Ecological Applications, 2(3), 1992, pp. 298–306

POTENTIAL CARBON LOSSES FROM PEAT PROFILES: EFFECTS OF TEMPERATURE, DROUGHT CYCLES, AND FIRE[1]

EDWARD H. HOGG, VICTOR J. LIEFFERS, AND ROSS W. WEIN
Department of Forest Science, 855 General Services Building, University of Alberta,
Edmonton, Alberta, Canada T6G 2H1

Abstract. Global warming and the resultant increase in evapotranspiration might lead to lowered water tables in peatlands and an increase in fire frequency. The objective of this study was to investigate some of the potential effects of these changes on peat decomposition. Dry mass losses and emissions of CO_2 and CH_4 from peat samples taken from three depth layers (0–10, 10–20, and 30–40 cm) of a black spruce peatland were measured in the laboratory at 8°, 16°, and 24°C under two moisture treatments. Effects of deep peat fire on decomposition were also simulated by burning the upper layer (0–10 cm) of peat and adding the ash to peat samples from the 10–20 cm layer. CH_4 release averaged $<1\%$ of total carbon loss in flooded samples. Release of CO_2 was 4–9 times greater from the 0–10 cm layer than from the 30–40 cm layer. After 120 d, the 30–40 cm layer had lost $<1\%$ of its original dry mass in all treatments. Higher temperatures strongly promoted decomposition of samples exposed to drying cycles but had little effect on decomposition of continuously flooded samples. Ash addition had variable effects on CO_2 emissions but may have promoted CH_4 production.

It is suggested that in certain situations, global warming may not cause appreciable increases in carbon loss from peat deposits. The results indicate that some deeper peats are resistant to decay even when exposed to warm, aerobic conditions. However, further experimental work is needed to predict the long-term response of peat deposits to changes in water levels in different peatland types.

Key words: ash; carbon dioxide; climate change; decomposition; drainage; fen; gas; greenhouse effect; methane; peat.

INTRODUCTION

In recent years there has been an increasing consensus that the observed increases in atmospheric CO_2 and CH_4 (Ehhalt 1988, Oeschger and Siegenthaler 1988) will produce a significant impact on global climate (e.g., Guthrie 1986, Ramanathan 1988, Aldhous 1991). High latitude regions are predicted to experience the most rapid increase in mean temperature coupled with possible increases in soil dryness (Manabe and Wetherald 1986, Billings 1987).

In their natural state, peatlands have been historic importers of CO_2, and represent a major global source of stored carbon. Canadian peatlands contain an estimated 168 Pg (168×10^9 Mg) of carbon (Tarnocai 1984) and represent about one-third of the world's total peatland area (Kivinen and Pakarinen 1981). The total carbon pool in boreal and arctic peatlands is an estimated 455 Pg (Gorham 1991), while the quantity of carbon released by world combustion of fossil fuels is ≈ 5 Pg/yr (Silvola 1986). Thus, northern peatlands may contain an amount of carbon equivalent to nearly 100 yr of global anthropogenic CO_2 emissions at current rates of energy consumption.

The waterlogged condition of virgin peatlands tends to maintain anaerobic conditions and slow rates of decay of organic deposits, except near the surface where aerobic conditions prevail (Ingram 1978, Clymo 1983). However, global warming and drying, coupled with continued drainage of peatlands for agriculture and forestry, are likely to cause lowering of water tables over extensive areas (Armentano and Menges 1986, Moore and Knowles 1989, Gorham 1991). Increases in the frequency and severity of organic terrain fires (Wein 1983, Maltby et al. 1990) can also be expected to cause widespread removal of surface peat layers. These effects would expose large quantities of deeper organic material to conditions more favorable to decomposition and CO_2 release. A few studies have experimentally examined the effect of peatland drainage on CO_2 and CH_4 emissions (Silvola et al. 1985, Moore and Knowles 1989), but the relative contribution of peat from different depths to greenhouse gas flux has received relatively little attention.

In this study we examined the potential for decomposition of three depth layers from a black spruce peatland in west-central Alberta, Canada. The first objective was to investigate potential effects of drought cycles and increased temperature on mass loss and gaseous carbon emissions from peat profiles. The second ob-

---

[1] Manuscript received 1 April 1991; revised 19 September 1991; accepted 24 October 1991.

TABLE 1. Characteristics of peat samples prior to treatment.

Depth interval (cm)	Bulk density (g/cm^3)	Ash (%)	C (%)	N (%)	P (%)	K (%)	TNC* (%)
0–10	0.067	7.6	40.6	1.0	0.10	0.21	2.0
10–20	0.102	5.1	41.4	1.6	0.09	0.10	0.9
30–40	0.083	5.4	41.5	1.3	0.04	0.04	0.3

* Total nonstructural carbohydrates (Smith 1981).

jective was to determine whether ash deposition after deep-burning peat fire is likely to stimulate decomposition of the remaining organic material.

METHODS

Peat samples were collected from a poor fen or muskeg dominated by black spruce, *Picea mariana* (Mill.) BSP. with occasional tamarack, *Larix laricina* (Du Roi) K. Koch. The site is located at 53°40′ N and 115°07′ W, some 110 km west of Edmonton, Alberta, Canada at 790 m above sea level. The vegetation, pH, and peat chemistry (Table 1) at this site appeared to be typical of treed, oligotrophic peatlands, which frequently predominate in the boreal forest region of western Canada (Zoltai and Johnson 1987). The shrub layer was composed mainly of *Ledum groenlandicum* Oeder., *Rubus chamaemorus* L., and *Vaccinium vitis-idaea* L. Hummocks were dominated by *Sphagnum fuscum* (Schimp) Klinggr., *Pleurozium schreberi* (Brid.) Mitt., along with several species of *Cladonia* and *Cladina.* There were occasional pools (water pH of 4.5) in depressions where *Sphagnum angustifolium* (Russow) C. Jens predominated. Mean temperatures are -15°C in January and 15° in July, and mean annual precipitation is 530 mm.

Cores measuring 15 cm diameter and 40 cm depth were collected in late October 1988 from microsites of intermediate elevation (i.e., hummock tops and low depressions were avoided). Throughout the 0–40 cm depth profile, the peat was composed mainly of *Pleurozium* or *Sphagnum* litter and often had a high content of woody material. At the core collection sites the water table was <30 cm deep in October 1988 and ≈ 10–20 cm deep in October 1989.

Unburned treatment samples consisted of the 0–10, 10–20, and 30–40 cm depth layers from 36 of the cores collected. These were oven-dried to constant mass at 75°C and weighed. The upper two layers from an additional 36 cores were used for the simulated burn treatment, as follows: after both layers had been oven-dried (75°C) and weighed, the upper 10 cm layer from each core was ashed at 650°C in a muffle furnace. The ash was then added to the peat from the 10–20 cm depth interval of the same core.

The dried peat samples were placed individually into 2.8-L plastic containers (approximate dimensions of 14 cm diameter and 18 cm height). An inoculum was prepared from 20 L of water that had been collected from peat hollows at the collection site. This peat water was combined with a mixture of three fresh peat samples from the collection site (one sample per depth interval) and filtered through a 0.2-mm mesh. The dried peat samples were first each inoculated with 100 mL of the peat water inoculum, and then rehydrated with a sufficient amount of deionized water to cover the peat surface. This resulted in a headspace height of ≈ 8 cm above the water level in each container.

Peat samples were assigned to three unlighted laboratory growth chambers held at 8°, 16°, and 24°C ($n = 48$ per chamber). Within each temperature treatment, six samples from each layer and six samples from the simulated burn treatment were chosen for each of two moisture treatments (flooded and drained, described directly below). A randomized selection procedure was used in which samples originating from the same core were assigned to the same combination of temperature and moisture treatments. Position of samples within each chamber was periodically randomized. Samples were incubated under these treatments for 125 d, a period corresponding approximately to the length of the ice-free period in northern Alberta peatlands (late June–late October).

In the flooded treatment, the water level was maintained 0–2 cm above the peat surface throughout the experiment. This was achieved by replacing evaporative losses with deionized water every 2–3 d. In the drained treatment, the peat samples were allowed to evaporate until their mass had decreased to a mean value of 500–550 g, corresponding to a volumetric moisture content of $\approx 25\%$. At this stage the surface of the peat samples was dry, and the water level had dropped to the base of the containers. All drained samples within a temperature treatment were then reflooded with sufficient deionized water to raise the water level to the peat surface. This procedure was repeated until the 125-d period of the experiment had elapsed. The drying cycles averaged 62 d in the 8°C treatment, 25 d in the 16° treatment, and 16 d in the 24° treatment; these differences reflect the more rapid evaporative losses with increased temperature.

Gas emissions were measured once for each flooded sample (after 39–41 d) and 4 or 5 times over one wet–dry cycle for each drained sample (beginning after 44 d). Prior to gas sampling, the samples were weighed for moisture content determinations, and the height of the headspace and the water table was measured. Gas samples were collected from the headspace after covering the containers with air-tight lids for 16–18 h. The gas samples were injected from a 1-mL syringe into a

Hewlett-Packard 5830A gas chromatograph. Separations were made at 50°C on a 2 m × 3 mm stainless steel column packed with Porapak Q (100/120 mesh = particle size 0.13–0.15 mm). A thermal conductivity detector was used to measure CO_2 concentrations, while CH_4 was measured with a hydrogen flame ionization detector (FID) using helium carrier gas. Readings were standardized against calibration mixtures of CO_2 and CH_4 (Medigas Alberta and Alltech Associates).

The rate (R) of gas flux from the samples (in milligrams per gram per day) was calculated as follows:

$$R = (DV/t)[(C - C_a)/M], \qquad (1)$$

where D = density of pure gas (i.e., CO_2 or CH_4) adjusted for ambient temperature, pressure, and humidity in milligrams per millilitre, V = volume of effective headspace (in millilitres), t = time interval (in days), C = final molar concentration of gas (proportion of H_2O-free air), C_a = initial (ambient) molar concentration of gas (proportion of H_2O-free air), and M = dry mass of peat sample (in grams).

Two methods were used to calculate the effective headspace volume (V). In the first method, we followed the common approach of assuming that V equals the enclosed volume above the peat surface (hereafter referred to as "external headspace"). However, this approach excludes any changes in gas concentrations below the peat surface when pails containing peat samples are covered. We observed that in uncovered peat samples in the drained treatment, CO_2 concentrations in gas-filled pore spaces above the water table were near ambient levels. This gas-filled pore space can therefore be viewed as part of an "internal headspace" where changes in CO_2 concentrations during the sampling procedure are presumably similar to those measured in the "external headspace." Calculations of V based on this second method (for drained samples only) were made as follows:

$$V = V_f + (M_f - M_i)/D_w, \qquad (2)$$

where V_f = external headspace volume immediately after flooding (in millilitres), M_f = total mass of pail and sample immediately after flooding (in grams), M_i = mass of pail and sample during gas sampling (in grams), and D_w = density of water (1 g/mL assumed).

The expected percentage mass loss of each peat sample over the 125-d period was calculated from measured CO_2 flux rate (R) by assuming a 0.68-g loss of organic material per gram of CO_2 released, i.e., $(CH_2O)_n + n\,O_2 \rightarrow n\,CO_2 + n\,H_2O$. For the drained treatment this was based on the mean value of R for each sample over one wet–dry cycle.

At the end of the experiment, all pails were placed in a large forced-air drying oven at 75°C to allow rapid evaporation of moisture. Samples were periodically reweighed until constant mass was reached (within 2–4 d).

For practical reasons (i.e., a limited number of growth chambers) the experimental design used did not achieve true replication with respect to temperature treatments (Hurlbert 1985). In the statistical analysis described below, we included temperature as a treatment effect, recognizing that differences among temperature treatments may also reflect slight differences in other factors among the three chambers used.

Three-way analysis of variance (ANOVA) was used to examine the effects of temperature, moisture treatment, and depth of peat on (1) mean CO_2 emission rates (logarithmic transformation) and (2) percentage mass loss. The core of origin for each sample was included as a fourth factor nested within temperature × moisture treatment combinations. We also used three-way ANOVA to examine the effects of ash addition on CO_2 emission rates and mass loss from the 10–20 cm depth peat layer. The analyses of CO_2 emission rates were conducted twice, using both methods of determining R.

For chemical analyses, dried subsamples from six untreated peat cores were pooled within each depth layer and ground through an 850-μm mesh screen in a Wiley mill. Duplicate samples were analyzed for total nitrogen and phosphorus on a Technicon autoanalyzer after digestion with concentrated sulfuric acid and peroxide (Department of Soil Science, University of Alberta). Potassium levels were determined on an atomic absorption spectrophotometer (Perkin-Elmer Model 500). Carbon levels were determined by Alberta Agriculture, Soils and Nutrition Laboratory. Subsamples of the peat ash (0–10 cm layer) used in this study were also analyzed for total N, P, and K. To obtain a measure of the most readily decomposable fraction, we analyzed the peat samples for total nonstructural carbohydrate using the Shaeffer-Somogyi titration method outlined by Smith (1981). We used a 0.5% solution of amyloglucosidase (16 h at 40°) followed by treatment with 0.1 mol/L sulfuric acid (Smith 1981) to hydrolyze starches and disaccharides to monomers prior to analysis.

RESULTS

Peat and ash characteristics

Total phosphorus, potassium, and total nonstructural carbohydrate (TNC) each showed strong decreases with increased peat depth (Table 1). In the upper 10-cm layer, P was more than twice as high as in the 30–40 cm layer, while K and TNC were ≈6 times higher. Total nitrogen was slightly higher in the 10–20 cm layer (1.6%) than in the upper and lower layers (1.0–1.3%), while carbon content was similar at all three depths (41%). Thus the C/N ratio varied according to differences in total N, being highest (40) in the 0–10 cm layer, and lowest (26) in the 10–20 cm layer. Bulk density was highest in the 10–20 cm layer, while ash content was highest in the 0–10 cm layer (Table 1). Nutrient analysis of ash from the 0–10 cm layer showed

TABLE 2. Results of three-way ANOVA (with core as nested variable) for estimated mean CO_2 emissions and dry mass losses. Logarithmic transformation of CO_2 emissions was used. Method 1 is based on external headspace volume; method 2 is based on internal + external headspace volume.

		CO_2 emissions					
		Method 1		Method 2		Loss in dry mass (%)	
Source of variation	df	*F*	*P*	*F*	*P*	*F*	*P*
Temperature (chamber)	2	38.12	<.001	40.34	<.001	31.49	<.001
Moisture	1	48.32	<.001	114.45	<.001	35.54	<.001
Layer	2	245.86	<.001	249.97	<.001	193.98	<.001
Temperature × moisture	2	10.70	<.001	11.60	<.001	13.28	<.001
Temperature × layer	4	0.80	.532	0.83	.513	10.01	<.001
Moisture × layer	2	3.14	.051	2.90	.063	19.90	<.001
T × M × L interaction	4	2.97	.026	2.90	.029	4.62	.003
Core within T × M interaction	30	1.09	.376	1.02	.463	3.53	<.001
Residual	60						

high levels of total P (1.0%) and K (1.2%), but levels of N were below detectable levels (<0.005%).

CO_2 emissions

Differences in CO_2 emissions were highly significant ($P < .001$) among the three peat depth layers (based on both methods, as shown in Table 2). Respiration rates of the upper (0–10 cm) layer ranged from 4 to 12 times higher than the lower (30–40 cm) layer under the different temperature and moisture treatments (Fig. 1).

As expected, average CO_2 production was greater ($P < .001$) in the drained moisture treatment (averaged over one drying cycle) than in the flooded treatment. Within the drained treatment, respiration rates increased as the peat became less saturated during drying cycles, but tended to decrease when very low levels of saturation were reached (Fig. 1).

The overall effect of temperature (i.e., differences among growth chambers) was highly significant ($P < .001$). Within the drained treatment, the rate of CO_2 emissions showed an exponential increase with temperature and the mean Q_{10} rates of increase between 8° and 24°C ranged from 1.9 to 2.2 for the three depth layers. However, there was a strong interaction between temperature and moisture treatments ($P < .001$), which reflected the much weaker effect of temperature on respiration of flooded samples, which had Q_{10} rates of only 1.0–1.5 (a Q_{10} of 1.0 indicates no increase with temperature). Indeed, when the statistical analysis was repeated using the flooded samples only, temperature effects were no longer significant at the 5% level (two-way ANOVA with core as nested variable: df = 2,30; $F = 2.93$; $P = .065$).

The three-way interaction between temperature, moisture, and peat depth was significant ($P < .03$, Table 2). This reflects a greater degree of drainage-induced stimulation of respiration in warm (24°C) samples from the upper layer.

The effects of ash addition to the second peat layer (10–20 cm) were highly variable among the different temperature and moisture treatments. Although the overall effect of ash was to promote respiration (three-way ANOVA: df = 1,60; $F = 5.39$; $P = .024$), this effect was noticeable only in the 8° and 24°C flooded treatment and in the 16° drained treatment. Ash tended to inhibit respiration in the 24° drained treatment (Fig. 1).

CH_4 emissions

CH_4 flux showed extreme variability among the flooded peat samples and in a high proportion of these,

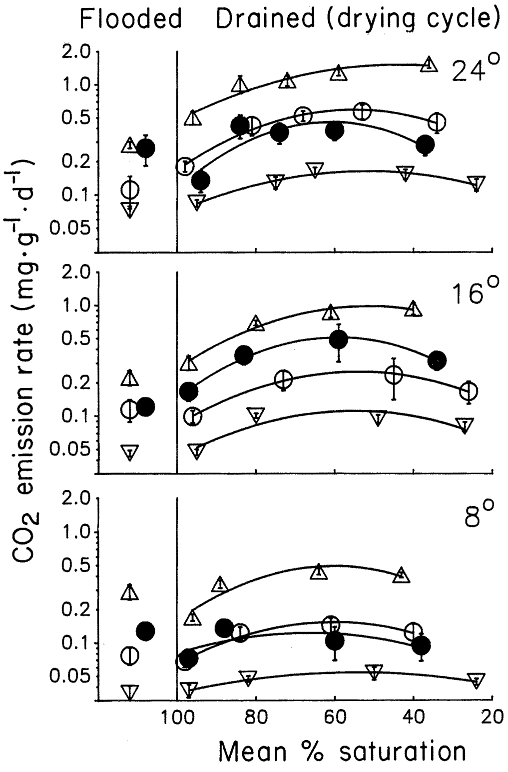

FIG. 1. Effects of temperature, moisture regime, and added ash on CO_2 emissions from peat profiles (mean ± 1 SE, $n = 6$ per treatment and depth combination). Samples were taken from the following depth intervals: 0–10 cm (△); 10–20 cm with (●) and without (○) added peat ash; and 30–40 cm (▽). Quadratic regressions are shown for drained samples.

TABLE 3. CH_4 emission rates from flooded peat samples under controlled treatment conditions (mean ± 1 SE, $n = 6$ for each combination of peat depth and treatment [°C]). Also shown are the number of samples with detectable fluxes of >0.01 $\mu g \cdot g^{-1} \cdot d^{-1}$.

Depth interval (cm)	CH_4 emission rate ($\mu g \cdot g^{-1} \cdot d^{-1}$)			Number of samples with detectable CH_4 emissions		
	8°	16°	24°	8°	16°	24°
0–10	<0.01	0.00	<0.01	1	0	1
10–20	0.00	0.00	0.80 ± 0.69	0	0	5
10–20 (ash added)	0.00	0.40 ± 0.17	6.5 ± 4.8	0	5	5
30–40	0.00	0.00	<0.01	0	0	1

no CH_4 was detected (Table 3). This precluded statistical analysis of individual treatment effects. However, the distribution of CH_4-producing samples among the 12 treatment combinations was found to be nonrandom (df = 2, $\chi^2 = 7.61$; $P < .025$), based on a test of goodness of fit to the Poisson distribution (Zar 1984). The general trends to be noted are (1) increased CH_4 flux with increased temperature; (2) greater flux from the 10–20 cm depth layer than from the other layers; and (3) a stimulating effect of ash addition on CH_4 flux from the 10–20 cm depth layer. The quantity of P and K present in the ash added to the 10–20 cm layer (Table 1) corresponds to an estimated 50–60% addition over that already present in the peat. The mean pH was higher (6.4–6.6) in the samples with added ash than in the corresponding peat samples without ash (5.3–5.8, Table 4).

CH_4 emissions represented a relatively insignificant proportion of total carbon loss during decomposition of peat samples. Estimated carbon flux as CH_4-C averaged <1% of the amount evolved as CO_2-C for the flooded samples taken as a whole. However, for one of the samples (10–20 cm depth with added ash, at 24°C) CH_4 made a substantial contribution (27%) to total carbon loss.

Flooded samples from treatment combinations with high CH_4 emissions were resampled 20 d after the main gas sampling period to determine if differences in CH_4 flux among samples were consistent over time or stochastic. These samples were all from the 10–20 cm depth layer (held at 24°C, with or without added ash; or at 16°, with added ash). CH_4 emissions were highly correlated between the two sampling dates [$r^2 = 0.877$, $n = 18$, based on $\log(R + 1)$ transformation].

None of the drained samples tested (using FID) had detectable CH_4 emissions. This analysis was conducted 3 d after reflooding for samples from the 10–20 cm depth layer, with and without added ash, under the 24°C temperature treatment.

TABLE 4. Water pH of flooded peat samples after 120 d under controlled treatment conditions.

Depth interval (cm)	Temperature (°C)		
	8°	16°	24°
0–10	5.6 ± 0.1	5.0 ± 0.4	4.6 ± 0.1
10–20	5.8 ± 0.1	5.3 ± 0.2	5.7 ± 0.1
10–20 (ash added)	6.6 ± 0.1	6.4 ± 0.1	6.5 ± 0.2
30–40	5.6 ± 0.1	5.6 ± 0.1	5.6 ± 0.1

Mass losses

The greatest percentage losses of dry mass (10.4 ± 1.4%) occurred in the upper (0–10 cm) peat layer in the warm (24°C), drained treatment (Fig. 2). In contrast, the lower (30–40 cm) peat layer lost <1% of its dry mass, even under these conditions most favorable to aerobic decomposition.

The patterns of mass loss from the peat samples were

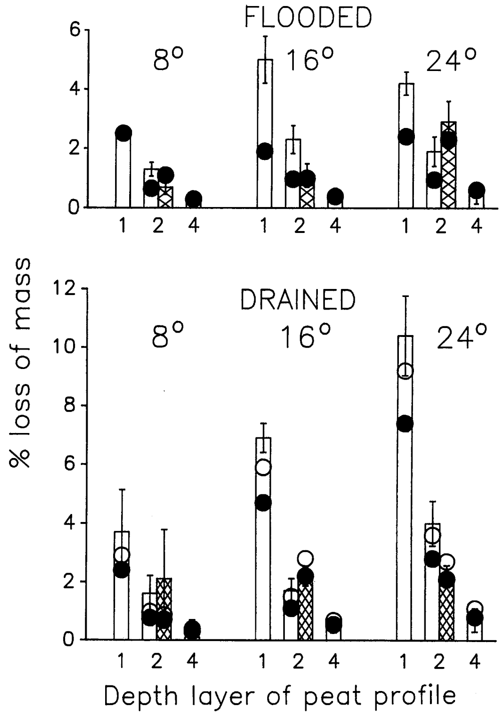

FIG. 2. Percentage mass loss of peat samples after 125 d under controlled treatment conditions (same as in Fig. 1). Layers 1, 2, and 4 refer to 0–10, 10–20, and 30–40 cm depth intervals, respectively. Shaded bars show effect of ash added to peat from the 10–20 cm depth layer. Mass loss estimates based on CO_2 emission rates are also shown, calculated using external headspace volume (●) and internal + external headspace volume (○).

similar to those expected on the basis of CO_2 emissions, though losses tended to be greater than expected in the upper layers of the flooded treatment at 16° and 24°C (Fig. 2). In the drained treatment, the second method of calculating headspace and emission rates resulted in predicted mass losses closer to the mass losses actually observed.

Estimates of dry mass losses were generally more variable than would be expected from CO_2 emissions. Slight errors in weighing were evident in a few samples from the 30–40 cm depth layer, where small increases in dry mass (up to 2%) were noted. Rewetting of oven-dried samples at the beginning of the experiment may have caused a transient increase in respiration rates (Orchard and Cook 1983). When samples were dried at the end of the experiment, microbial respiration (particularly in flooded samples) may have been briefly stimulated before lethal temperatures were reached. Thermal degradation could have also promoted carbon loss during the oven-drying process (Taylor and Parkinson 1988).

The main results of ANOVA based on percent mass loss were generally in agreement with those based on CO_2 emissions (Table 2), despite the inherent potential for error in each of these methods. Temperature, moisture regime, and peat depth each had significant effects ($P < .001$) on mass loss. All possible interactions among these three factors were also significant ($P < .005$). Although ash had no overall effect on percent mass loss of the 10–20 cm depth layer (three-way ANOVA: df = 1,60; $F = 0.58$; NS), there was a significant three-way interaction among ash, temperature, and moisture treatments (df = 2,60; $F = 3.50$; $P = .036$).

Discussion

CO_2 *losses and decay resistance*

The results indicate that deeper peat strata were much more resistant to decay than surface peat. When compared within each combination of temperature and moisture treatments, CO_2 emission rates from the 0–10 cm depth layer were 2–4 times greater than from the 10–20 cm layer, and 4–9 times greater than from the 30–40 cm layer (Fig. 1). Mass losses from the deeper layer were very low (<1%) even after 3 mo exposure to aerated conditions at 24°C. The large difference in decomposition rates between the 0–10 and the 30–40 cm depth layers was not accompanied by a difference in the C/N ratio, suggesting that this factor is a poor indicator of decay potential when comparing peat from different depths (see also Fyles and McGill 1987). However, the strong differences in total P, K, and TNC levels (Table 1) among the three peat strata suggest that these substances could have had a controlling influence on microbial respiration rates. When samples were collected, the uppermost layer contained living mosses and a greater abundance of living and senescent vascular plant roots than in the lower layers. These were killed by drying at the start of the experiment but presumably contained higher concentrations of P, K, and TNC than the peat (Malmer 1962, 1988, Heal et al. 1978). Thus the more rapid rate of carbon loss from the 0–10 cm depth may reflect a greater abundance of freshly killed plant biomass in this layer. In the deeper layers, respiration rates may have been limited by the accumulation of components unfavorable to microbiological activity, such as lignins and phenolic or humic substances (e.g., Ivarson 1977, Heal et al. 1978, Dickinson 1983, Anderson and Hepburn 1986).

In a few other studies it has been observed that deeper peats respire more slowly than surface peats when incubated under common environmental conditions (Lähde 1969, Farrish and Grigal 1988), even when given adequate supplies of mineral nutrients (Ivarson 1977). Studies of decomposition in peatlands using the litter bag technique suggest that the rate of mass loss of *Sphagnum* species decreases as they decompose (Clymo 1965, Rochefort et al. 1990, Johnson and Damman 1991). Similarly, Heal et al. (1978) found that the rate of oxygen consumption by vascular plant litter on a blanket bog decreased substantially during decomposition over a 5-yr period, based on measurements made at 10°C on litter of different ages.

To our knowledge, the question of decay resistance in older peats has not been addressed in previous discussions on the carbon balance of peatlands following drainage or climate change (e.g., Silvola and Hanski 1979, Armentano and Menges 1986, Silvola 1986, Billings 1987, Gorham 1991). Decay resistance is potentially important because it could strongly influence the rate of carbon loss from organic deposits under changing environmental conditions.

Reliable predictions of carbon loss from peat deposits following climate change require an improved understanding of the factors controlling the peat accumulation process. The accumulation of organic material in peatlands is often attributed to the slow microbial decay that occurs under anaerobic conditions in deeper peat strata (Clymo 1983, 1984). In cold climates, the seasonally constant low temperatures of deeper peats also result in a thermally less favorable environment for microbial activity than at the peat surface. If these are the main factors causing peat accumulation, then lowered water tables and warmer temperatures would be expected to produce a very strong and rapid increase in the rate of carbon loss from organic deposits. However, in situations where decomposition leads to the formation of highly decay-resistant organic material, the rate of carbon loss would be less affected by changes in environmental conditions. The intrinsic chemical and physical characteristics of certain peat-forming plants such as *Sphagnum* may also lead to decay-resistant peat, even in the early stages of decomposition (Coulson and Butterfield 1978, Clymo and Hayward 1982, Johnson and Damman 1991).

Although the present study compares the decomposition of peat layers from only one peatland, it does suggest that some deeper peats are composed of decay-resistant material. A major implication of decay resistance in deeper peat strata is that lowered water tables may not necessarily cause a rapid increase in CO_2 release from peatlands, particularly those that already have water tables >20 cm below the peat surface for most of the summer.

The expected increase in CO_2 release rates with increased temperature (Silvola et al. 1985) was observed in the present study for the samples exposed to drying cycles. However, temperature had little effect on CO_2 release from continuously flooded samples. This presumably reflects the dependence of aerobic respiration on the rate of oxygen diffusion across the flooded peat surface. Thus, in areas where global warming is not accompanied by lowered water tables, there may not be a substantial increase in CO_2 emission rates from continuously flooded peat deposits.

Postfire losses of CO_2

The addition of peat ash to samples from the 10–20 cm depth layer caused an increase in pH under each of the three temperatures in the flooded treatment, but appeared to have a variable effect on peat respiration. This may be expected in light of the microbial diversity of peatlands (Christensen and Cook 1970, Williams and Crawford 1983*a*) and the highly diverse physiological response of microbes to pH, temperature, and aeration (Williams and Crawford 1983*b*). Silvola et al. (1985) noted that addition of wood ash (3000 kg/ha) to three peatlands caused consistent long-term increases in pH, but CO_2 fluxes increased in only one of the peatlands treated.

Several factors also need to be considered when predicting the effects of deep-burning fire on the subsequent decomposition of organic soils, including postfire changes in water tables and substrate temperatures. If deeper peats are resistant to decay, then the removal of surface peat layers by fire should result in an overall decrease in the subsequent CO_2 emissions. Thus the immediate release of CO_2 in organic terrain fires would be much more significant than postfire changes in microclimate or the potentially stimulating effect of ash on peat respiration.

Release of CH_4

CH_4 emissions were highly variable, as has been reported elsewhere (Svensson and Rosswall 1984, Moore and Knowles 1987, 1989, Hogg and Wein 1988). When expressed on the basis of peat surface area, the data in Table 3 correspond to mean CH_4 emission rates of up to 8 $mg \cdot m^{-2} \cdot d^{-1}$ for samples without added ash and up to 66 $mg \cdot m^{-2} \cdot d^{-1}$ for samples with added ash at 24°C. These values are in the low portion of the range of field measurements of CH_4 emission rates (0–130 $mg \cdot m^{-2} \cdot d^{-1}$) reported for comparable sites (Moore and Knowles 1987, Crill et al. 1988, Moore et al. 1990). Although the experimental conditions used in the present study do not mimic present-day field conditions, the results indicate that even after severe drought, methanogenic bacteria would be capable of rapid recolonization if water levels subsequently increased and anaerobic conditions were restored. The results also suggest that after reflooding for several weeks, CH_4 flux should increase to higher levels under warmer thermal regimes (Svensson 1984, Williams and Crawford 1984). The tendency for increased CH_4 emissions in the samples with added ash suggests that peat fires during drought periods can indirectly promote methanogenesis in peatlands. CH_4 production could be stimulated by the P and K present in the ash or by the increased pH associated with ash addition (see Williams and Crawford 1984, Shotyk 1989). These effects are potentially important because CH_4 is estimated to be 3–33 times more efficient than CO_2 in producing global warming (Guthrie 1986, Mooney et al. 1987, James 1990, Lashof and Ahuja 1990, Gorham 1991). However, further experimentation is needed to determine the long-term importance of these effects. For example, warmer temperatures or nutrient additions might not promote CH_4 production in deep, anaerobic peats if the rate of methanogenesis is limited by the buildup of toxic, metabolic end products (Williams and Crawford 1984). Also, changes in CH_4 production within peat deposits may be poorly correlated with CH_4 emissions at the peat surface because some, or even all of the CH_4 produced may be consumed by CH_4-oxidizing bacteria in the aerobic zone (Shotyk 1989).

There are several points concerning experimental methodology that should also be considered. First, we suggest that in future studies of peat respiration using the static chamber method, a high ratio of air headspace volume to peat volume should be used. This reduces the potential for error in determining the effective headspace volume and hence also, CO_2 emission rates. A second problem is the question of whether fresh samples or dried, rewetted, and re-inoculated samples are most appropriate for this type of study. Fresh, intact peat should be generally superior in simulating field conditions, but living belowground plant biomass contributes a disproportionately high amount of CO_2 through plant respiration, particularly in surface peats (E. H. Hogg, *unpublished data*). Drying of samples is essential for studies of mass loss and has the advantage of eliminating the influence of vascular plant respiration, but high temperatures may be required to kill some bryophyte species (Proctor 1981). However, drying of samples may affect decay rates after re-wetting because of chemical changes in the organic material, disturbance to microbial populations, and nutrient release from dead microbial biomass (Taylor and Parkinson 1988, Okano 1990). Thus, the measurement of carbon flux from fresh peat following the removal of living plant material should be more effective in simulating peat decay rates in the field, except in studies specifically investigating the effects of severe drought and fire. Finally, it is evident from this study and others that CH_4 flux shows much more variability among samples than CO_2 flux, and thus experimental designs need to include a higher number of replicates to adequately assess CH_4 emissions from peatlands.

CONCLUSIONS

The present study indicates that the two potential effects of global change, i.e., increased temperature and lowered water tables, could operate synergistically in promoting respiration of peat substrates. This should be particularly important in peatlands where organic strata near the surface have been continuously inundated. However, we have indicated several situations where global warming may have little effect on CO_2 release from decomposing peat deposits. First, we suggest that peats that have already been exposed to long periods of aerobic decay may be highly resistant to further decay. Thus microbial respiration in these peats might not increase appreciably following lowered water levels and fire. Second, we suggest that increased temperature alone will not strongly promote CO_2 emissions from waterlogged peat deposits because the rate of aerobic decay is largely determined by the rate of oxygen diffusion.

In the present study we have restricted our discussion to the topic of carbon losses from peatlands, but changes in primary productivity and carbon storage of the peat-forming vegetation (including trees) are equally important in understanding future changes in the carbon balance of peatlands (Billings 1987, Gorham 1991). Also, future change in species composition of the vegetation will affect the rates of both primary production and decay, because the decomposability of litter being added to peatlands differs dramatically among species (Coulson and Butterfield 1978, Heal et al. 1978).

There is a clear need for more experimental work, particularly on the respiration potential of organic substrates from different types of peat-forming systems. Changes in carbon flux from anaerobic peats as they are re-exposed to aerobic conditions need to be examined experimentally over longer time periods. The effects of deep-burning fire and ash deposition on CH_4 emissions from peatlands also warrant further study. Such studies would assist in the prediction of future changes in peatland carbon balance and CH_4 emissions, as well as providing better estimates of carbon losses that have already occurred in response to anthropogenic peatland disturbance (Armentano and Menges 1986).

ACKNOWLEDGMENTS

S. C. Zoltai provided useful comments on the manuscript, and the assistance provided by J. Niederleitner and D. Stelter is also gratefully acknowledged. This work was funded by a Forestry Transition grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to R. W. Wein and V. J. Lieffers, and an NSERC Postdoctoral Fellowship to E. H. Hogg.

LITERATURE CITED

Aldhous, P. 1991. Climate change—1990 warmest year on record. Nature **349**:186.

Anderson, H., and A. Hepburn. 1986. Variation in humic substances within peat profiles. Pages 177–194 *in* C. H. Fuchsman, editor. Peat and water. Aspects of water retention and dewatering in peat. Elsevier, London, England.

Armentano, T. V., and E. S. Menges. 1986. Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. Journal of Ecology **74**:755–774.

Billings, W. D. 1987. Carbon balance of Alaska tundra and taiga ecosystems: past, present and future. Quaternary Science Reviews **6**:165–177.

Christensen, P. J., and F. D. Cook. 1970. The microbiology of Alberta muskeg. Canadian Journal of Soil Science **50**: 171–178.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. Journal of Ecology **53**:747–758.

———. 1983. Peat. Pages 159–224 *in* A. J. P. Gore, editor. Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. General studies. Elsevier, Amsterdam, The Netherlands.

———. 1984. The limits to peat bog growth. Philosophical Transactions of the Royal Society of London **B 303**:605–654.

Clymo, R. S., and P. M. Hayward. 1982. The ecology of *Sphagnum*. Pages 229–289 *in* A. J. E. Smith, editor. Bryophyte ecology. Chapman and Hall, London, England.

Coulson, J. C., and J. Butterfield. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bogs. Journal of Ecology **66**:631–650.

Crill, P. M., K. B. Bartlett, R. C. Harriss, E. Gorham, E. S. Verry, D. I. Sebacher, L. Mazdar, and W. Sanner. 1988. Methane flux from Minnesota peatlands. Global Biogeochemical Cycles **2**:317–384.

Dickinson, C. D. 1983. Micro-organisms in peatlands. Pages 225–245 *in* A. J. P. Gore, editor. Ecosystems of the world 4A. Mires: swamp, bog, fen and moor. General studies. Elsevier, Amsterdam, The Netherlands.

Ehhalt, D. H. 1988. How has the atmospheric concentration of CH_4 changed? Pages 25–32 *in* F. S. Rowland and I. S. A. Isaksen, editors. The changing atmosphere. John Wiley & Sons, New York, New York, USA.

Farrish, K. W., and D. F. Grigal. 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Science **145**:353–358.

Fyles, J. W., and W. B. McGill. 1987. Decomposition of boreal forest litters from central Alberta under laboratory conditions. Canadian Journal of Forest Science **17**:109–114.

Gorham, E. 1991. Northern peatlands: role in the global carbon cycle and probable responses to climatic warming. Ecological Applications **1**:182–195.

Guthrie, P. D. 1986. Biological methanogenesis and the CO_2 greenhouse effect. Journal of Geophysical Research **91(D10)**: 10847–10851.

Heal, O. W., P. M. Latter, and G. Howson. 1978. A study of the rates of decomposition of organic matter. Pages 136–159 *in* O. W. Heal and D. F. Perkins, editors. Production ecology of some British moors and montane grasslands. Ecological Studies Analysis and Synthesis **27**.

Hogg, E. H., and R. W. Wein. 1988. Seasonal change in gas content and buoyancy of floating *Typha* mats. Journal of Ecology **76**:1055–1068.

Hurlbert, S. H. 1985. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

Ingram, H. A. P. 1978. Soil layers in mires: function and terminology. Journal of Soil Science **29**:224–227.

Ivarson, K. C. 1977. Changes in decomposition rate, microbial population and carbohydrate content of an acid peat bog after liming and reclamation. Canadian Journal of Soil Science **57**:129–137.

James, C. G. 1990. Natural gas and the greenhouse. Nature **347**:720.

Johnson, L. C., and A. W. H. Damman. 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos **61**:234–242.

Kivinen, E., and P. Pakarinen. 1981. Geographical distribution of peat resources and major peatland complex types in the world. Annales Academiae Scientiarum Fennicae A III **132**:1–28.

Lähde, E. 1969. Biological activity in some natural and drained peat soils with special reference to oxidation–reduction conditions. Acta Forestalia Fennica **94**:1–69.

Lashof, D. A., and D. R. Ahuja. 1990. Relative contribution of greenhouse gas emissions to global warming. Nature **344**: 529–531.

Malmer, N. 1962. Studies on the mire vegetation in the archaean area of southwestern Götaland (south Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. Opera Botanica **7(2)**:1–67.

———. 1988. Patterns in the growth and the accumulation of inorganic constituents in the *Sphagnum* cover on ombrotrophic bog sites in Scandinavia. Oikos **53**:105–120.

Maltby, E., C. J. Legg, and M. C. F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78**:490–518.

Manabe, S., and R. T. Wetherald. 1986. Reduction in summer soil dryness induced by an increase in atmospheric carbon dioxide. Science **232**:626–628.

Mooney, H. S., P. M. Vitousek, and P. A. Matson. 1987. Exchange of materials between terrestrial ecosystems and the atmosphere. Science **238**:926–932.

Moore, T. R., and R. Knowles. 1987. Methane and carbon dioxide evolution from subarctic fens. Canadian Journal of Soil Science **67**:77–81.

Moore, T. R., and R. Knowles. 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science **69**:33–38.

Moore, T., N. Roulet, and R. Knowles. 1990. Spatial and temporal variations of methane flux from subarctic/northern boreal fens. Global Biogeochemical Cycles **4**:29–46.

Oeschger, H., and U. Siegenthaler. 1988. How has the atmospheric concentration of CO_2 changed? Pages 5–23 *in* F. S. Rowland and I. S. A. Isaksen, editors. The changing atmosphere. John Wiley & Sons, New York, New York, USA.

Okano, S. 1990. Availability of mineralized-N from microbial biomass and organic matter after drying and heating of grassland soils. Plant and Soil **129**:219–225.

Orchard, V. A., and F. J. Cook. 1983. Relationship between soil respiration and soil moisture. Soil Biology and Biochemistry **15**:447–453.

Proctor, M. C. F. 1981. Physiological ecology of bryophytes. Advances in Bryology **1**:79–166.

Ramanathan, V. 1988. The radiative and climatic consequences of the changing atmospheric concentration of trace gases. Pages 159–186 *in* F. S. Rowland and I. S. A. Isaksen, editors. The changing atmosphere. John Wiley & Sons, New York, New York, USA.

Rochefort, L., D. H. Vitt, and S. E. Bayley. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology **71**:1986–2000.

Shotyk, W. 1989. An overview of the geochemistry of methane dynamics in mires. International Peat Journal **3**:25–44.

Silvola, J. 1986. Carbon dioxide dynamics in mires reclaimed for forestry in eastern Finland. Annales Botanici Fennici **23**:59–67.

Silvola, J., and I. Hanski. 1979. Carbon accumulation in a raised bog. Simulation on the basis of laboratory measurements of CO_2 exchange. Oecologia (Berlin) **37**:285–295.

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

Smith, D. 1981. Removing and analyzing total nonstructural carbohydrates from plant tissue. University of Wisconsin, College of Agriculture and Life Sciences Publication **R-2107**.

Svensson, B. H. 1984. Different temperature optima for methane formation when enrichments from acid peat are supplemented with acetate or hydrogen. Applied and Environmental Microbiology **48**:389–394.

Svensson, B. H., and T. Rosswall. 1984. In situ methane production from acid peat in plant communities with different moisture regimes in a subarctic mire. Oikos **43**:341–350.

Tarnocai, C. 1984. Peatland resources of Canada. National Research Council of Canada, NRCC Number 24140, Ottawa, Ontario, Canada.

Taylor, B. R., and D. Parkinson. 1988. Does repeated wetting and drying accelerate decay of leaf litter? Soil Biology and Biochemistry **20**:647–656.

Wein, R. W. 1983. Fire behaviour and ecological effects in organic terrain. Pages 81–95 *in* R. W. Wein and D. A. MacLean, editors. The role of fire in northern circumpolar ecosystems. John Wiley & Sons, Toronto, Ontario, Canada.

Williams, R. T., and R. L. Crawford. 1983*a*. Microbial diversity of Minnesota peatlands. Microbial Ecology **9**:201–214.

Williams, R. T., and R. L. Crawford. 1983*b*. Effects of various physicochemical factors on microbial activity in peatlands: aerobic biodegradative processes. Canadian Journal of Microbiology **29**:1430–1437.

Williams, R. T., and R. L. Crawford. 1984. Methane production in Minnesota peatlands. Applied and Environmental Microbiology **47**:1266–1271.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Zoltai, S. C., and Johnson, J. D. 1987. Relationships between nutrients and vegetation in peatlands of the prairie provinces. Pages 535–542 *in* C. D. A. Rubec and R. P. Overend, editors. Proceedings of the 1987 Symposium on Wetlands/Peatlands, Edmonton, Alberta, Canada. August 23–27, 1987. Canada Committee on Ecological Land Classification, Ottawa, Ontario, Canada.