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Beaver population fluctuations and tropospheric methane emissions in boreal wetlands

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Abstract. Measurements of net methane flux were made during the 1988 ice-free season (May–October) at a beaver-meadow complex in northern Minnesota, USA. The site included upland boreal forest, sedge meadow, submerged aquatic plants, and the open water of a beaver pond. Annual fluxes were 8–11 g C/m^2 in the permanently wetted zones and 0.2–0.4 g C/m^2 at the occasionally inundated meadow and forest sites. These data, when coupled with long-term (46 yr) data on beaver (*Castor canadensis*) population size and habitat alteration, suggest that about 1% of the recent rise in atmospheric methane may be attributable to pond creation by beaver in North America.

Introduction

Habitat alteration and feeding by large animals can profoundly influence the broader biotic community, with the effects reverberating throughout the ecosystem for decades to centuries (Naiman 1988). However, observations of ecosystem changes are seldom related to population dynamics, even though animal population sizes respond to predators, food limitation, disease, and habitat variability over many decades (Andrewartha & Birch 1954; Starfield & Bleloch 1986). These adjustments in population size have profound implications for longer-term ecosystem processes but have received little attention because there are few data coupling population dynamics with ecosystem-level processes.

In North America, beaver (*Castor canadensis*) provide a good example for linking long-term population dynamics to ecosystem-level processes. At the time Europeans arrived in North America, the beaver population exceeded 60 million individuals (Jenkins & Busher 1979). These beaver created extensive wetlands throughout their 15 × 10^6 km^2 range. Yet, by 1900 AD the beaver was nearly extinct and much of their former habitat had reverted to dry-land (Naiman et al. 1988). At the beginning of this century, with a relative absence of predators, laws regulating trapping, and an abundance of forage and habitat, beaver began a rapid population increase throughout most of their former range.

Beaver alter the landscape by cutting forests within about 100 m of water courses and by changing the hydrologic regime through dam building. These activities are readily quantified from aerial photographs taken since the mid-1920s (Johnston & Naiman 1990a, b).

The alteration of the hydrologic regime has a profound influence on the emission of methane to the atmosphere (Harriss et al. 1982; Richey et al. 1988). Beaver create conditions for organic matter accumulation, hydrologically providing anoxic conditions suitable for methanogenesis (Ford & Naiman 1988). Recent evidence of steadily rising tropospheric methane concentration (Rasmussen & Khalil 1983, 1984) has prompted investigation of methane sources. Methane is an important 'greenhouse' gas with significant environmental consequences should the 0.8–1.0%/yr increase in its atmospheric concentration continue.

Methane, a radiatively active gas, absorbs energy in a relatively unsaturated region of the infrared. Therefore, small concentration changes are expected to have large atmospheric warming effects (Dickinson & Cicerone 1986; Blake & Rowland 1988; Mitchell 1989). Methane plays an important role in tropospheric chemical reactions involving the OH radical; methane escaping the troposphere and oxidized in the stratosphere contributes H_2O to stratospheric clouds, which are radiatively and chemically important to the Earth's climate (Blake & Rowland 1988).

It is thought that 40% of the global emissions of methane are from wetlands (including rice paddies) which are mostly located in the boreal zone and in the tropics and subtropics (Matthews & Fung 1987; Cicerone & Oremland 1988; Devol et al. 1988). Yet, methane emissions from northern wetlands remain a major uncertainty in global methane budgets (Nisbet 1989). Recent atmospheric measurements, models, and budgets suggest that high-latitude wetland methane sources are important in driving annual variations in northern hemisphere methane concentration and in maintaining the interhemispheric methane concentration gradient (Whalen & Reeburgh 1988). Therefore, newly created beaver-maintained northern wetlands may be an important additional source of methane.

This article examines methane evasion rates from four hydrologically and vegetatively distinct zones of a beaver-meadow complex in northern Minnesota, USA. Atmospheric evasion rates are related to soil redox potential, temperature, and carbon storage. The data are then combined with information on beaver induced habitat changes over a 46 yr (1940–1986) period to evaluate beaver mediated alterations to the annual flux of tropospheric methane.

Methods and materials

Study area

The Kabetogama Peninsula in Voyageurs National Park (VNP), Minnesota, is a roadless 294 km^2 wilderness area. Vegetation on the Peninsula is primarily secondary-growth boreal forest, the overstory being dominated by aspen (*Populus tremuloides and P. grandidentata*) and paper birch (*Betula papyrifera*), with understory balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) (Kurmis et al. 1986). As of 1986 beaver-created habitat covered approximately 13% of the peninsula (Naiman et al. 1988; Johnston & Naiman 1990a, b).

The pond complex studied on Shoepack Creek covers 0.02 km^2 (2.24 ha). Vegetation in the pond complex is primarily (70%) grass and sedge meadow with a few rocky islands covered with spruce. Four zones were represented in the study: upland forest (*Populus* and *Betula*); sedge meadow (*Carex* spp., *Calamogrostis canadensis, Scirpus cyperinus*); submergent aquatic plants (*Utricularia* spp., *Potamogeton* spp.); and deep water. Plants capable of direct transport of methane to the atmosphere were occasionally present (e.g., *Nuphar*) but were not sufficiently abundant to justify sampling. Depths of water in the last two zones were approximately 45 cm and 125 cm, respectively. This pond complex was chosen for study because of its typical vegetation zonation pattern, ease of access, and the availability of extensive data on other biogeochemical cycles (G. Pinay & R.J. Naiman, unpublished data).

Access to the Peninsula is restricted by the National Park during late April and early May because of unsafe ice on the large lakes surrounding the Peninsula. These lakes must be crossed to reach the study sites. The beaver ponds on the Peninsula lose their ice cover about 10 d before the ice disappears from the large lakes.

Methane flux measurements

Sampling apparatus

The methane gas collectors were modeled after those described in Ford & Naiman (1988). Bell jars (10 L) were covered with aluminum foil and the edges set 5 cm into the ground at the forest and meadow sites. For submergent and deep water sites, the gas collectors were mounted on wooden frames, stabilized with polystyrene floats and anchored with ropes to shore. The edges of the floating gas collectors were always under the surface of the water but above the surface of the sediment. A glass sampling tube with a gas-sampling septum extended into the jar through a rubber stopper. A total of 16 such gas collectors were used, four in each of the four vegetative zones.

Matthias et al. (1978) have critiqued chamber techniques used to measure gas fluxes from soil and water surfaces. This found that under certain conditions closed chambers may underestimate the flux rate by as much as 55% due to soil disturbance and changing concentration differentals between soil or water and atmosphere over time. In our experiments the chambers collected methane for one week before sampling which, from similar studies (e.g., Ford & Naiman 1988), is an appropriate period for methane concentrations to reach measurable levels ($\sim$ 5 ppm).

Sampling procedure

Gas samples were collected weekly from late May through late October, 1988. Unsafe ice conditions on access lakes before 10 May prevented earlier sampling. Gas was collected with 60-ml plastic syringes. The syringe was used first to mix the air in the jar by filling and flushing several times, then the sample (50 ml) was drawn into the syringe via a needle and gas septum. Samples sealed in the syringes with septa were placed in PVC tubes and the tubes sealed with rubber stoppers. These were then transported to the laboratory in insulated ice-chests. Gas samples were kept cool (~ 10° C) during transport to the laboratory, then allowed to equilibrate to room temperature (20° C) before analysis. Analyses were completed within 24 hr of collection.

For the forest and meadow sites, jares were flushed with ambient air after sampling and moved to a new patch of ground in the immediate vicinity. For the flooded zones, samples were taken in a manner that minimized the disturbance of water and sediment below the collecting jars, and the jars were thoroughly flushed with ambient air immediately after sampling.

Chromatography

Gas samples were analyzed on a Carle Series S Analytical Gas Chromatograph using a flame ionization detector, helium carrier gas and a Poropak Q column at 75° C. The instrument was calibrated immediately before and after each analysis of weekly samples. Sample methane concentrations were compared with a 1500 ppm methane standard and data were converted to milligrams carbon (as methane) per unit area per day.

Annual methane evasion

It was assumed that methanogenesis continues under ice (Rudd & Hamilton 1978) but at a reduced rate because of low winter temperatures (Whalen & Reeburgh 1988). Evasion rates observed soon after ice-out, and just before heavy ice formation were averaged, and this average was used as an estimate of the winter rate (usually < 10% of summer rates). These calculations also assume that all methane produced during winter evades to the atmosphere, and that none is oxidized. The estimated winter rate was combined with the measured summer rates to calculate the annual evasion of methane (Ford & Naiman 1988).

Soil characteristics

Redox potential and temperature

Soil oxidation-reduction potential (Eh) was measured weekly at each collection site using a millivolt meter, a calomel reference electrode and platinum-tipped redox probes (DeLaune et al. 1980). In early June 1988 three probes were placed about 5 cm deep in the soil at each gas-collection site and left *it situ* throughout the study to minimize soil disturbance. The readings from the three replicate probes were averaged and the means compensated for soil temperature, soil pH and individual variations among the electrodes (Bohn 1968; G. Pinay, pers. comm.). The redox probes were not set in completely anaerobic zones. They were placed at a constant depth to monitor temporal and spatial changes in redox potential and to develop predictive equations for methane flux from different zones. After the field season, all probes were checked in the laboratory for conformity to theoretical values (DeLaune et al. 1980).

Soil and sediment temperatures were recorded at the same time and depth as redox potential. Temperatures were converted to cumulative degree-days for the May–October sampling period. The total number of degree-days was calculated by summing the average daily temperature (°C) over the sampling period.

Soil pH

Soil pH was determined with a Beckman Phi-31 pH meter. Dried soil samples, collected in August 1988 and including the entire organic horizon, were mixed with water in the ratio of 2.5 volumes of deionized water to each volume of dry soil. The resulting slurry was mixed well and pH was determined immediately at 22° C (Page 1982).

Total carbon content

Total carbon content (by percent dry weight) of soil in the four vegetative zones was estimated from ten 4.5 cm diameter cores taken from each zone in August 1988. In each case an effort was made to sample the entire thickness of the O and A horizons, which contained most of the organic carbon in the soil profile. Mean depth of these highly organic horizons varied from 9 cm in the forest zone to over 17 cm in the meadow zone. Cores were dried in an oven at 75° C. Dry mass of each visibly distinguishable layer was recorded. Carbon content was determined from three replicates from each layer using a LECO carbon-hydrogen-nitrogen analyzer. Total carbon ($g\,C/m^2$) was calculated by factoring the mass of each soil layer with the area represented by the sample for each zone.

Hydrology

Changes in water table elevation were recorded continuously with a Leupold & Stevens Model 71-A strip chart hydrologic recorder located in the meadow zone. These water levels were correlated with those measured in six reference wells placed in a transect from the forest to the pond. Depth to water table was measured weekly at the reference wells.

Statistical treatment

One-way analysis-of-variance was used to test for significant differences in all variables among the four zones of the pond complex. Where data did not conform to ANOVA assumptions, the non-parametric Kruskal-Wallis Test was used. The Scheffe's Test was used to identify which means differed significantly.

Stepwise multiple regression analyses were used to determine which of four independent soil variables (temperature, redox potential, total carbon content and pH) were correlated with methane evasion. First, the data were analyzed for relationships between daily methane evasion rate and the independent soil variables within each of the four zones. Second, relationships between annual methane evasion rate and soil variables were sought for all four zones combined by summing the weekly flux data for each of the 16 collectors to obtain total carbon flux. This approach relates methane flux to soil conditions throughout the growing season, rather than at any time during that season. All statistical analyses were performed with the PC SAS statistical package (SAS Institute, Inc. 1985).

Results

Physical measurements

Soil and sediment temperatures were 7–11° C at the beginning of the study in early May. Except for the meadow they rose steadily until June, remaining relatively constant at 13–21° C until mid-August (Fig. 1). They decreased rapidly from mid-August, with the onset of autumn, to about 2–3° by the end of October. Cumulative soil and sediment temperatures (expressed as annual degree-days) in the submergent and deep zones were 33% greater than in the forest and meadow zones ($P < 0.01$). Annual degree-days in the submergent and deep zones could not be distinguished from each other, nor could degree-days in the forest and meadow zones (Table 1).

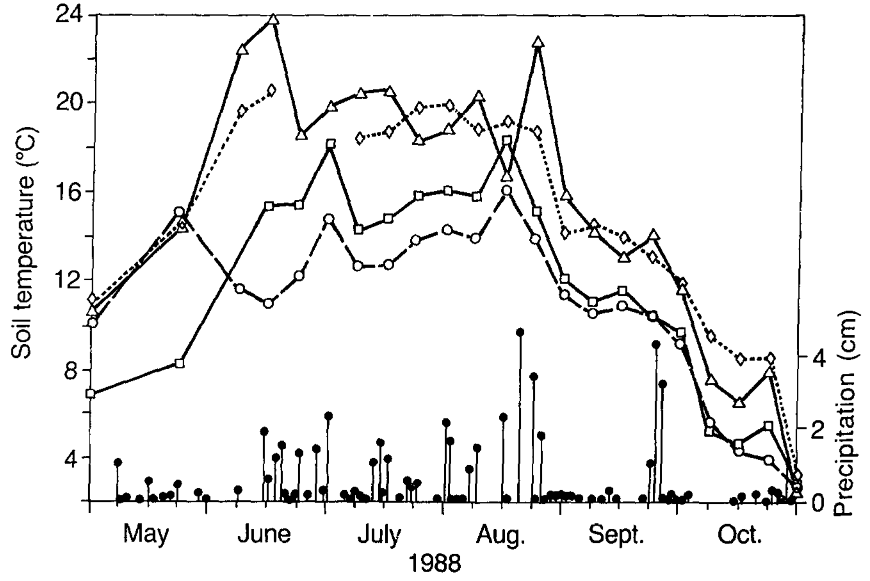

Fig. 1. Seasonal variations in soil temperature (5 cm depth) for each vegetative zone. Key: forest (□), meadow (○), submergent (◇), and deep (△). Daily precipitation events are also shown.

Table 1. Cumulative soil temperatures and mean redox potential for each vegetative zone.

Vegetative zone	Sample size (n)	Temperature (Annual degree-days, °C/yr)			Redox Potential (mv)		
		mean	SE	Scheffe's*	mean	SE	Scheffe's*
Forest	80	2083.5	21.1	A	727.1	26.6	A
Meadow	80	2078.4	18.1	A	196.2	28.4	B
Submergent	80	2759.7	19.0	B	– 108.2	3.1	C
Deep	80	2783.5	21.1	B	164.5	21.5	B

*Groups with different letters are statistically different.

Table 2. Total soil carbon and soil pH for each vegetative zone.

Vegetative zone	Sample size (n)	Total Carbon ($g\ C/m^2$)			pH		
		mean	SE	Scheffe's*	mean	SE	Scheffe's*
Forest	9	4247	428.5	A	5.45	0.06	A
Meadow	9	9619	658.1	B	4.80	0.13	B
Submergent	9	5285	404.7	A	5.12	0.03	C
Deep	10	5920	808.9	A	4.95	0.05	BC

*Groups with different letters are statistically different.

Soil oxidation-reduction (redox) potential was significantly higher ($\bar{x} = 727$ mv; $P < 0.01$) at the forest site as compared to the other zones. In addition, meadow and deep zone redox potentials were significantly higher ($\bar{x} = 164$ to 196 mv; $P < 0.01$) than in the submergent zone ($\bar{x} = -108$ mv), but could not be distinguished from each other (Table 1). Seasonal and spatial coefficients of variations for all zones were 3–15% of the mean.

Total carbon (Table 2) in the meadow soils were nearly twice that in the other zones (9618 $g\,C/m^2$; $P < 0.01$). The other three zones ranged from 4247 to 5919 $g\,C/m^2$ and could not be distinguished on the basis of total soil carbon.

Soil pH was significantly higher ($\bar{x} = 5.45$; $P < 0.01$) in the predominantly typic eutroboralf (e.g., alfisols) forest soils than in the other zones, and significantly higher in the submergent soils than in the meadow soils ($P < 0.01$; Table 2). Soils in the submergent zone were typic haplaquents (entisols) and those in the meadow zone were typic ochraqualfs (alfisols).

Methane flux

Methane flux from the forest was low ($< 0.002\,g\,C/m^2/d$) except for brief periods immediately following heavy rainfalls in mid-June and mid-October (Fig. 2). Methane flux from the meadow paralleled that in the forest from May to July, but had slightly greater and more variable flux during the mid-summer period. Methane flux from the submergent and deep sites increased rapidly just after ice-off, being nearly 40 times that in the forest and meadow zones. Flux was

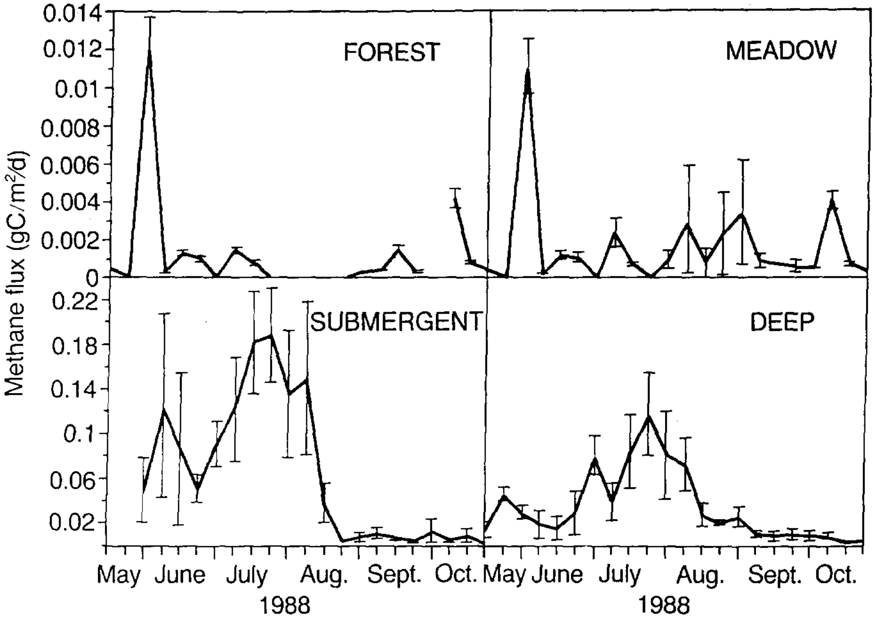

Fig. 2. Seasonal variations in net daily methane flux for each vegetative zone. Bars are ± 2 SE.

Table 3. Total annual methane flux (g $C/m^2/yr$) from each vegetative zone.

Vegetative zone	Sample size (n)	mean	SE	Scheffe's test*
Forest	4	0.25	0.04	A
Meadow	4	0.36	0.04	A
Submergent	4	10.78	1.87	B
Deep	4	8.73	1.72	B

*Groups with different letters are statistically different.

highest from May to August approaching 0.1–0.2 g $C/m^2/d$. Flux decreased in mid-August with the decline in temperature, remaining low throughout the remainder of the ice-free season (Fig. 2).

Annual methane flux in the submergent and deep zones approached 8–11 g C/m^2; 24–43 times greater than in the forest or meadow zones (ANOVA, $P < 0.01$). No significant differences were found between the submergent and the deep sites, or between the forest and the meadow sites (Table 3).

Regression analyses

Daily methane flux was significantly correlated with temperature in the submergent zone ($r^2 = 0.56$, $P < 0.01$, Table 4). In the deep zone, both temperature and redox potential significantly influenced the daily methane evasion rates

Table 4. Summary of multiple regression results of annual methane flux against physical variables for each vegetative zone and for all zones combined.

Vegetative zone	Independent variables retained	Coefficient of determination (r^2)	Significance (P)
Forest	Temperature	0.14	< 0.01
Meadow	Temperature Redox potential	0.08	0.05
Submergent	Temperature	0.56	< 0.01
Deep	Temperature Redox potential	0.40	< 0.01
All zones[a]	Temperature Redox potential	0.79	< 0.01

[a] Annual methane evasion can be estimated from the following equation:

$$\text{Log}(F) = 0.0005T - 0.0002R - 0.7725$$

where, F = annual methane flux ($gC/m_2/yr$)
T = annual degree-days (°C/yr)
R = mean redox potential (mV)

($r^2 = 0.40$, $P < 0.01$, Table 4). Daily methane flux was weakly related to all physical parameters measured in the forest and meadow zones ($r^2 = 0.08$–0.14, $P < 0.05$; Table 4) but temperature and redox potential remained the most important variables. Soil pH and total soil carbon were not retained in any of the stepwise multiple regressions.

Using stepwise multiple regression, we found that temperature and redox explained 79% of the variation in methane flux from soils in the beaver-meadow complex (Table 4). Temperature (annual degree-days) was the most important variable and was correlated positively with methane flux, explaining 73% of variation. Oxidation-reduction potential was the second most important variable, but was correlated negatively with CH_4 explaining only 6% of the variation.

Discussion

Factors influencing methane flux

Annual methane flux from the permanently flooded zones (i.e., submergent and deep) was 43 times that of the dryer upland forest and the intermittently flooded sedge meadow. This suggests that beaver, by impounding streams and flooding forests, might alter atmospheric trace gas balances.

The maximum flux rates observed (10.78 g $C/m^2/yr$) are somewhat lower than most other published estimates for wetlands (Baker-Blocker et al. 1977; Bartlett et al. 1987, 1988; Cicerone & Oremland 1988; Cicerone & Shetter 1981; Cicerone et al. 1983; Conger 1943; Devol et al. 1988; Ehhalt & Schmidt 1978; Koyama 1963; Seiler et al. 1984; Sheppard et al. 1982). This may be a factor of our gas sampling apparatus (c.f. Sebacher & Harriss 1982; see Matthias et al. 1978 for a critique of closed-chamber experiments for measuring gas fluxes from soil and water surfaces). Another possible reason for the low annual rate is the cool temperature regime of the boreal location. Sebacher et al. (1986) and Whalen & Reeburgh (1988, 1989), however, found results similar to ours in subarctic boreal marsh and in tundra environments, respectively. Yet, the late onset of sampling also may have missed an initial pulse of methane at ice-off.

The close temperature-dependence for methane flux ($r^2 = 0.73$) has also been found in other studies (Atkinson & Hall 1976; Baker-Blocker et al. 1977; Bartlett et al. 1987; Ford & Naiman 1988; Harriss et al. 1982; Kelly & Chynoweth 1981; King & Wiebe 1978; Koyama 1963; Seiler et al. 1984; Svennson 1980; Williams & Crawford 1984; Zehnder 1978; Zeikus & Winfrey 1976), although Kelly & Chynoweth (1981) argued that given stable high temperatures, methanogenesis can be limited by carbon input. Temperature, however, is closely related to the hydrologic zone. The aquatic areas (deep and submergent) accumulated more degree-days than the terrestrial areas (forest and meadow) because of the high heat capacity of water.

The lack of a relationship between methane flux and redox potential ($r^2 = 0.06$) is surprising since all methanogenic microbes are strict anaerobes (Hungate 1966; Zehnder 1978). Perhaps the placement of redox probes only 5 cm deep into the soils did not detect lower redox potentials in deeper layers, thus resulting in the apparent lack of a relationship between flux and redox potential.

The unimportance of total carbon standing stock to methane flux suggests that flux in this stystem was not substrate-limited. If temperatures in the system had been maintained at a high level for a longer period, some substrate limitation might have become apparent, as described by Kelly & Chynoweth (1981). Also the annual carbon supply rate appeared sufficient to maintain the system. In another study of a beaver pond Naiman et al. (1986) showed that methane evasion was < 7% of the annual carbon supply.

Measurements reported here are of net methane release to the atmosphere with no attempt made to account for bacterial oxidation of methane within the water column. Oxidation presumably increases with water column height and degree of stratification; thus, with all other factors being equal, one would expect greater oxidation of methane with deeper water, and consequently a lower net flux (Rudd & Taylor 1980). Yet fluxes in the deep and submergent zones were not significantly different. Perhaps greater methanogenesis in the deep sediments was compensated for by greater oxidation in the overlying water column. Recall that the deep zone had a slightly higher carbon standing stock, yet lower measured flux rates, than the submergent zone. In the deep zone only 0.15% of the carbon standing stock annually escaped to the atmosphere as methane, as compared to 0.20% in the submergent zone. This compares to 0.12% found by Ford & Naiman (1988) for fine sediments in the deep zone of a beaver pond (e.g., excluding wood and coarse detritus). These differences were not statistically significant suggesting that oxidation in the water column was minor. The annual percentages for the conversion of the carbon standing stock to methane for the forest and meadow sites were 0.01% and < 0.01%, respectively.

Methane flux from the sedge meadow was lower than might be expected given the redox potential. We believe this is due primarily to significantly lower temperatures in the meadow soils relative to the submergent and deep soils. These low temperatures may have been the result of shading and evapotranspiration by sedge vegetation. Additionally, redox potential in the meadow was significantly higher than in the submergent zone, possibly due to the intermittent draining of the meadow during dry periods. This could also decrease methane flux in the meadow zone by allowing greater oxidation at the soil surface.

Implications for atmospheric methane flux

Atmospheric methane is considered one of the most important of the greenhouse gases, with the potential to affect the earth's radiation balance (Lacis et al. 1981; Mitchell 1989). Much attention has centered on the increase in tropospheric methane concentrations of about 1% per year in the last three decades (Cicerone 1988; Khalil & Rasmussen 1983). The major sources for this increase are anthropogenic and include ruminant husbandry, rice cultivation, burning biomass, fossil fuel mining, solid waste landfills and possibly even human-induced increases in termite populations (Khalil & Rasmussen 1983; Zimmerman et al. 1982).

There is a strong concentration of global methane production in the northern hemisphere (Khalil & Rasmussen 1983; Rasmussen & Khalil 1984; Blake & Rowland 1988; Nisbet 1989). Much of this northern bias may be due to methane production in boreal wetlands between 50° and 70° N latitude, which produce perhaps 10–20% of total global methane emissions (Matthews & Fung 1987). If beaver are expanding the area of boreal wetlands by additional water impoundment, then the increasing beaver population over the last half century may be influencing the recent rise in atmospheric methane.

Through the creation and expansion of wetlands in the boreal forest, beaver promote net methane flux to the atmosphere in several ways. First, flooding of soils creates anaerobic conditions necessary for methanogenic bacteria. Second, creation of shallow ponds with large surface areas for absorption of solar radiation result in greater thermal inertia than in forest soils, maintaining high temperatures that facilitate methanogenesis. Third, the increase in habitat for emergent aquatic plants, which transfer large quantities of methane directly from sediments to the atmosphere and circumvent oxidation in the water column, may be a major factor in increasing net flux to the atmosphere (Cicerone & Shetter 1981; Dacey 1980; Dacey & Klug 1979; Sebacher et al. 1985). Finally, the geat quantities of carbon that are accumulated by beaver ponds (Francis et al. 1985; Naiman & Melillo 1984; Naiman et al. 1986) may enhance methanogenesis (Ford & Naiman 1988), if circumstances are such that the process is not temperature-limited.

It is possible to derive a preliminary estimate of the amount of carbon released as methane from the surface of beaver meadow complexes in the boreal forest of North America. We make the following assumptions in our calculations. First, all significant methane evasion takes place from the flooded areas of the system and not from peripheral intermittently flooded areas. This seems justifiable in light of the results of this study yielding a mean estimate of 9.76 g C/m^2/yr for the flooded areas and 0.31 g C/m^2/yr for the dryer zones. Second, the system studied here is representative of the boreal forest. This is not a desirable assumption but is made necessary by the spatially limited scope of this investigation. Third, the abundance of beaver on the Kabetogama Peninsula is representative of boreal North America. This is probably an overestimate but could be corrected easily with better population data from other areas (Broschart et al. 1989). Finally, temperature and insolation differences within the boreal region are minor. Again, this assumption is correctable given proper climatic data.

In 1986 the Kabetogama Peninsula had about about 13.7 km^2 of recently created flooded surface (Naiman et al. 1988). When combined with data on methane flux this yields an estimate of 4.55×10^5 g C/km^2/yr for the 294 km^2 Peninsula. Woodwell et al. (1978) estimate the global area of boreal forest to be 12×10^6 km^2; about 40% of this is in North America yielding as estimate of 4.8×10^6 km^2 of boreal forest with potential for beaver impoundment. Following these calculations and the assumptions listed above, an estimate of 2.18×10^{12} grams carbon (as methane) released each year for beaver created wetlands in the North American boreal forest is probably a maximum, given that beaver are probably not generally as dense elsewhere as they are on the Kabetogama Peninsula (Broschart et al. 1989). The open-water area of beaver ponds on the Kabetogama Peninsula increased 86-fold (from 0.16 km^2 to 13.7 km^2) between 1940 and 1986 (Naiman et al. 1988; Johnston & Naiman 1990a, b). Assuming that this rate of increase can be generalized across the boreal ecosystem of North America, we estimate that the emission of methane to the atmosphere from beaver ponds in 1940 was 0.03×10^{12} g C/yr.

Natural wetlands release about 115×10^{12} g C/yr of methane to the atmosphere (Cicerone & Oremland 1988). This represents about 21% of the annual release from all known sources. Beaver-meadow complexes in the boreal forest contribute approximately 1.9% of the total released from natural wetlands. The beaver-induced influence on methane flux is, however, comparable to that estimated from all other freshwaters (5×10^{12} g C/yr).

Termites (40×10^{12} g C/yr) and enteric fermentation from ruminant animals (80×10^{12} g C/yr) are the major animal-related sources of atmospheric methane. Beaver-induced methane flux is small compared to these wide ranging sources.

Cicerone & Oremland (1988) estimated the global steady-state flux (source = sink) of methane to the atmosphere as 500×10^{12} g C/yr (range 405–595). We estimate that the corresponding figure for 1940 is 284×10^{12} g C/yr (range

260–308), assuming that the recent rate of increase has remained between 0.8–1.0%/yr (op. cit.). Thus, in accordance with our preliminary estimate of beaver-caused methane emissions above, beaver accounted for about only 0.01% of net global methane flux to the atmosphere in 1940, compared with about 0.44% in 1988. In other terms, the difference between the 1940 and 1988 beaver methane flux equals about 0.99% of the difference between the 1940 and 1988 global steady-state flux. Thus, about 1% of the recent rise in net methane input to the atmosphere is attributable to the actions of beaver in North America alone. Relaxing the above assumptions, particularly the overestimate of beaver density and homogeneity of temperature regimes throughout the boreal zone, should decrease this estimate. We assume that contributions of European beaver populations to atmospheric methane are presently minor enough to disregard, since those populations have not recovered as dramatically as those in North America (Tyurnin 1984).

In conclusion, we find that beaver, through impoundment of streams, and consequent alterations to hydrology, vegetative patterns and biogeochemical cycling, represent a minor but measurable factor in the recent increase in tropospheric methane concentration. Yet, beaver are just one of many species that may have measureable effects on ecosystem processes that will respond to long-term changes in population size. We suggest there remains a need to link population cycles with ecosystem-level processes to better understand landscape scale characteristics of the Earth's atmospheric and surficial processes.

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