone that is dominant to the pelagic zone (Wetzel 1990). For instance, in Finland, lakes cover ca. 10% of the surface area, and more than 95% of the 190 000 lakes are smaller in area than 1 km^2 (Raatikainen and Kuusisto 1990). A special characteristic of northern lakes, due to the glaciation history, is that shoreline displacement is common. Thus, numerous lakes with flooded ancient shores exist (cf. Lappalainen 1962; Saarnisto 2000), some of which have originally been peatlands.

Earlier studies from the littoral emergent vegetation zones of boreal lakes have shown higher emissions of methane per area unit (Alm et al. 1996; Hyvönen et al. 1998; Juutinen et al. 2001) than those commonly measured from boreal peatlands (Nykänen et al. 1998). Thus, we wanted to study spatial and temporal variation of methane release in a littoral zone with a high biomass of emergent vegetation to find out how the methane emissions are related to the dynamics of vegetation during the growing season and to the variation in temperature, solar radiation and water level. The study was carried out in a reed-dominated (*Phragmites australis* (CAV.) TRIN. EX STEUD) littoral zone of a boreal lake over a three-year period (1997–1999). Due to shoreline transgression, this area is a submerged ancient peatland. Preliminary results on seasonal and diel variations of methane emissions from the area in 1997 have been published in Ojala et al. (2000). A more detailed description of the diel cycle of methane emissions can be found in Käki et al. (2001). The results on the impact of detritus quality on methane production potential, and the relationship between methane emission and production of all littoral vegetation (including algae and free-floating plants) are presented in Kankaala et al. (in press).

Materials and methods

Study site

Lake Vesijärvi is located in southern Finland (61°05′ N, 25°30′ E). The lake was badly eutrophicated by sewage waters but was restored in the 1990s by large-scale biomanipulation through coarse fish removal. Lake Vesijärvi is divided into four main basins by sounds and shallows. Its surface area is 109 km^2, mean depth 6.0 m and shoreline length 180 km (Keto et al. 1992). According to a geological study, the lake is tilting because of postglacial rebound, which is more rapid at the NW than SE shore (Saarnisto et al. 1994). Our study area on the SE shore is an ancient peatland with a peat cover of several metres (Dr. H. Pajunen, Geological Survey of

Table 1. Mean content of organic matter (± SE) in the uppermost 30-cm layer of the sediment expressed as loss on ignition (LOI,% of dry weight). Samples were taken on 2 September 1998 (n = 3). Root and rhizome biomass of macrophytes (20 August 1999, n = 5) and mean densities of shoots in July–August (1997–1999) in different vegetation zones are also displayed. (nd = no data).

Vegetation zone	Sediment LOI	Root and rhizome biomass kg DW m^{-2}	Mean density of shoots m^{-2}
Inner reed zone	84.7 ± 3.4	2.6 ± 0.3	78
Inner cattail-reed zone	84.6 ± 5.7	nd	44
Outer cattail-reed zone	68.8 ± 6.9	3.6 ± 0.5	46
Outer reed zone	54.5 ± 4.6	2.0 ± 1.2	24
Yellow water lily zone	43.6 ± 2.1	nd	6

Finland, personal communication), but due to shoreline transgression, the area has been flooded and presently supports a dense, reed-dominated vegetation stand. The study site is located in the sheltered bay Kilpiäistenpohja. The area of the bay is 49.1 ha and vegetation covers 20.3 ha. The most dominant species of the emergent vegetation is common reed (*Phragmites australis* (CAV.) TRIN. EX STEUD.), which covers 7.8 ha. Cattail (*Typha latifolia* L.) is also abundant, comprising 1.9 ha. In the community of floating-leaved plants, yellow water lily (*Nuphar lutea* L. Sibth. and Sm.) predominates and covers 3.6 ha. Among ceratophyllids, ivy-leaved duckweed (*Lemna trisulca* L.) is most abundant.

The study was carried out within a perpendicular transect extending from the outer edge of the grass meadow to the outer edge of the zone of floating-leaved plants. The length of the transect was 60 m, which was divided into five zones based on the dominating species, its abundance and water depth. These zones (from innermost to outermost) are the inner reed zone, the inner cattail-reed zone, the outer cattail-reed zone, the outer reed zone and the yellow water lily zone (cf. Käki et al. 2001). The mean shoot number in summer in the inner reed zone was 78 m^{-2}; in other zones, the density was considerably lower (Table 1). The inner reed zone and the cattail-reed zones were in an area where the water table was usually < 10 cm, and only during the spring flood it was > 20 cm above the peat layer. In the outer reed zone and the water lily zone, the water depth was 30–70 cm, and ivy-leaved duckweed (*Lemna trisulca*) formed thick mats between the sparse shoots. In the inner cattail zone, mosses (*Sphagnum* spp., *Calliergon* sp.) and willows (*Salix* spp.) grew among emergent macrophytes. The organic matter content of the sediment, sampled on 2 September 1998 and analysed with standard methods (loss on ignition,% of DW; Table 1), was highest in the two inner zones, decreasing towards the outer zones.

Measurements

The methane emission measurements were carried out from boardwalks using static chambers made of transparent acrylic plastic. Three replicate chambers were used in each vegetation zone. For a more detailed description, see Käki et al. (2001). In late summer and autumn, when the reeds had reached their maximum length (1.5–2.5 m), the plants were gently folded in the chambers. At the time of gas sampling, air temperature inside the chamber was measured with a mercury thermometer. The number of samplings per year varied according to the zone; it was 8–11 and 11–12 during 27 May–5 November 1997, and 19 May–16 December 1998, respectively, when samples over the open-water period were taken fortnightly. In 1999, samples were taken once a month from January to September. In December–March, when the lake had an ice cover and snow on top of that, only the space above the snow surface was taken into account in determining the volume of measuring chambers.

Gas samples for methane analyses were collected into 60-ml syringes equipped with three-way stopcocks at 3-min intervals for a period of 9 min. In 1997, the interval was 4 min and the period was 16 min. The samples were analysed by gas chromatography (5710A, Hewlett Packard). The rate of methane increase within the chambers was calculated from linear regressions of concentration measurements versus time. Only time series with t_0 values < 2 ppm were regarded as undisturbed and thus accepted in the estimates. In the outer reed zone, the increase in concentration was often step-wise, indicating that methane emissions largely occurred by ebullition; in these cases, the rates were calculated from the difference between two points (0 and 9 min). For the outer reed zone, the results were expressed separately for plant-mediated emissions and total emissions, the latter also including emissions from ebullition. For a more detailed description of gas analyses, see Käki et al. (2001). The information on diel variations in emission rates (Käki et al. 2001) was applied in calculations of daily rates. For the time periods when solar radiation was < 20 W m^{-2}, night values of emissions were applied; for all other times, we used day values. In the inner reed zone, night emissions were 40% lower than day time emissions, whereas in the outer cattail-reed zone, the corresponding proportion was 50%. Because no significant diel changes in methane emissions were present in the outer reed zone, daytime values were used for day and night. From the daily values, total emissions over open-water period and annual total emissions (g CH_4 m^{-2} a^{-1}) were estimated by areal integration for each zone separately. Since the dominating plants of the study area apply a pressurized ventilation mechanism for gas exchange (Dacey 1981; Armstrong and Armstrong 1991), the results obtained by using the static chambers without cooling underestimate rather than overestimate the methane emissions.

In the yellow water lily zone, gas bubble formation was quantified with six subsurface bubble collectors (area 0.03 m^2) fastened to the boardwalks (Huttunen et al. 2001). The gas collections lasted 1–3 days and the volume of trapped gas was checked from the displacement of water in a 60-ml syringe. Ivy-leaved duckweed occasionally blocked some of the collectors or water level was so low that the collectors did not work; the number of successful collections thus varied between 2 and 6. Methane concentration of bubble gas was determined with gas chromatography on 17 September 1999 from gas trapped in bubble collectors (n = 4) immediately after disturbing the sediment.

Sediment temperature at a 30-cm depth was recorded on a continuous basis with Tinytag IP 68 loggers (Orion Group). In 1997, two loggers, one in the inner reed zone and another in the inner fringe of the outer reed zone, were installed for the time period 1 August–4 November. In 1998 and 1999, only one logger in the outer cattail-reed zone was in use for recording periods 19 May–4 November and 29 April–15 September, respectively. The recording interval was 15 min in 1997 and one hour in 1998 and 1999. Air temperature (1.7 m above the sediment surface) was recorded continuously by a Tinytag with a recording interval of 15 min. Solar radiation (Wm^{-2}) (pyranometer CM6B; Reino Rehn Ky) in 1997–1999 and air temperature in 1997 were measured on the roof of a building ca. one kilometre from the study area. The time interval between these measurements was 2 min. Official hydrographs for water level fluctuation in Lake Vesijärvi were available for the measuring periods.

At each sampling, the above-ground biomass of green shoots in the chambers was determined; 15–30 stems growing close to the particular measuring chamber were cut, oven-dried at 60 °C to constant mass and weighed. The shoot biomass was calculated by multiplying the shoot number by the average weight of the shoot. The below-ground biomass was sampled on 20 August 1999 in the inner reed zone, outer cattail-reed zone and outer reed zone with a steel corer (length 70 cm, diameter 8 cm, n = 5 in each zone). The roots (including fine and coarse material) and rhizomes were gently washed, oven-dried at 60 °C to constant mass and weighed.

The differences in seasonal methane emissions were analysed statistically using one- way ANOVA (Systat 5.0 or 9.0 program packages). Tukey's honestly significant difference (HSD) test was applied as a post hoc test. The roles of shoot biomass and sediment temperature were analysed using non-linear and linear regression models. For the methane emission vs. sediment temperature relation, an exponential model $y = a*e^{bx}$ was applied, and for the emission vs. shoot biomass relation, we used the linear equation $y = a + bx$. In both equations, y refers to methane emissions; however, in the first equation x refers to sediment temperature and in the second equation to shoot biomass.

Results

Seasonal variation

During the ice-free period methane emissions from the inner reed zone showed a significant seasonal pattern (ANOVA, $p < 0.05$). The emissions (range 11–1180 mg CH_4 m^{-2} d^{-1}; Figure 1) were highest in July and August. In the inner cattail-reed zone, the seasonal pattern of methane emissions (range 31–1130 mg CH_4 m^{-2} d^{-1}) was less pronounced than in the inner reed zone, and only in 1998 did the maximum values in July differ significantly from most of the determinations (ANOVA, $p < 0.05$). In the outer cattail-reed zone, the CH_4 emission rates were

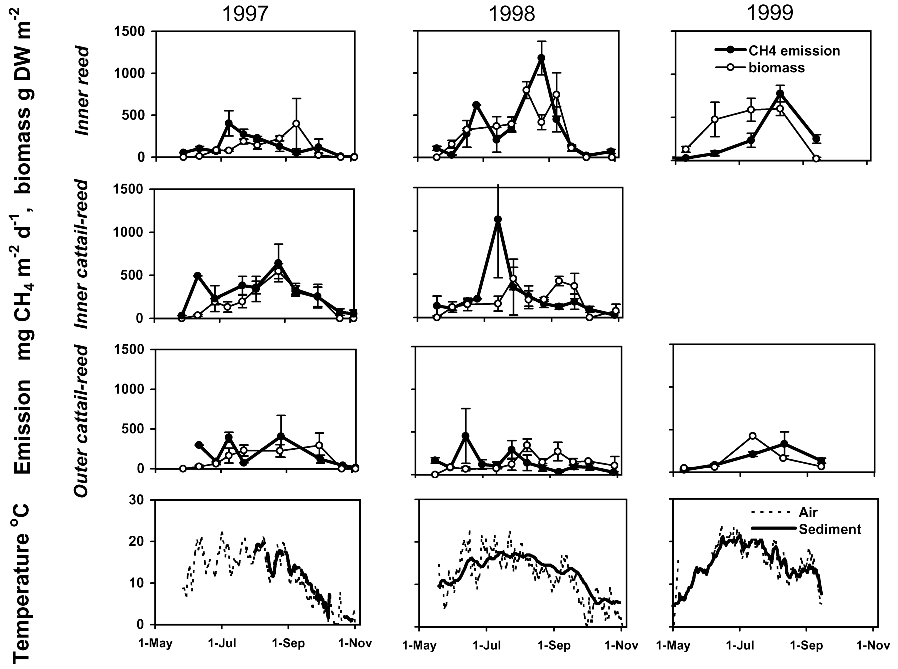

Figure 1. Seasonal variation in plant-mediated methane emission (mg CH_4 m^{-2} d^{-1}) and biomass (g DW m^{-2}) of green shoots in 1997–1999 in the inner reed, inner cattail-reed and outer reed zones. The bars are for values of SE. Also displayed are daily means of air and sediment temperature (°C).

slightly lower (range 33–450 mg CH_4 m^{-2} d^{-1}) than in the other zones and show no strong seasonal patterns during the ice-free period (Figure 1).

In the outer reed zone, a large proportion of measurements failed because of difficulties in sampling due to bubbling of gas from underlying peat. During the ice-free period the pattern of methane emissions from this zone was irregular, but emissions were considerably higher than from the other zones studied (range 12–3570 CH_4 m^{-2} d^{-1}; Figure 2). The regularly observed step-wise increase in methane concentration in chambers indicated that methane emissions in this zone largely occurred by ebullition. Especially in 1997 and 1999, when the water level was lower than in 1998 (Figure 2), the role of ebullition was significant. When methane concentration increased linearly in the chambers, emissions were interpreted to be plant-mediated and are shown separately in Figure 2 (range 12–2050 CH_4 m^{-2} d^{-1}).

In the yellow water lily zone, the methane emissions largely occurred by ebullition (range 5–690 CH_4 m^{-2} d^{-1}; Figure 2). Reliable values for plant-mediated CH_4 emissions could only be obtained for summer 1998 (range 0–610 mg CH_4 m^{-2} d^{-1}), whereas in summer 1997, observations were sporadic. Plant-mediated emissions were not measured in this zone in summer 1999. The seasonal pattern of bubbling, recorded by bubble collectors, was irregular, and each year, the maximum ebullition rate was recorded at different times between June and August. In 1999, autum-

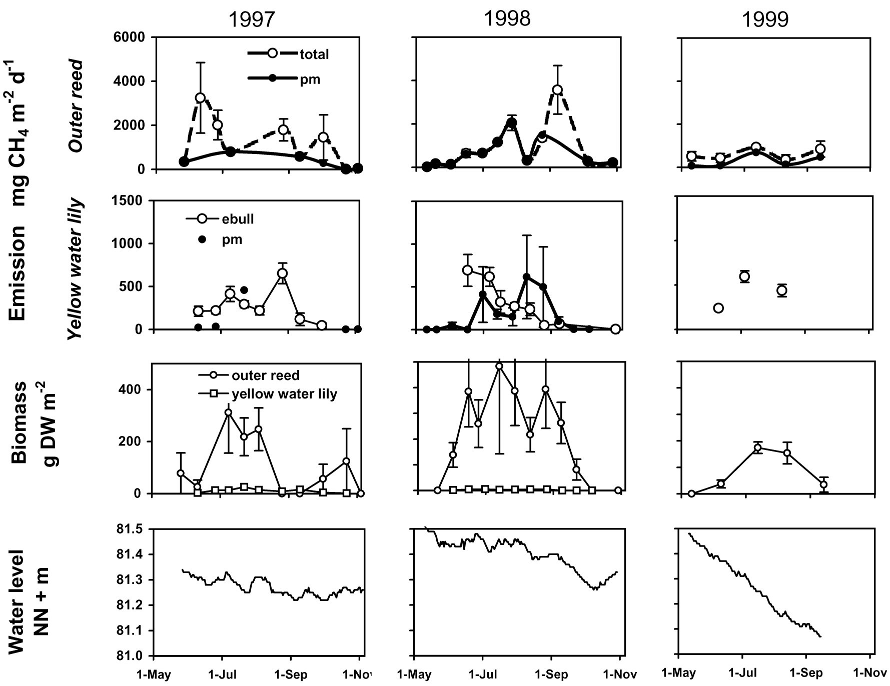

Figure 2. Seasonal variation in methane emission (mg CH_4 m^{-2} d^{-1}) and biomass (g DW m^{-2}) of green shoots in 1997–1999 in the outer reed and yellow water lily zones. In the outer reed zone, total emission estimates include release of CH_4 by ebullition and through plants, with the share of plant-mediated (pm) emission shown separately. In the yellow water lily zone, plant-mediated (pm) CH_4 emissions and those by ebullition are shown separately. The bars are for values of SE. Water level fluctuation in Lake Vesijärvi during the study period is also displayed (NN = mean sea level at Helsinki port in 1900).

nal emissions could not be estimated since, due to the decreasing water level (Figure 2), use of gas collectors was terminated in August.

In winter, when the lake was covered by ice and snow, diffusion of methane from the zones of emergent vegetation was measured regularly; these methane emissions were lower (range 0–74 CH_4 m^{-2} d^{-1}; Figure 3) and the spatial and temporal variation of emissions was less clear than those observed during the ice-free period.

Annual variation

In the inner reed zone, the calculated total methane emission for the open-water period varied between 22 and 58 g CH_4 m^{-2}, and the interannual variation was thus > 100% (Table 2). In the inner cattail-reed zone, the total methane emissions for the open-water season (43–51 g CH_4 m^{-2}) were higher than in the outer cattail-reed zone (23–30 g CH_4 m^{-2}).

In the outer reed zone, the total plant-mediated methane emissions during the open-water periods in 1997, 1998 and 1999 were ca. 81, 123 and 38 g CH_4 m^{-2},

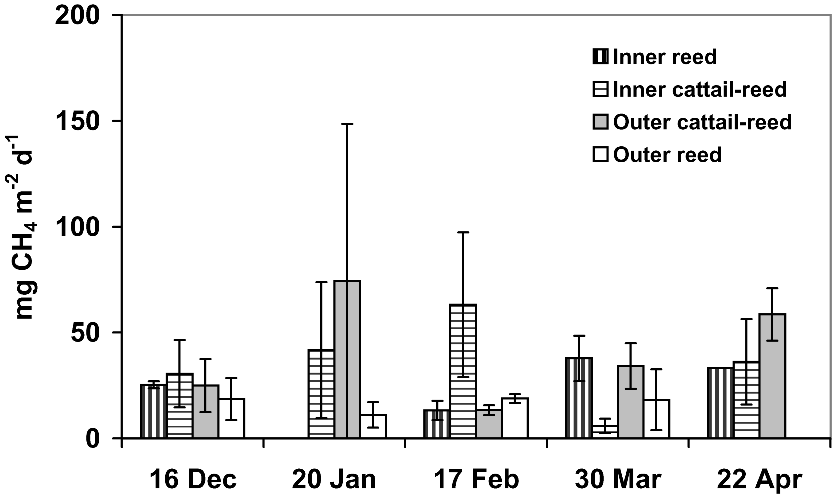

Figure 3. Variation of methane emissions (mg CH_4 m^{-2} d^{-1}) in winter 1998–1999 in the different vegetation zones. The bars are for values of SE.

Table 2. Total emissions of methane (g CH_4 m^{-2}) from the different vegetation zones during open-water periods in 1997–1999 and during winter 1998–1999. For the yellow water lily zone, the estimate of methane release through ebullition is based on results from bubble collectors, whereas in the outer reed release through ebullition is estimated from chamber measurements.(nd = no data).

Vegetation zone	Open-water period			Winter
	1997	1998	1999	1998–1999
Inner reed zone	22	58	40	4
Inner cattail-reed zone	51	43	nd	6
Outer cattail-reed zone	30	23	23	7
Outer reed zone, plant-mediated	81	123	38	5
through ebullition	123	51	39	nd
Yellow water lily zone, plant-mediated	nd	28	nd	nd
through ebullition	33	30	nd	nd

respectively, i.e., the interannual variation in this zone was large (Table 2). The corresponding proportions of emissions through ebullition were 60%, 29% and 51%. Since the total area of Kilpiäistenpohja Bay covered by this type of vegetation is known, we could calculate the total annual emission from the whole outer reed zone; in 1997, it was 2530 kg a^{-1}, and in 1998, 2158 kg a^{-1}.

In the yellow water lily zone, the total CH_4 emission through plants could only be calculated for 1998, when it was ca. 28 g CH_4 m^{-2} (Table 2). The emission due to ebullition was as high as plant-mediated CH_4 release in this zone (33 and 30 g CH_4 m^{-2} in 1997 and 1998, respectively). Based on the emission rates and the total area covered by yellow water lily in Kilpiäistenpohja Bay, the total annual plant-mediated emission from this vegetation zone was estimated to be 1008 kg a^{-1}.

No large differences were present in wintertime emissions between the different vegetation zones; the fluxes varied from 4 to 7 g CH_4 m^{-2} (Table 2). Thus, only 6–23% of the annual methane emissions were released in winter. The estimated total annual emission of methane from the littoral zone of Kilpiäistenpohja bay was ca. 9 322 kg a^{-1}, i.e., 701 kg ha^{-1} a^{-1}.

Correlation with sediment temperature and other environmental variables

The seasonal variation in plant-mediated methane emissions during the open-water periods was significantly correlated with the daily mean of sediment temperature (Figure 4). When data for three years were pooled, sediment temperature explained 50.3–60.7% of the variation in emissions in the reed and cattail-reed zones. Since data from the yellow water lily zone were only available for 1998, this zone was excluded from analysis. The correlation between seasonal variation of plant-mediated methane emissions and green biomass of vegetation was less obvious, although the seasonal maxima of CH_4 emissions and shoot biomass often seemed to coincide (Figures 1 and 2); only in the inner cattail-reed zone in 1997 and in the outer reed zone in 1998 were the correlations significant ($p < 0.05$, $r^2 = 0.537$ and 0.592, respectively). Methane emissions from the study area were related to neither daily mean solar radiation (data not shown) nor water level (Figure 2).

When the CH_4 emission estimates of the open-water periods for different vegetation zones were analysed together, no significant correlations between methane emissions and shoot biomass were found. However, total plant-mediated emissions during the growing season were significantly correlated with the maximum shoot biomass when the vegetation zones continuously flooded with water > 25 cm (outer reed zone and yellow water lily zone) were analysed separately from the other zones of water depth < 10 cm (Figure 5). Emission dependence on biomass was greater in the flooded sites ($y = 20.646 + 0.211x$, $r^2 = 0.94$) than in the drier area ($y = 2.89 + 0.071x$, $r^2 = 0.68$). The intercepts of the equations also revealed that non-plant-mediated emissions were of greater importance in the flooded areas; ca. 21 g CH_4 m^{-2} was emitted to the atmosphere by routes other than aerenchymal tissues of green shoots. Ebullition of CH_4 from the outer reed and yellow water lily zones was not correlated with any of the measured environmental variables.

Discussion

A pronounced seasonal variation of methane emissions, i.e., maximum in July and August and low but clearly detectable emissions in winter, typically observed in boreal peatlands (e.g., Dise et al. 1993; Shannon and White 1994; Nykänen et al 1998; Alm et al. 1999), was also found in the vegetated littoral zone of boreal Lake Vesijärvi. Since the seasonal variation in plant-mediated methane emission was more closely correlated with variation of sediment temperature than with fluctuation of other environmental factors (plant biomass, solar radiation, water level), the

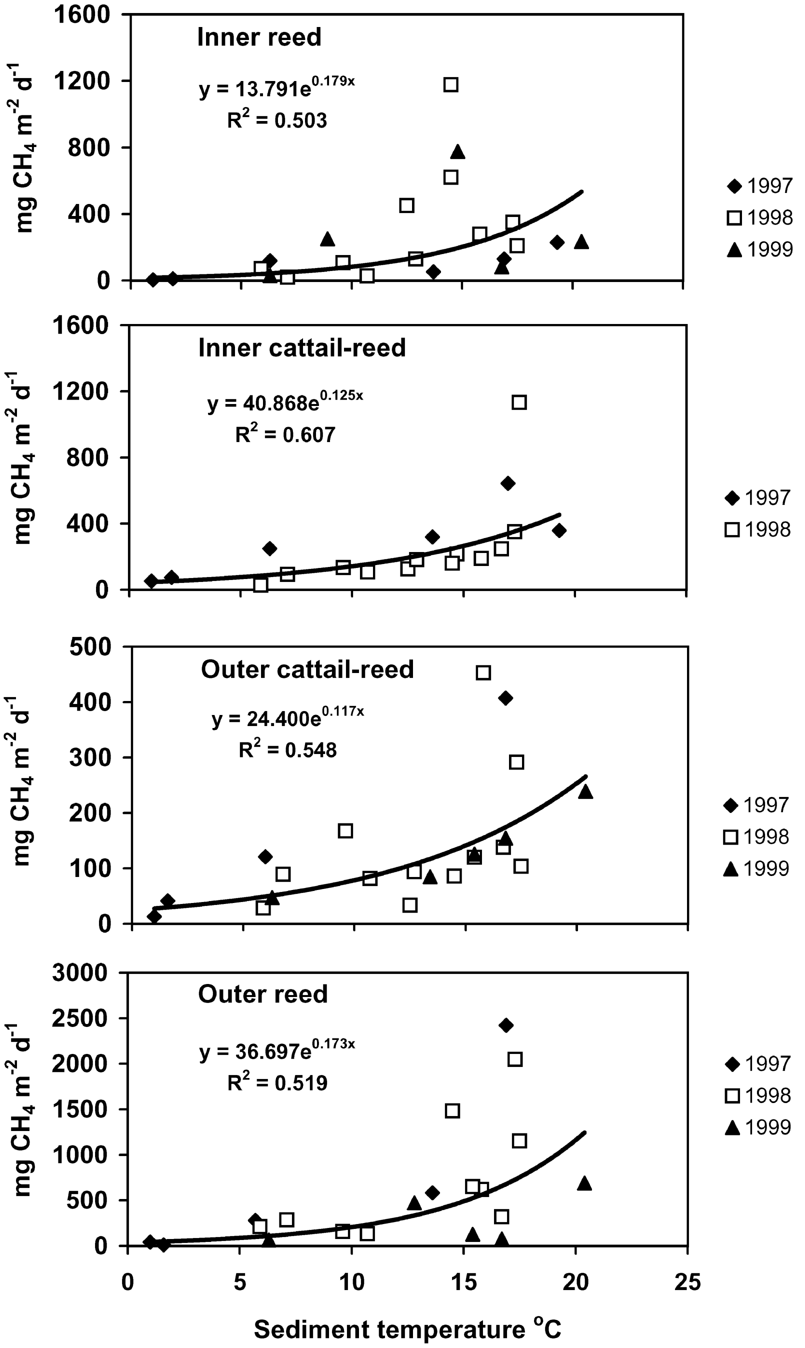

Figure 4. Relation between plant-mediated methane emission (mg CH_4 m^{-2} d^{-1}) and daily mean of sediment temperature (°C) in the different vegetation zones in the 1997–1999 open-water periods.

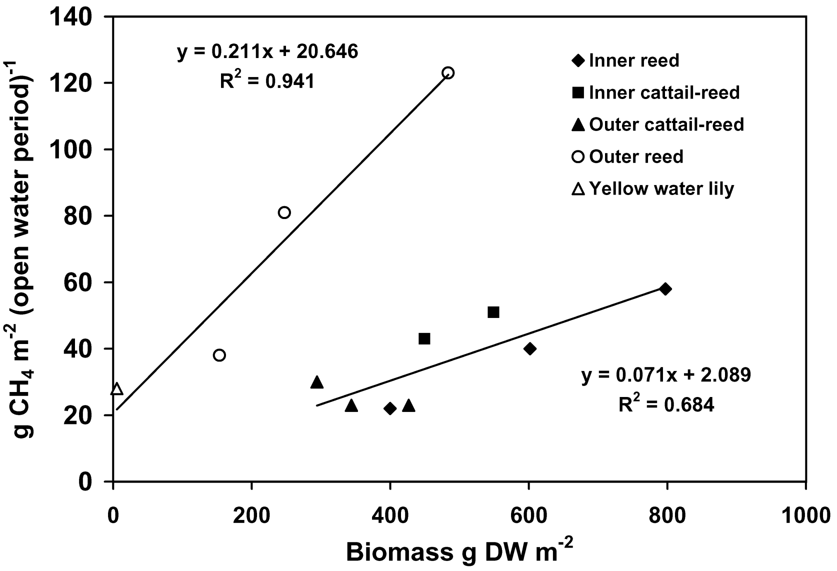

Figure 5. Relation between the seasonal maximum of green shoot biomass and total plant-mediated methane emission during the open-water period. The regression equations are calculated separately for continuously flooded (> 25 cm) vegetation zones (outer reed and yellow water lily zones) and those covered with < 10 cm of water in summer.

temperature-regulated production of CH_4 by methanogens seemed to be the most important controlling factor of CH_4 emissions in our study area. Plant growth has often been shown to control seasonal cycles of methane emissions in vegetated areas of wetlands (e.g., van der Nat and Middelburg 1998a, 2000; Joabsson and Christensen 2001). In *Phragmites*-dominated wetlands, this is related both to effective pressurized ventilation and oxidation of methane in the rhizosphere of the actively growing plants and to release of low-molecular-weight substrates from rhizomes available for methanogens (Kim et al. 1998; van der Nat and Middelburg 1998a, 1998b; Brix et al. 2001). In the field, these factors, together with sediment temperature and water level fluctuation, act simultaneously, and thus, the relationship between plant growth dynamics and methane emission is not always straightforward. For example, in a temperate *Phragmites*-dominated marsh in Nebraska (USA), Kim et al. (1998) observed peak methane emission during the time of highest sediment temperature in August, which occurred 2–3 weeks after the peak shoot biomass production, whereas in a Danish *Phragmites* wetland, the methane emission was maximal during spring and early summer, before the maximum shoot biomass; this was the time of high water table and high availability of labile organic compounds for methanogens (Brix et al. 2001).

Although in our study area seasonal dynamics of methane emission was more weakly related to the variation of plant biomass than to sediment temperature, a clear relationship was found between annual plant production and methane emission; total plant-mediated methane emission of the open-water period was strongly correlated with the seasonal biomass maximum of green shoots. These findings are in accordance with those of Whiting and Chanton (1993) and Joabsson and Christensen (2001), and reflects the importance of plants producing substrates for methanogens and the well-developed root system acting as a gas conduits from the anoxic layer to the atmosphere. Since the seasonal net production of vegetation often correlates with the seasonal maximum of plant biomass (Westlake 1982; Figure 5), we could, by applying the mean carbon content of 38% of DW (Duarte 1992) for *P. australis*, *T. latifolia* and *N.lutea* in Lake Vesijärvi, estimate the proportion of released CH_4 in relation to net production of emergent and floating-leaved vegetation. On a molar basis, in the zones where water depth was < 10 cm (inner reed and both cattail-reed zones), 13.9% of net carbon fixation (above-ground parts) during the open-water period was released as CH_4. This finding is in consistent with Brix et al. (2001), who estimated in *Phragmites* wetlands that up to 15% of net carbon fixation, including below-ground parts, was emitted as CH_4. When water depth was > 25 cm in the littoral of Lake Vesijärvi, the proportion went up to 41.5%; emissions through ebullition were excluded from these calculations, and the estimate is thus very conservative. Although the standing green shoots of plants using pressurized ventilation are overwhelmingly important in gas transport, the role of other routes during the open-water period can also be considerable. In the continuously flooded vegetation zones of Lake Vesijärvi (outer reed and yellow water lily zone), ca. 21 g CH_4 per square metre was emitted to the atmosphere, probably via diffusion through the water column and through standing dead culms. Of the total emission, about 30–60% was released via ebullition, which is typical of non-vegetated or sparsely vegetated water-logged areas (Chanton and Dacey 1991).

Spatial variation in methane emission from the transgression shore of Lake Vesijärvi was influenced by growth conditions created by the ancient anoxic peat layer for *P. australis* and *T. latifolia* and also by high productivity of free-floating plants (Kankaala et al. in press). The sparsely vegetated outer reed zone, where culms of previous growing seasons are accumulated through wave and ice action and free-floating plants, such as *Lemna trisulca* and *Elodea canadensis*, grow on the decomposing culms, is typical of Lake Vesijärvi as a whole (Keto et al. 2000). In our study area, *Lemna trisulca* formed thick mats between the shoots of *P. australis*. In a laboratory experiment, fresh detritus from *Lemna trisulca* supported much higher CH_4 production than detritus from *P. australis* leaves (Kankaala et al. in press). Thus, the high CH_4 emissions from the outer reed zone were influenced by availability of substrates for methanogens. On the other hand, the oxidation potential of the peat was higher in the innermost vegetation zones, which were healthier and denser than the outer zones. In actively growing vegetation stands, the proportion of methane oxidized is usually higher than among senescent plants (van der Nat and Middelburg 1998b; Popp et al. 2000).

Compared with boreal peatlands, the emissions of methane from vegetated littoral areas are high. According to Crill et al. (1992) and Bartlett and Harriss (1993), the daily methane emissions from the northern peatlands during the growing season vary from less than 1 mg to > 2000 mg CH_4 m^{-2} d^{-1}, a range resembling that observed in Lake Vesijärvi. The mean total emissions from May to September at 17 Finnish peatland sites were clearly lower than from the littoral of Lake Vesijärvi: for ombrogenous bogs 8 g CH_4 m^{-2} and for minerogenous fens 19 g CH_4 m^{-2} (Nykänen et al. 1998). In Lake Vesijärvi, methane emissions were highest in stands of reed, especially in the outer reed zone, where total methane emissions were 77–204 g CH_4 m^{-2} during the open-water seasons. These are very high values compared with the June–September emissions from reed and sedge marshes in the littoral zone of two boreal mesoeutrophic lakes (eastern Finland), where Juutinen et al. (2001) measured emissions of 11–13 g CH_4 m^{-2}. In stands of water horsetail in Lake Pääjärvi, which is located only 40 km west of Lake Vesijärvi, the total methane emission over the open-water period was 44 g CH_4 m^{-2} (Hyvönen et al. 1998), comparable with our estimates for the inner reed and the cattail-reed zones (23–58 g CH_4 m^{-2}). In temperate *Phragmites* marshes, the emissions of methane have been within the range observed in the reed zones of Lake Vesijärvi: in Ballards Marsh, Nebraska, USA, 64 g CH_4 m^{-2} in April–October, 80 g CH_4 m^{-2} a^{-1} (Kim et al. 1998); in Vejlerne Nature Reserve, Denmark, ca. 64 g CH_4 m^{-2} a^{-1} (Brix et al. 2001); and in a tidal freshwater marsh in the Scheldt Estuary, the Netherlands, ca. 76 g CH_4 m^{-2} a^{-1} (van der Nat and Middelburg 2000).

In conclusion, total emissions of CH_4 in the littoral zone of boreal lakes may be related to maximum biomass of green shoots. However, in sparsely growing stands, ebullition is of great importance as a route for CH_4, with part of the CH_4 escaping via diffusion and dead culms. The most important environmental factor behind seasonal variation in emissions is probably sediment temperature, which regulates the production of CH_4 by methanogens. CH_4 is emitted throughout the year, although the proportion of CH_4 released in winter is usually low. From a flooded transgression shore, emissions of CH_4 generally tend to be higher than from boreal peatlands, but the role of ancient lacustrine carbon stores as a substrate supply relative to recent anthropogenic eutrophication remains unknown.

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References

Alm J., Juutinen S., Saarnio S., Silvola J., Nykänen H. and Martikainen P.J. 1996. Temporal and spatial variations in CH_4 emissions of flooded meadows and vegetated hydrolittoral. In: Laiho R., Laine J. and Vasander H. (eds), Proceedings of the International Workshop Northern Peatlands in Global Climate Change, Hyytiälä, Finland. Publications of the Academy of Finland, Helsinki, pp. 71–76, 1/96.

Alm J., Saarnio S., Nykänen H., Silvola J. and Martikainen P.J. 1999. Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands. Biogeochemistry 44: 163–186.

Armstrong J. and Armstrong W. 1991. A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. Ex. Steud. Aquat. Bot. 39: 75–88.

Bartlett K.M. and Harriss R.C. 1993. Review and assessment of methane emissions from wetlands. Chemosphere 26: 261–320.

Brix H., Sorrell B.K. and Lorenzen B. 2001. Are *Phragmites*-dominated wetlands a net source or net sink of greenhouse gases? Aquat. Bot. 69: 313–324.

Bubier J.L. and Moore T.R. 1994. An ecological perspective on methane emissions from northern wetlands. Tree 9: 460–464.

Chanton J.P. and Dacey J.W.H. 1991. Effects of vegetation on methane flux, reservoirs and carbon isotopic composition. In: Sharkey T. and Mooney H. (eds), Trace Gas Emissions by Plants. Academic Press, San Diego, pp. 65–92.

Crill P., Bartlett K. and Roulet N. 1992. Methane flux from boreal peatlands. Suo 43: 173–182.

Dacey J.W.H. 1981. Pressurized ventilation in the yellow waterlily. Ecology 62: 1137–1147.

Dise N.B., Gorham E. and Verry E.S. 1993. Environmental factors controlling methane emissions from peatlands in northern Minnesota. J. Geophys. Res. 98: 10 583–10 594.

Duarte C.M. 1992. Nutrient concentration of aquatic plants: Patterns across species. Limnol. Oceanogr. 37: 882–889.

Hein R., Crutzen P.J. and Heinmann M. 1997. An inverse modeling approach to investigate the global atmospheric methane cycle. Global Biogeochem. Cycles 11: 43–76.

Houghton J.T., Ding Y., Griggs D.J., Noguer M., van der Linden P.J. and Xiaosu D. (eds) 2001. Climate Change 2001. The Scientific Basis. Cambridge University Press, Cambridge, UK, 944 p.

Huttunen J.T., Lappalainen K.M., Saarijärvi E., Väisänen T. and Martikainen P.J. 2001. A novel sediment gas sampler and a subsurface gas collector used for measurement of the ebullition of methane and carbon dioxide from a eutrophied lake. Sci. Tot. Environ. 266: 153–158.

Hyvönen T., Ojala A., Kankaala P. and Martikainen P.J. 1998. Methane release from stands of water horsetail (*Equisetum fluviatile*) in a boreal lake. Freshwat. Biol. 40: 275–284.

Joabsson A. and Christensen T.R. 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology 7: 919–932.

Joabsson A., Christensen T.R. and Wallén B. 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Tree 14: 385–387.

Juutinen S., Alm J., Martikainen P. and Silvola J. 2001. Effects of spring flood and water level drawdown on methane dynamics in the littoral zone of boreal lakes. Freshwat. Biol. 46: 855–869.

Kankaala P., Käki T. and Ojala A. Quality of detritus impacts on spatial variation of methane emissions from littoral sediment of a boreal lake. Arch. Hydrobiol. (in press).

Keto A., Hellsten S., Lammi E., Partanen S., Visuri M. and Lampolahti J. 2000. Ruovikoituminen: täydentävät erikoistutkimukset. In: Hellsten S. (ed.), Development of Regulation of Lake Päijänne – Present State of Littoral Zone and Effects of Different Environmental Factors. The Finnish Environment 357., Helsinki, pp. 90–110, (In Finnish with English summary).

Keto J., Horppila J. and Kairesalo T. 1992. Regulation of the development and species dominance of summer phytoplankton in Lake Vesijärvi: predictability of enclosure experiments. Hydrobiologia 243/244: 303–310.

Khalil M.A.K. and Shearer M.J. 2000. Sources of methane: an overview. In: Khalil M.A.K. (ed.), Atmospheric Methane: Its Role in the Global Environment. Springer Verlag, Berlin, pp. 98–111.

Kiene R.P. 1991. Production and consumption of methane in aquatic systems. In: Rogers J.E. and Whitman W.B. (eds), Microbial Production and Consumption of Greenhouse Gases: Methane and Nitrogen. American Society for Microbiology, Washigton, pp. 111–146.

Kim J., Verma S.B. and Billesbach D.P. 1998. Seasonal variation in methane emission from a temperate *Phragmites*-dominated marsh: effect of growth stage and plant-mediated transport. Global Change Biol. 5: 433–440.

Käki T., Ojala A. and Kankaala P. 2001. Diel variation in methane emissions from stands of *Phragmites australis* (Cav.) Trin ex Steud. and *Typha latifolia* L. in a boreal lake. Aquat. Bot. 71: 259–271.

Lappalainen V. 1962. The shore-line displacement on southern Lake Saimaa. Acta Bot. Fennica 64: 1–125.

Lelieveld J., Crutzen P. and Dentener J.F. 1998. Changing concentration, lifetime and climate forcing of atmospheric methane. Tellus 50B: 128–150.

Nykänen H., Alm J., Silvola J., Tolonen K. and Martikainen P.J. 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochem. Cycles 12: 53–69.

Ojala A., Käki T. and Huttunen J. 2000. Methane emissions from a boreal meso-eutrophic lake: an assessment of seasonal and diel variation among emergent vegetation. Verh. Int. Verein. Limnol. 27: 1420–1423.

Popp T.J., Chanton J.P., Whiting G.J. and Grant N. 2000. Evaluation of methane oxidation in the rhizosphere of a *Carex* dominated fen in north central Alberta, Canada. Biogeochemistry 51: 259–281.

Raatikainen M. and Kuusisto E. 1990. Suomen järvien lukumäärä ja pinta-ala. Terra 102: 97–110, (in Finnish).

Saarnisto M. 2000. Shoreline displacement and emergence of lake basins. Geological Survey of Finland, Special Paper 29: 25–34.

Saarnisto M., Kutvonen H. and Rainio H. 1994. Salpausselkä ja jääkausi. In: Saarnisto M., Rainio H. and Kutvonen (eds), Salpausselkä ja jääkaudet. Geologian tutkimuskeskus Opas 36. Geological Survey of Finland, Lahti, pp. 5–43, (in Finnish).

Shannon R.D. and White J.R. 1994. A three-year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry 27: 35–60.

van der Nat F.-J.W.A. and Middelburg J.J. 1998a. Effects of two common macrophytes on methane dynamics in freshwater sediments. Biogeochemistry 43: 79–104.

van der Nat F.-J.W.A. and Middelburg J.J. 1998b. Seasonal variation in methane oxidation by the rhizosphere of *Phragmites australis* and *Scirpus lacustris*. Aquat. Bot. 61: 95–110.

van der Nat F.-J. and Middelburg J.J. 2000. Methane emission from tidal freshwater marshes. Biogeochemistry 49: 103–121.

Westlake D.F. 1982. The primary productivity of water plants. In: Symoens J.J., Hooper S.S. and Compère P. (eds), Studies on Aquatic Vascular Plants. Royal Botanical Society of Belgium, Brussels, pp. 165–180.

Wetzel R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. Verh. Internat. Verein. Limnol. 24: 6–24.

Whiting G.J. and Chanton J.P. 1993. Primary production control of methane emission from wetlands. Nature 364: 794–795.