Fluxes of CO_2 and CH_4 in high latitude wetlands: measuring, modelling and predicting response to climate change

Nicolai S. Panikov

This review covers selected aspects of recent international efforts to measure and model greenhouse gas emission from northern wetlands, to identify the environmental factors that control gas emission, and to investigate wetlands' responses (particularly with respect to gas emission) to global change. Both bottom-up and top-to-bottom approaches, based respectively on local observations plus inventory of gas fluxes and inverse modelling of global circulation, agree on the size of the high latitude (>60°N) contribution to global methane, which should be about 13% or 70 Tg/year. It has been shown that winter and spring fluxes are an essential part in the annual budget of CH_4 and especially CO_2 exchange (varying from 5 to 50%). Soil micro-organisms were shown to be able to respire during winter even at −16°C. In comparison to aerobically respiring organisms, anaerobic methanogenic bacteria were less active in frozen soil, although they are subjected to significant stimulation by soil freeze-thaw cycles. The absence of immediate coupling of methanogenesis with plant photosynthesis implies that substrates for methane formation are derived from peat decomposition rather than from root exudation.

N. S. Panikov, Institute of Microbiology, Russian Academy of Sciences, Prospect 60-Let Octyabrya 7/2, Moscow 117811, Russia.

Introduction

Increases in the concentration of greenhouse gases since pre-industrial times (i.e. since 1750) have led to a positive radiative forcing of climate, tending to warm the surface and to produce other changes in climate (Houghton et al. 1995). Global circulation models (GCMs) predict an increase in global mean temperature of 3°C by the end of next century; they also indicate that high northern latitudes will warm more than the global mean in winter (Walsh 1991; Maxwell 1997). Warming is indicated by: reduction in sea ice extent and snow cover, particularly in spring (Robinson & Dewey 1990); lowering of surface-based temperature inversion depths (Bradley et al. 1993); retreat of mountain glaciers; and rise of near surface air temperature by 0.3–0.6°C since the late 19th century (Houghton et al. 1995).

The northern ecosystems are a significant source of greenhouse gases. Even if the present-day fluxes are modest, the large size of the reserves of conserved organic matter implies that potential, warming-induced CO_2, CH_4 and non-methane hydrocarbons (NMHC) fluxes could be very large (Vourlitis & Oechel 1997). Warming and drying of tundra areas could result in massive losses of CO_2. There are data indicating that some tundra areas have already shifted from net carbon sinks to sources in the last 10–15 years (Oechel, Vourlitis et al. 1995). Warming of areas which remain wet could stimulate methane formation and increase already large methane releases to the atmosphere. Trace gas fluxes are also expected to be sensitive to changes in plant and microbial community distribution, which might be driven by perturbations of biological equilibrium and have a counter-intuitive response.

Trace gas fluxes vary in a complex way across space and over time; gas formation and transport involve various physiological and physico-chemical mechanisms. The most evident gaps in this field were identified as follows (see IASC-GCTE Working Group's FATE [Feedbacks from Arctic Terrestrial Ecosystems] document, accessible via the internet): deficiency of flux data on gas,

especially on winter emissions from northern Eurasia and the high Arctic; poor understanding of the mechanisms behind observed fluxes at a physiological level (formation of belowground substrates, microbial, enzymatic, and microfaunal interactions, etc); the lack of generalized integrated approaches, and long-term and spatially extensive measurements. The progress achieved recently by the international efforts of Arctic scientists to fill in the indicated gaps is summarized here.

Contribution of northern wetlands to global methane budget

One of the most important objectives is to determine circumpolar CO_2 and CH_4 fluxes, quantify the rates of gas emission in different parts of the Arctic and reveal the trends associated with global climatic change. There are two complementary approaches to this: bottom-up and top-down approaches. The first one is based on the long-term monitoring of gas emission via a network of field stations or sites that cover the main types of habitats. At its simplest, the total circumpolar emission, E is estimated as a sum:

$$E = \sum_{i=1}^{n} A_i F_i$$

where n is the number of the types of northern ecosystems differentiated in terms of easily mapped features like vegetation, soil properties, relief, geomorphology, etc.; A is the area of each type; and F is characteristic annual emission. The sets of A_i and F_i are assumed to be constants. Instead of sum, one can use the more or less complicated functional dependence of F on environmental parameters, say on soil/air temperature, water table level, mineral content in soil, etc., to evaluate regional emission (Bouwman et al. 1999).

Bottom-up approach: geographical coverage, variation in spatial and temporal fluxes

A thorough survey of available data is beyond the scope of this paper; readers are referred to reviews by Harris et al. (1993) and Vourlitis & Oechel (1997). The most intensive studies and the longest observations of gas fluxes have been obtained in North America, mainly the Alaskan North Slope (Whalen & Reeburgh 1988, 1992; Oechel, Vourlitis et al. 1995; Baldocchi et al. 1996; Oechel, Cowles et al. 1994, 1995). Currently these sites are the main focus of the Atmospheric Radiation Measurement (ARM) programme, supported by the US Department of Energy, and the US National Science Foundation Land-Atmosphere-Ice-Interactions (LAII) flux programme (Weller et al. 1995). There are similar programmes funded by EU and national IGBP programmes of several European countries (LTEEF-Finland, BERI, Danish Trace Gas Flux Study, CONGAS, etc.).

In northern Eurasia, extensive measurements of gas emission were initiated in the late 1980s. These were either short-term measurements across geographical transects or long time series of flux at single sites. The first approach is illustrated by chamber measurements of CO_2 and CH_4 fluxes across the Russian Arctic (Christensen, Jonasson et al. 1995). The second approach is realized in a number of field stations where gas fluxes are measured mainly during the summer season (Zimov et al. 1993; Panikov, Sizova et al. 1995; Panikov, Glagolev et al. 1997).

The general tendencies of spatial and temporal flux variation can be formulated as follows. First, there are evident temperature related variations: even within northern wetlands the highest net fluxes occur in warmer soils, the maximal values being attained in the boreal zone. Seasonal variation also follows a temperature dynamic curve, although winter, autumn and spring emission are often essentially non-zero (see below). Second, there is always enhanced emission from wetlands patches covered by vascular plants (*Eriophorum*, *Carex*, *Menianthes*) as compared with pure *Sphagnum* lawn (due to the effects of vascular transport of methane and higher productivity of graminoids as compared with mosses). Third, variations of the water table affect CO_2 and CH_4 emission in an opposite ways, methane fluxes being stimulated and carbon dioxide suppressed by a rising water table. However, the range of fluxes varies so widely that uncertainty in regional and global estimates remains large and very much dependent on site-specific features of each particular study. For example, extensive measurements by various techniques over Hudson Bay Lowland (Roulet et al. 1994) lead to the conclusion that

northern wetlands are a modest source of atmospheric methane, with an average July emission of 10–20 mg CH_4/d/m^2 and a regional flux no more than 0.5 Tg CH_4 per year. On the other hand, Alaskan wet meadow and shrub/tussock tundra have an average summer emission up to 100–700 mg CH_4/d/m^2 (Whalen & Reeburgh 1992), extrapolating to 42 ± 26 Tg CH_4/year. A similar or even higher emission level was found in the boreal zone both in Minnesota (Dise 1992; Melloh & Crill 1993) and in west Siberia (Panikov, Sizova et al. 1995; Panikov, Glagolev et al. 1997). A modelling approach based on empirical relationships between CH_4 fluxes, environmental factors and NPP provides some compromise between the two cited extremes, say, 20 ± 16 Tg CH_4/year from northern wetlands globally (Christensen, Prentice et al. 1996). However, the uncertainty in regional/global estimates is very disappointing and calls for alternative ways to solve the problem. An inverse modelling approach is one such solution.

Top-down approach: inverse modelling

Information on temporal and spatial variation of CH_4 and CO_2 emissions from soils is deduced from observational data on gas mixing ratios in air (obtained via a network of NOAA/CMDL field stations scattered over the globe, mainly in oceanic regions far from industrial sources). These data are fitted to a 3-D atmospheric transport model, which is combined with a tropospheric background chemistry module and accounts for all essential sources and sinks of gas. The model is validated against an "internal standard," such as methyl chloroform. For this volatile man-made compound, the chemical industry has reliable data on its annual production, as well as the kinetics of its elimination from the atmosphere through photochemical reactions involving the same OH radicals as in the case of atmospheric methane (Hein et al. 1997). The inverse modelling method optimizes the agreement between calculated and observed methane mixing ratios by adjusting the magnitudes of the various methane sources and sinks. The adjustment is constrained by specified *a priori* information, e.g. methane emission from wetlands and rice paddies is allowed to vary in seasonal dynamics, while methane from anthropogenic sources (fossil fuel escaping from oil wells, natural gas pipelines, coal mains, etc.) is not. Additional constraints come from 13C/12C isotopic ratios of gas in the atmosphere, driven by isotopic fractionation factor having different values for biological and abiotic catalysers. A similar approach was used to assess CO_2 sources (Fan et al. 1998).

Table 1. Contribution of northern area (above 60°N) to global methane emission (based on Hein et al. 1997).

Source	Tg/year	% from global emission*
Wetland	28.7	12.3
Animals	2.6	3.1
Biomass burning	0	0
Landfills	2.2	5.6
Fossil sources	40.7	38.9
Sum	74.3	12.9

*540 Tg/year.

Currently available results of inverse modelling (Hein et al. 1997) do not deviate significantly from data obtained by bottom-up approaches (Table 1). The contribution of high latitude areas (>60°N) to global methane levels was less than 13% or 70 Tg/year, and northern wetlands are responsible for emissions of less than 30 Tg of CH_4 per year. Such conclusions seems to contradict the latitudinal gradient pattern of atmospheric methane with a maximum over the Arctic. However, this maximum can be attributed to a smaller sink (slower removal of CH_4 in photochemical reactions with OH at lower temperatures), rather than by more intense gas emission from northern terrestrial as compared with mid-latitude sources. At the same time, Hein et al. admit that simulation of CH_4 seasonal dynamics in Arctic air was poor, reflecting that some essential mechanistic considerations behind gas emission were missed.

Mechanistic understanding of biological and environmental control of gas emission

To clarify such mechanisms we require a holistic view of the functioning of the whole ecosystem, including photosynthesis, respiration, C-flows between plants, micro-organisms and animals, as well as decomposition and conservation of soil organic matter (OM), nutrient dynamics, water

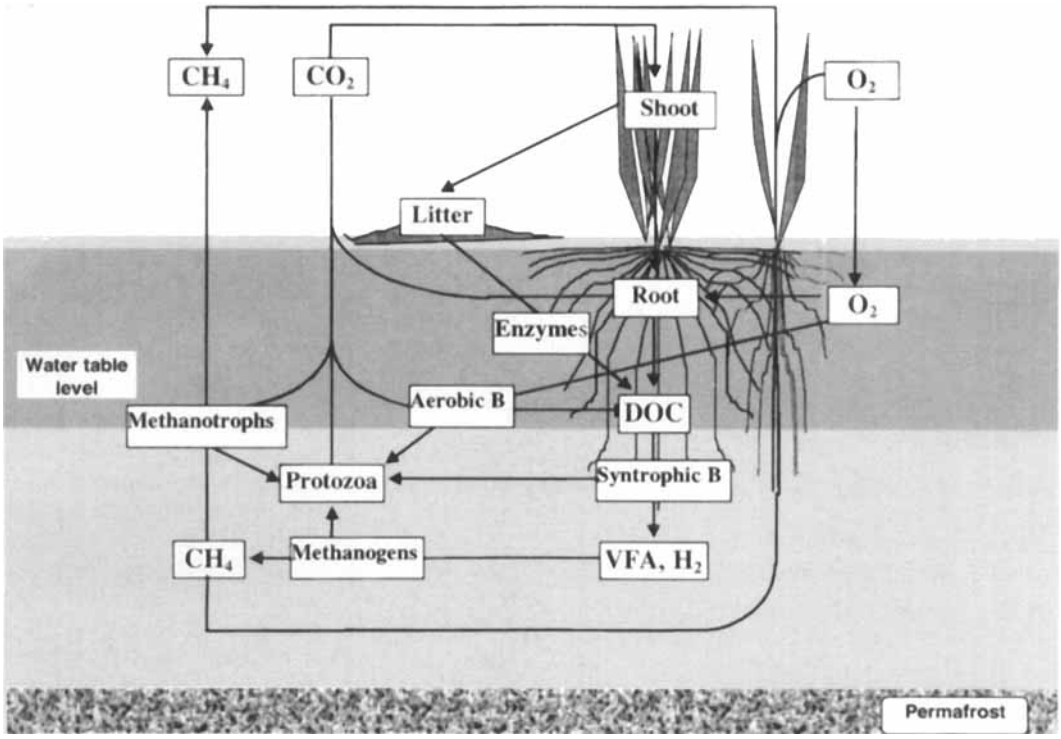

Fig. 1. Schematic representation of biological processes in wetland soil responsible for methane formation, uptake and emission.

regime, etc. (Fig. 1). Methane is the end product of an anaerobic metabolic network, which starts with the hydrolytic split of plant litter polymers (lignocellulose, pectin). The next step is fermentation of monomeric soluble products into volatile compounds (fatty acids, alcohols, H_2 and CO_2). Fatty acids containing three or more carbon atoms are resistant to instant assimilation under anaerobic conditions, but are converted to acetate and H_2 by enigmatic soil microbes called syntrophic bacteria. Their functioning is permitted by the second law of thermodynamics only under conditions of continuous removal of produced H_2 and acetate (Stams 1994). The removal is performed by methanogens and their competitors, acetogenic and sulfidogenic bacteria. Under some environmental conditions (e.g. if sulphate content is high enough) methanogens are suppressed by their competitors and anaerobic soils do not produce methane. Gases formed anaerobically move across a concentration gradient (molecular diffusion, ebullation or vascular transport) to atmosphere, being partly scavenged by methanotrophic bacteria occupying the aerobic/anaerobic interface. All microbial cells are subjected to elimination by grazing protozoa.

Even a simplified scheme (Fig. 1) illustrates a very important feature of the anaerobic metabolic network: CH_4 formation proceeds through a number of alternative pathways and methane can be substituted by competitive end products (fatty acids, acetate or sulphide). This feature of anaerobic soil calls for adequately structured mathematical simulations aimed at understanding and predicting ecosystem dynamics under climate change (warming/cooling, soil flooding or draining, fertilization, etc.). It is not enough to relate methane emission to the water table level without considering the nutrient status of the soil environment and the possibility of one or several competing pathways.

Plant-microbial interactions

It is well known that CO_2 exchange in aerobic soils is entirely controlled by the carbon and nutrient

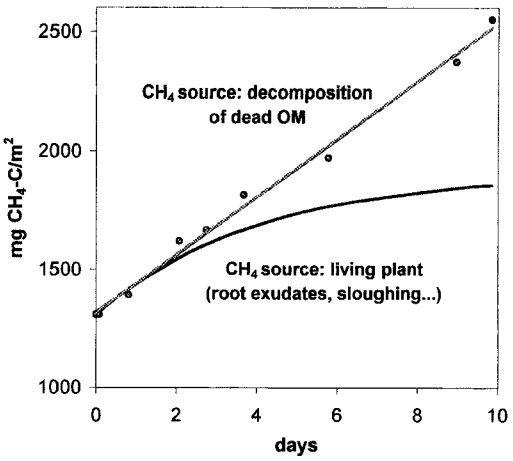

Fig. 2. Dynamics of methane formation in the peat soil under sedges (Plotnikovo, West Siberia) after clipping plants and enclosing the soil in a stainless steel cylindrical frame (28 cm diameter, 32 cm long). During 10 days of anaerobic *in situ* incubation the peat water was sampled at different depths and analysed for dissolved methane content (Panikov, unpubl. data).

flows between the plant and microbial communities (Panikov & Gorbenko 1992). Photosynthetic uptake of CO_2 initiates plant growth (shoots and roots), as well as the formation of rhizodeposition (root sloughing and exudation) which is the main C and energy source for soil microbes. On the other hand, micro-organisms are the main suppliers of N, P and hormones regulating plant growth. The immediate link between plants and soil methane is less obvious. Do methanogens consume root exudation products or do they utilize peat decomposition products? This question was addressed in a number of recent studies with $^{14}CO_2$ labelling of plants which traced the label in methane emitted from submerged soil to the atmosphere. Clear-cut results were obtained with rice paddies (Minoda & Kimura 1994): incorporation of photosynthetically derived ^{14}C to methane was highest (72–110%) in young plants and then declined to 13–17% at senescence. In our preliminary experiments with natural northern wetlands we came to the opposite conclusion (Fig. 2): the prevention of photosynthesis by plant clipping or shading and the subsequent prevention of root exudation did not affect a steady rate of methane formation. In other words, we have not found any significant short-term response of methanogens to changes in photosynthetic activity. This indicates that anaerobic processes in wetlands are mainly driven by peat decomposition rather than by root exudation.

Temperature effects, cold season fluxes

Temperature stimulation of methanogenesis and methane emission is probably the main focus in the majority of ecological and biogeochemical studies of trace gas fluxes. The mechanism of such stimulation seems to be counter-intuitive. Indeed, summer temperatures rise more in the top methanotrophic soil layer or, at least, should stimulate both methane formation and uptake. Therefore, net emission (formation minus uptake) was expected to decline or remain more or less constant under soil warming. However, in reality, net CH_4 emission is always accelerated by warming, indicating that methane formation is more responsive to temperature than methane uptake. Although a molecular mechanism for such a phenomenon is still unknown, we have reliable estimates of empirical Q_{10} coefficient that varies between 5–8 for methanogens and around 2 for methanotrophs.

Several recently published papers deal with winter fluxes and belowground processes in frozen soils. Whalen & Reeburgh (1988) noted in Alaskan sites episodic release of CH_4 amounting to 41% of the annual flux from moss-covered areas. Winter CH_4 emission from various bogs and fens were found to account for 4–21% of annual fluxes in Minnesota (Dise 1992) and 2–10% in the temperate poor fen in New Hampshire (Melloh & Crill 1993). February fluxes of CH_4 in west Siberia were 5.0 ± 3.7 mg m^{-2} per day, which corresponds to 3.5 to 11% of annual budget (Panikov, Dedysh et al. in press).

Winter CO_2 emission to the atmosphere was shown to be even higher: average values for the entire cold season (October–May) were 150 mg C m^{-2} d^{-1} in subarctic Kolyma soils (Zimov et al. 1993) and 300 and 80 mg C m^{-2} d^{-1} for moist tussock tundra and coastal wet sedge ecosystems, respectively (Oechel, Vourlitis & Hastings 1997). The cold season loss of C then should be 20–70 g m^{-2}, which is up to 80% of the total annual net loss. The reason for the difference in contributions of CH_4 and CO_2 winter fluxes to the annual budget stems first of all from the algebra behind flux calculation. Indeed, the net

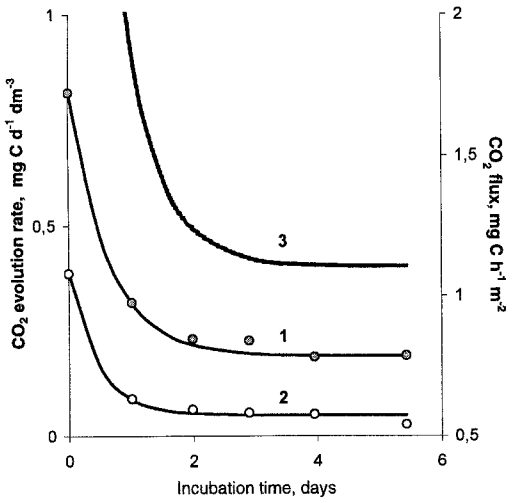

Fig. 3. Dynamics of peat respiration (CO_2 formation) during winter sample incubation at -16 ± 1°C: CO_2 evolution rate in peat from 1–10 cm (1) and 10–20 cm (2). The deeper peat layers are not shown. The total flux (3) was calculated as the sum of respiration rates over all peat depths.

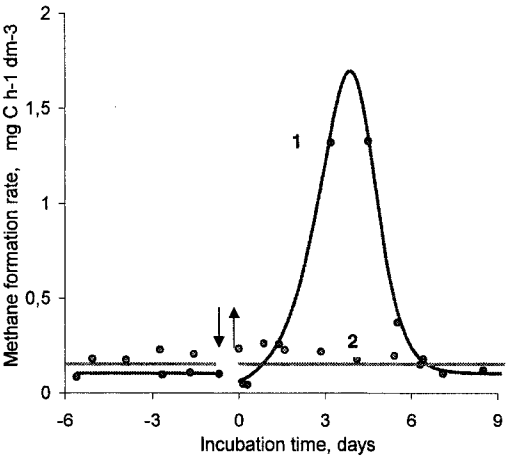

Fig. 4. The effects of freeze-thawing on soil methanogenic activity. Peat sampled from 15–20 cm depth was incubated at 20°C for 6 days, then frozen (↓) and allowed to thaw (↑), with subsequent incubation at 20°C (Panikov, Dedysh et al. in press). Peat was sampled in April (1) and July 1998 (2).

annual CO_2 flux is a difference between two high numbers:

$$\text{net C-flux} = R - Ph = R_{sum} + R_{win} - Ph = (1 - k_2)R + k_2R - k_1R = (1 - k_1)R$$

where R is total ecosystem respiration, Ph is plant photosynthesis, and R_{sum} and R_{win} are summer and winter respiration, respectively. Since $R_{sum} \approx Ph$ (summer respiration is almost balanced by photosynthesis), then net CO_2 flux is very much influenced by cold season emission, when $Ph = 0$, even if the $R_{win} >> R_{sum}$. For example, if $k_1 = 0.9$ and $k_2 = 0.05$ (i.e. winter respiration is only 5% of the annual respiration as in the case of methane), then the contribution of winter to the annual net CO_2-flux would be very high anyway:

$$R_{win}/\text{net } CO_2 \text{ flux} = k_2/(1 - k_1) = 0.5 \text{ or } 50\%!$$

The mechanisms of cold season emission are intensively discussed. Some authors explain winter fluxes by the mechanical release of CO_2 from soil during ice formation (Coyne & Kelley 1971). Oechel, Vourlitis & Hastings (1997) hypothesize that frozen soil retains the respiratory activity of cold-tolerant organisms; potential candidates are soil fungi, which display a wider temperature range of metabolic activity than bacteria (Flanagan & Bunnell 1980). Zimov et al. (1993) assume uninterrupted activity of soil micro-organisms due to their self-heating; biogenic heat production can be viewed in biochemical terms as deliberate adaptive uncoupling of oxidative reactions from ATP-generation to convert chemically usable energy to heat. We have recently obtained direct experimental evidence for this phenomenon (Panikov, Dedysh et al. in press).

We have found that fresh samples of frozen peat soil incubated under laboratory conditions at a constant temperature of -16°C displayed very slow but steady respiration. This varied from 0.05 to 0.2 mg CO_2-C d^{-1} dm^{-3}, depending on peat sampling depth (Fig. 3). Although this activity was 200–300 times lower than summertime soil respiration, it was enough to support the observed *in situ* winter CO_2 emission. There are at least three convincing arguments confirming that observed CO_2 evolution is caused by instant microbial activity, but not diffusion of gas accumulated in soil crumbles during the warm season:

1) The dynamic pattern of CO_2 evolution from frozen soil, which follows an asymptotic curve, approaches a low but constant steady gas formation rate, rather than a gradual decline to zero which would be expected from mechanisms based on release of accumulated CO_2.
2) The vertical distribution of the respiration rate

along a profile of frozen soil has its maximum on the top, where highest biological activity occurs. It is clear that opposing mechanisms (release of accumulated gas) would require more intensive CO_2 flux from bottom layers, where CO_2 concentration is higher.
3) The proportionality between respiration rates of soils at low and high temperatures indicate that the forces driving the process are basically the same at both temperatures.

Other interesting effects observed at low temperatures are activation of soil respiration and especially high methanogenic activity. The thaw and subsequent peat incubation at 15°C accelerated gas formation by one order of magnitude followed by a decline, approaching a steady state level (Fig. 4). Although the mechanism of freeze-thaw activation needs further clarification, it was nevertheless possible to simulate the observed activation dynamics with a mathematical model, which accounts for the burst of microbial growth on nutrients released into soil from frost-damaged cells.

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