

The Annual Carbon Budget for Fen and Forest in a Wetland at Arctic Treeline

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ABSTRACT. Three separate research efforts conducted in the same wetland-peatland system in the northern Hudson Bay Lowland near the town of Churchill, Manitoba, allow a comparison of two carbon budget estimates, one derived from long-term growth rates of organic soil and the other based on shorter-term flux measurements. For a tundra fen and an open subarctic forest, calculations of organic soil accumulation or loss over the last half-century indicate that while the fen on average has lost small amounts of carbon from the ecosystem, the adjacent forest has gained larger amounts of atmospheric carbon dioxide. These longer-term data are supported by shorter-term flux measurements and estimates, which also show carbon loss by the fen and carbon uptake by the forest. The shorter-term data indicate that the fen's carbon loss is largely attributable to exceptionally dry years, especially if they are warm. The forest may gain carbon at an increased rate as it matures and during warm growing seasons. Also, the changes in relief of the dynamic hummock-hollow landscape in the fen may inhibit photosynthesis.

Key words: Subarctic fen and forest, net carbon loss, temperature and water balance variability

RÉSUMÉ. Trois travaux de recherche distincts portant sur le même système de marécages/tourbières situés dans la partie septentrionale des basses-terres de la baie d'Hudson, près de la ville de Churchill au Manitoba, permettent de comparer deux estimations du budget de carbone, l'une tirée des taux de croissance à long terme du sol organique et l'autre fondée sur des mesures du flux à plus court terme. Pour une tourbière basse de toundra et une forêt claire subarctique, les calculs de l'accumulation ou de la perte de sol organique au cours des cinquante dernières années révèlent que, si la tourbière basse a perdu en moyenne de petites quantités du carbone présent dans l'écosystème, la forêt adjacente a acquis des quantités plus grandes de bioxyde de carbone atmosphérique. Ces données établies sur une période relativement longue sont étayées par des mesures et estimations du flux à plus court terme, qui révèlent également une perte de carbone par la tourbière basse et une absorption de carbone par la forêt. Les données à plus court terme montrent que la perte de carbone par la tourbière basse est due en grande partie à des années de sécheresse exceptionnelle, surtout s'il fait chaud. Il se peut que la forêt acquière du carbone à une vitesse accrue en devenant mature et au cours des saisons de croissance chaudes. Il est en outre possible que les changements dans le relief dynamique en bosses et en creux de la tourbière basse bloquent la photosynthèse.

Mots clés: tourbière basse et forêt subarctiques, perte nette de carbone, variabilité du bilan de température et d'eau

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INTRODUCTION

This study arises from the congruence in time of three separate research efforts conducted in a wetland-peatland system in the northern Hudson Bay Lowland near the town of Churchill, Manitoba, Canada (Fig. 1). Carbon budget estimates derived from accumulation rates of organic soil for a tundra fen and an open subarctic forest are compared with estimates from flux measurements. The former apply to a 53-year period (1947–99), while the latter apply to a recent period (1994–99) of measurements in the fen and forest.

Carbon budgets in northern wetland-peatland systems are important to the global carbon budget in a number of respects. First, these systems are important to the net gain

and storage of atmospheric carbon dioxide during the post-glacial period. Gorham (1991) estimates that northern peatlands contain about one-third of the global pool of carbon in soil and a little less than two-thirds of the carbon stored in the atmosphere. Second, the stored carbon in northern ecosystems appears to be vulnerable to climate change (Oechel et al., 1993; Griffis, 2000a, b). As northern wetlands have the potential to influence the carbon storage in the atmosphere and hence the greenhouse effect, it is important to understand the carbon budget of northern peatlands and how it might be changing.

The Hudson Bay Lowland is the second-largest contiguous wetland-peatland system in the world, but only in the last decade has there been an effort to understand its carbon budget in terms of process magnitudes and

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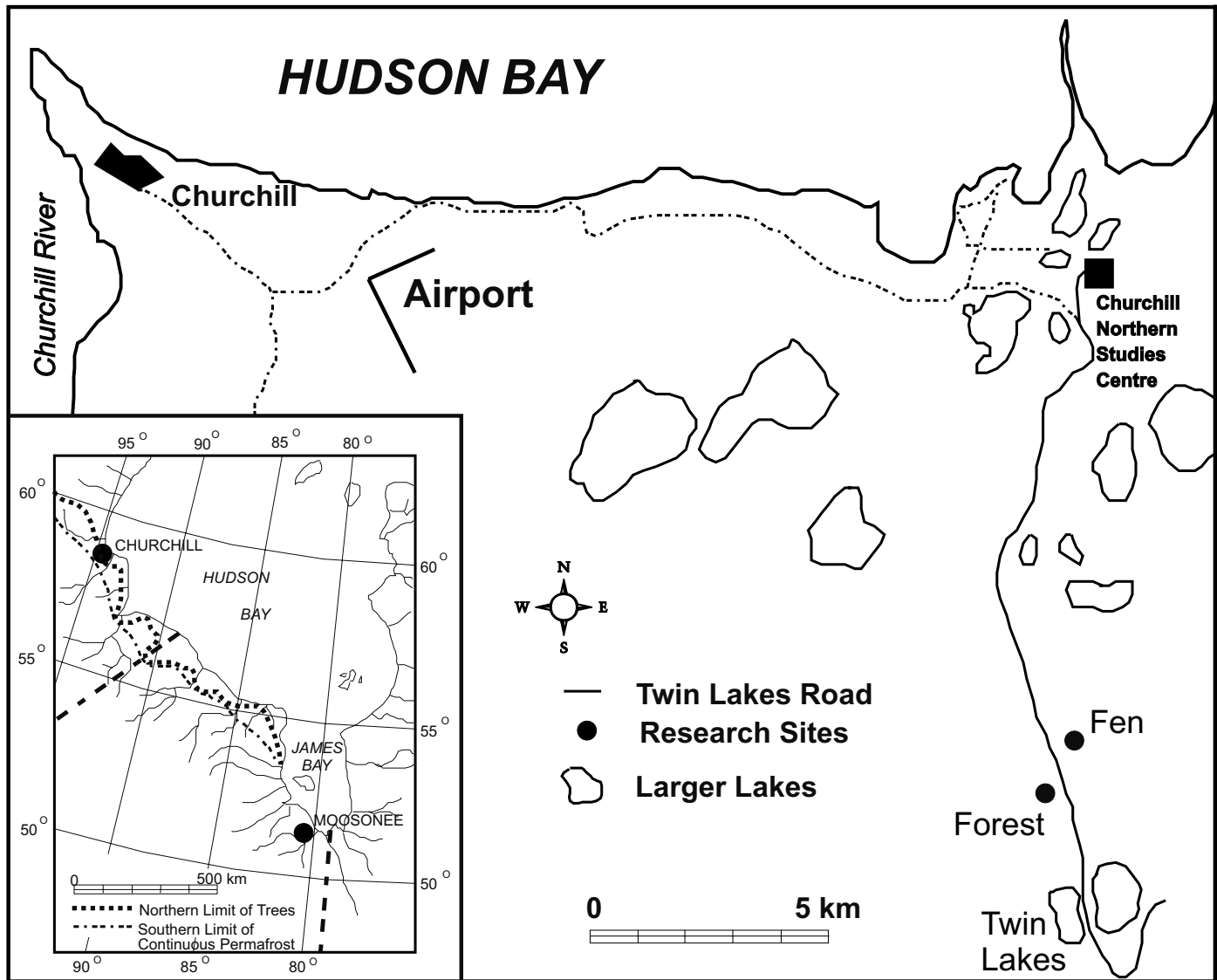


FIG. 1. Location of research area and sites.

controls. Important and definitive research into the net methane effluxes was undertaken during the Northern Wetland Ecosystem Study (e.g., Roulet et al., 1994), and there have been limited studies of the carbon dioxide budget (Neumann et al., 1994; Whiting, 1994; Burton et al., 1996; Schreuder et al., 1998; Waddington et al., 1998; Joiner et al., 1999; Lafleur, 1999; Griffis et al., 2000a, b). A number of studies have investigated landscape-scale net ecosystem CO_2 exchange at Alaskan high-latitude wetlands (e.g., Coyne and Kelly, 1975; Peterson et al., 1984; Fan et al., 1992; Oechel et al., 1993; Vourlitis and Oechel, 1997; McFadden et al., 1998). Most of these studies have been of short duration (1 to 3 years). Moreover, their results differ, some indicating that wetlands act as net carbon sources, and others, that they act as net carbon sinks (Griffis et al., 2000a). The present report attempts to extend our knowledge to a period spanning the last half-century and to place recent carbon budget measurements into that perspective.

METHODS

Site Description

The research area is located near the southwest coast of Hudson Bay, within the northern Hudson Bay Lowland (Fig. 1). It lies poleward of the southern limit of continuous permafrost and at the northern extent of the boreal tree line. The research sites are located 20 km east of the town of Churchill, Manitoba ($58^{\circ}45'N$, $94^{\circ}04'W$), and from 10 to 15 km south of the Hudson Bay coastline, which trends east-west at this location.

The fen research sites comprise an extensive freshwater system with restricted drainage, low oxygen saturation, and a limited mineral supply. The contemporary fens are characterized by hummock and hollow surface relief (Fig. 2). The relief between hummock and hollow averages 0.25 m. Hollows make up 48%, small hummocks 47%, and large hummocks 5% of the fen landscape

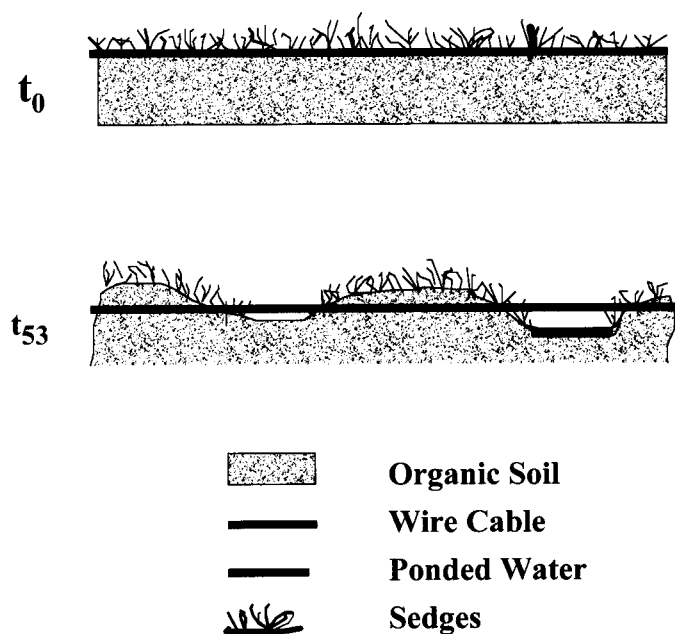


FIG. 2. Schematic diagram of the fen showing the development of hummock-hollow topography over time and the location of the communications wire.

(Schreder et al., 1998). This hummocky landscape is dynamic, increasing and then decreasing in vertical relief over time. This is visually evident in the larger frost mounds, which grow to a certain size and then collapse. The general relief in the research area appears to have been increasing in the last half-century. The base of the soil profile is composed of glaciomarine fine silts and clays. Above this, the accumulated peat layer is from 0.3 to 0.4 m thick. The site lies in an area of rapid isostatic rebound following the last ice age. From its mean elevation of 22 m ASL, we estimate that the site emerged from the sea about 2200 years ago. On the hummocks, the vegetation is dominated by sedges (*Carex aquatilis*, *C. limosa*, *C. saxatilis*, *C. gynocrates*) and sparsely populated with a vascular shrub canopy of dwarf birch (*Betula glandulosa*), Labrador tea (*Ledum decumbens*), and arctic willow (*Salix arctophila*). Beneath the vascular plants, the ground is covered in lichen (*Cladina stellaris*, *C. rangiferina*). The hollows are dominated by brown moss (*Scorpidium turgescens*). On average, the growing season commences about 20 June (initial green leaf emergence of sedges), and maximum growth rates occur during mid-July, when the maximum leaf area index (ca. 0.4) for the vascular plants (mainly sedges) is achieved. The maximum canopy height of about 0.18 m is reached in late July, and senescence of the vascular plants (biomass decrease) usually begins during the first half of August. However, during favourable warm and moist weather conditions, the growing season can start a week earlier and last several weeks later than average (Griffis et al., 2000a).

The forest research area extends southward from the fen and is better drained because of a gradient caused by the rise onto a kame terrace (Twin Lakes in Fig. 1). Topographically, it consists of uneven, hummocky terrain

interspersed with small, shallow pools of highly acidic bog water. The open canopied lichen-woodland has an upper canopy that is 52% spruce (*Picea mariana* and *P. glauca*) and 48% tamarack (*Larix laricina*). The mean height of trees is 5.4 m (Lafleur et al., 2001). The understory comprises sphagnum moss mounds (*Sphagnum* spp.), bog cranberry, crowberry, willows, Labrador tea, and lichens in the drier areas, and horsetail (*Equisetum arvense*) and sedges (*C. aquatilis* and *C. vaginata*) in the wetter areas. The soil consists of 0.2 to 0.3 m of fibrous peat overlying a marine clay/silt stratum. The leaf area index for the trees is estimated at 1.5, but if one includes shrubs, it is more than 2.0 (Lafleur et al., 2001). Also the moss and lichen ground cover is much thicker in the forest than in the fen. The presence of evergreen spruces in this landscape enables photosynthesis to begin earlier in the spring and persist later into the fall than does the sedge-dominated fen.

The fluxes of CO₂ from the fen were measured continuously during the summer period in the five years 1994, 1996, 1997, 1998, and 1999 (Schreder et al., 1998; Griffis et al., 2000a). The methodology involves a flux-gradient approach, the details of which are outlined in Burton et al. (1996). The flux-gradient system employs vertical profiles of CO₂, wind speed, vapour pressure, and temperature measured at six levels above the fen surface. The Bowen ratio-energy balance is used to derive the turbulent transfer coefficient for CO₂. That coefficient is then applied to the CO₂ vertical gradients to determine the CO₂ flux into the atmosphere. This approach has been one of the accepted methods for determining CO₂ fluxes (e.g., Neumann et al., 1994), but recently it has been largely replaced by the eddy correlation approach, which has been used above the forest. This latter approach is a measurement of the CO₂ flux computed directly from the covariance of the instantaneous deviations in vertical wind and CO₂ concentration of the air above the surface. Its use in the Hudson Bay Lowland is described in detail in Neumann et al. (1994), Lafleur (1999), and Joiner et al. (1999). Neumann et al. (1994) show good agreement between the flux-gradient and eddy correlation approaches as applied to wetlands in the southern Hudson Bay Lowland, and our shorter-term comparisons over wetlands in the northern Hudson Bay Lowland confirm this result. However, the errors associated with both methods can be substantial when atmospheric conditions are stable and wind speeds are low. Error analyses for the flux-gradient measurements (Griffis et al., 2000a) and eddy correlation measurements (Joiner et al., 1999; Lafleur, 1999) indicate that the maximum probable errors can approach $\pm 25\%$ over the course of a typical day.

Most of the flux measurements at fen and forest sites incorporate only the period from early June to the end of August. Thus the late growth and senescence periods, the winter snow-cover period, and the spring snowmelt period are not included in these measurements. These latter periods, which comprise about three-quarters of the year, are times of soil and plant respiration and net carbon loss.

Even in mid-winter under cold conditions, there can be small but persistent respiration losses from Arctic soils (Zimov et al., 1993; Oechel et al., 1997). The following methods were employed to estimate unmeasured fluxes during these periods. Following Griffis et al. (2000a), we used nocturnal measured flux data to estimate ecosystem respiration as a function of surface temperature ($ER = aT_s + R_{max}$) and adjusted this relationship for different phenological periods during the growing season. T_s is soil surface temperature. R_{max} describes the maximum respiration rate at 0°C and is adjusted through the season to ensure that the estimated respiration matched the observed nighttime respiration. This relation was derived from data collected when surface temperature ranged from -1.5° to 15.5°C. The correlation coefficient for the 2°C binned observations is $r = 0.83$. Other respiration functions, derived from scaled chamber measurements at the fen, yield similar parameter estimates (Waddington et al., 1998; Griffis et al., 2000b). The pre-growing and senescence relationships adjusted for R_{max} were applied to the snow-free periods before measurements began in the spring and to the fall period after measurements ceased.

Following Zimov et al. (1993), we have taken a mean daily carbon loss of -0.5 g CO₂ per m² and applied it to the period with snow cover. In the case of the fen, this is sometimes enough to change a measured carbon gain during the growing season to a net annual loss. However, that is not the case for the forest. From observations and the above assumptions, we estimate that our measured flux data represent approximately 60% (range 33% to 75%) of the total annual carbon exchange.

In addition to the CO₂ flux, there is also a small carbon loss due to methane flux (CH₄) from the wetlands. During an earlier two-year study, Rouse et al. (1995) showed that for the fen, water-filled hollows were an important source of methane, and that the fen methane flux could be modelled as a function of depth to water table and temperature. The functional relationships developed during that study have been applied to the five years of this study to estimate carbon losses due to CH₄ emissions. These emissions are significant and variable for the fen. For the acidic bog soils and ponds of the forest, the methane flux is very small and does not appear to vary significantly from year to year.

The second method of estimating the carbon budget uses an inactive telephone transmission wire that runs along the ground from the former Churchill Rocket Range (Churchill Northern Studies Centre) to Twin Lakes (Fig. 1). The wire parallels the west side of the Twin Lakes road at a distance of 5 to 10 m from the shoulder of the gravel roadbed. It is composed of a twisted pair of 20 gauge stranded, stainless steel conductors covered with black insulation. The wire was strung along the surface in 1947, so the peat accumulation around it represents a 53-year interval.

As the communications wire was not anchored artificially, it is surprising that the wire is perched horizontally above the surface of the hollows by up to 3 cm (Fig. 2). The

anchoring mechanism, which is quite secure, is provided naturally by the peat that has accumulated over the wire on the adjacent hummocks (Fig. 2). When the wire is cut above a hollow, there is no sagging of the wire in the adjacent hollows because of the anchoring action of the peat in the hummocks. The horizontal position of the wire relative to the hummocks and hollows suggests that when it was first laid out, the ground was flatter, and the wire made contact with the surface in most places. The hummocks and hollows appear to have increased their vertical relief during the 53-year period that the wire has been in place.

Samples were extracted during July and August 1999. Ten sites were selected in the fen, and two in the forest, roughly equidistant from one another. We avoided sites in the forest where shrub or tree branches had forced the wire above the soil surface. Each site was 20 m long and was subdivided into 0.5 m increments. Ten locations along each 20 m transect were selected randomly for the removal of soil blocks. On average, this would theoretically result in a 50%, equally distributed sample at all sites. In practice, some individual sites yielded spatially biased data because soil blocks were selected for analysis only where the wire was completely buried. The removal procedure involved cutting the transmission line and then excavating a rectangular block of peat of approximately 20 cm in length and 10 cm in width extending approximately 10 cm below the wire. The intact block (with the cut wire still inside it) was sealed in a plastic bag and frozen for approximately 12 hours. This sampling yielded 100 sample blocks for the fen and 20 for the forest.

In the lab, the peat block was inverted and a sharp, serrated knife was used to remove the portion of the peat that had accumulated below the wire. The above-wire portion of the frozen peat was then sectioned into smaller rectangular blocks and the dimensions were measured to estimate the sample volume. The fresh samples were weighed on a digital balance, then oven-dried at 75°C until no further weight changes were observed (approximately 48 hours). Samples were re-weighed to determine volumetric soil moisture content and bulk density.

The dried samples were crushed and thoroughly mixed in a plastic bag, after which a subsample of approximately 30 ml was removed for loss-on-ignition tests. The oven-dried subsamples were weighed on a second digital balance and then incinerated in ceramic crucibles in a muffle furnace at 450°C for two to five hours. The ash weight was used to determine the organic fraction. These values were combined with the corresponding bulk densities and multiplied by 0.50 to derive organic carbon contents. The reported proportions of peatland organic matter composed of carbon vary moderately around the most commonly used value of 0.50 (see Robinson and Moore, 1999).

For each 20 m site, the sequence and length of exposed and buried wire segments were recorded. Microtopography was measured (0.01 m resolution) at 0.5 m intervals along the 20 m transect, using a laser diode mounted on a self-indicating carpenter's level attached to a tripod. At each

measurement point, the thickness of the accumulated peat layer overlying the buried wire was also recorded. In flat terrain, the exposed wire lies directly on the soil surface in several locations, indicating no net accumulation over the time period. In hummocky terrain, the wire is presently suspended above the soil surface over hollows. In such locations, the displacement of the soil surface below the wire was also recorded. Negative carbon accumulations in the hollows were determined by using the mean bulk density and organic fractions at that site with the measured displacements for individual hollows.

Inferences regarding the initial placement of the wire on the ground surface are required because the spooling-out procedure was not directly observed. The generally flat nature of the terrain suggests that the wire was in direct contact with the surface. With the possible exception of small shrubs intervening, it is not considered plausible that the transmission line would have been laid with sufficient tension that it would remain suspended a few centimetres above the surface over typical spans of several metres. In one instance, the wire was observed to cross a deep pool (3 m diameter) bounded by two tall hummocks (> 0.75 m high). Rocks had been placed on top of the wire at some time in the past, presumably to prevent it from sagging into the pool. This site was not sampled. At another site in the fen, the hollow between two hummocks showed evidence of the accumulation of aquatic organic matter, as the wire was buried under presently growing benthic algae. The local microtopography at this site did not differ substantially from that at other sites where the wire was suspended above hollows. Third, at several locations near the edges of pools, the wire revealed local undulations that can best be interpreted as relicts of the original pond boundaries. This interpretation is consistent with the initial conformity of the wire with the underlying terrain, even where there are relatively abrupt changes in microtopography.

These inferences regarding the initial repose of the wire are important because they support its use as a datum. The sometimes large negative rates of carbon accumulation derived from the downward displacement of the present-day surface of hollows from the suspended wire are responsible for the negative average net accumulations in the fen. However, these negative wetland results are most likely conservative. In extensive zones where the wire is presently resting on the surface, the net accumulation is recorded as zero. In reality, there is potentially an overall negative accumulation, which is undetected because of the absence of any anchoring system for the wire. Similar biases towards underestimating peatland degradation may also exist if perennial stretching of the wire occurred over hollows during successive winters.

These two very different methods of estimating the carbon budget allow us to compare the average annual rate of carbon accumulation over a 53-year period to the rate at the end of that period (over five years for the fen and three years for the forest).

RESULTS AND DISCUSSION

The five years of flux measurements and estimates for the fen indicate that carbon was lost from the peatlands in the form of CO₂ during three of the five years, and that carbon loss in the form of CH₄ was variable and small, but significant each year. The average annual carbon loss was substantial: ca. 12 g per cm² (Table 1).

If this loss all took place from the organic soils, then they lost the equivalent of around 1.3 mm depth of peat (Table 2). However, much of this loss is attributed to 1994 (Table 1), a very dry and warm year (Schreder et al., 1998; Griffis et al., 2000a), particularly at the start of the growing season, which is critical to the full seasonal CO₂ budget (Griffis et al., 2000a). In 1994, the equivalent loss of organic soil depth was about 1 mm. Two other years showed substantial net gains (Table 1), equivalent to about 0.40 mm depth of peat. Table 1 indicates that the CO₂ flux is the important variable in determining the overall carbon budget changes from year to year. Under dry conditions, as in 1994, the CO₂ carbon loss is large and the CH₄ loss is small, whereas under wet conditions, as in 1996, there is large CO₂ uptake and relatively large CH₄ loss.

The wire carbon budget estimates concur with the flux estimates, indicating a net carbon loss for the fen over the longer 53-year time period, but a loss of much lesser average magnitude than indicated by the flux estimates for the five-year period (Table 3). Over the total period, the equivalent loss in peatland depth was only about 0.5 mm (Table 2).

Table 3, which represents the 100 soil samples, indicates a large spatial variability. As noted in the Methods section, the flat profile of the wire relative to the variations in topography caused by the present-day hummocks and hollows indicates that the terrain has undergone an increase in relief between hummocks and hollows during the past 53 years. It is these undulations that give the large spatial variation in the carbon budget estimates.

One is faced with a number of possibilities to account for the substantial differences in magnitude between the flux and the wire estimates of carbon loss from the fen. One possibility is error. The flux estimates rely on relationships of CO₂ to temperature during the nonmeasurement period, which are imprecise. The CH₄ estimates rely on relationships to temperature and moisture derived for the same site but for different time periods. The wire estimates refer to a more heterogeneous spatial sample than do the flux measurements, and there are potentials for error in the sampling protocol and in the assumptions of peat depth to carbon conversions. It is difficult to compile all of the potential errors into an overall value. However, factoring in the total carbon flux during measurement and nonmeasurement periods, as well as maximum error estimates for each of the sources listed above, results in a maximum probable RMS error of $\pm 29\%$ for the annual carbon budget comparison. If one postulates the maximum probable error, there is still a significant difference between the magnitudes of the results from the two methods.

TABLE 1. Annual carbon budget of fen and forest estimated from flux measurements. ΔCO_2 , ΔCH_4 , and C_{NET} are the annual net carbon fluxes of carbon dioxide, methane, and the two totalled, respectively. Positive values indicate a carbon uptake and negative values a carbon loss.

Date	FEN (g Cm ² per year)			FOREST (g Cm ² per year)		
	ΔCO_2	ΔCH_4	C_{NET}	ΔCO_2	ΔCH_4	C_{NET}
1994	-53.5	-1.5	-55			
1996	31.4	-8.3	23.1			
1997	-19.4	-4.5	-23.9	2.7	-0.8	2
1998	30	-7.5	22.5	73.1	-0.8	72.3
1999	-24.5	-3.8	-28.3	81.8	-0.8	81.1
Mean	-7.2	-5.1	-12.3	52.5	-0.8	51.8

TABLE 2. Change in equivalent depth of peat in the fen, estimated from carbon change calculations.

Measurement Method	Period	Change in Depth of Peatlands (mm)
Wire Estimate	53 Years	-0.55
Flux Estimate	1 Year Average	-0.26
Flux Estimate	5 Years	-1.28
Flux Estimate	1996	0.42
Flux Estimate	1994	-0.99

This raises a second possibility: that the rates of carbon measured during five years for the fen were substantially different from the average rates for the 53-year period. This scenario has plausible support. As indicated by the wire measurements, the fen has apparently slipped into a neutral or negative carbon budget after accumulating 0.2 to 0.3 m of peat over the past 2200 years. This negative budget could have become accentuated during the 53-year period. Associated with this conclusion is the evidence that hummock and hollow development may inhibit photosynthesis. Griffis et al. (2000b) show that hummocks are much more effective in photosynthesis than are hollows, and Rouse et al. (1995) show that wet hollows lose substantially more CH_4 than do hummocks. This difference is relevant to the comparison of methodologies, because if methane emissions were large in hummocks, they would be originating from the peat in the saturated zone below the zone of peat accumulation and would not influence the measured changes in peat accumulation.

Further support for the second scenario is the fact that the growing seasons during the five years of flux measurements averaged 1.7°C warmer than those of a 35-year period (1965–99) for which we are able to model the energy and water balance (Table 4 and Fig. 3) using the methodology of Rouse (1998). Table 4 indicates that the five years of measurement had a soil moisture deficit about the same as the 35-year average (1965–99). However, the very warm and dry year of 1994, with its large carbon loss, stands out as anomalous. If one excludes 1994 from the data, then the net carbon loss is very close to zero (Table 4). This raises the question, How anomalous was 1994? In terms of soil moisture deficit, Figure 3 indicates that during the 35

TABLE 3. Average annual carbon budget of fen and forest estimated from measured accumulation around a wire during a 53-year period. The sites represent the intervals where intensive measurements were made. C_{POS} represents the carbon equivalent of organic soils accumulated above the wire, and C_{NEG} , the carbon equivalent of height of the wire above the soil surface. C_{NET} is the sum of C_{POS} and C_{NEG} .

Site	FEN (g Cm ² per year)			FOREST (g Cm ² per year)		
	C_{POS}	C_{NEG}	C_{NET}	C_{POS}	C_{NEG}	C_{NET}
1	14.93	-0.36	14.57	16.46	-2.51	13.95
2	6.46	-3.23	3.22	20.04	-7.16	12.88
3	5.22	-9.78	-4.57			
4	10.2	-36.25	-26.05			
5	10.17	-10.3	-0.13			
6	12.91	-3.59	9.33			
7	8.18	-24.89	-16.71			
8	14.83	-10.75	4.08			
9	13.7	-6.96	6.74			
10	15.04	-11.28	3.75			
Average	11.16	-11.74	-0.58	18.25	-4.83	13.41

years of our record, three other years equalled 1994 in dryness and one year (1966) exceeded it. As noted in Rouse (1998), the amount of summer rainfall is the main determinant of whether a growing season is dry or wet and, as indicated by Griffis et al. (2000a), this is most critical to the carbon budget in the early part of the growing season. On the basis of this evidence, we suggest that very dry years occur more than 10% of the time, and that they apparently give rise to most of the net carbon loss in the system. It is evident that wetlands are very responsive to climate variability (Rouse et al., 1997; Rouse, 1998) and that a combination of higher temperatures and lower rainfall, as shown in Table 4, must lead to substantial drying of the landscape. Since the largest CO_2 sinks in the fen are the mosses (Griffis et al., 2000b), much of the interannual variability is a response to the wetting and drying of the wetland hollows. As the hummock-hollow terrain has increased in relief during the 53-year period, the importance of the wet hollows in the carbon budget has likely become enhanced.

The three years of flux measurements from the adjacent forest give a substantially different result. All three years indicate a carbon gain to the forest, and in 1998 and 1999 this gain was substantial (Table 1). The carbon loss due to methane flux is estimated to be minimal, since the wet hollows in the forest are acidic bogs and produce little CH_4 (Roulet et al., 1994; Rouse et al., 1995). The strength of the CO_2 flux therefore dominates the carbon budget.

Wire estimates of the forest carbon budget indicate a net gain over the 53-year period. The annual average of this carbon uptake is about one-quarter as large as uptakes from the flux estimates for the three-year period (Table 5). The flux estimates, however, include the carbon assimilation by the forest canopy, whereas the wire estimates comprise only the net peat accumulations. If one assumes that the uptake is proportional to the respective leaf-area

TABLE 4. Net carbon fluxes from the fen for the detailed study period and their accompanying environmental energy and water budget parameters in terms of the 35-year average (1965–99). C_{NET} is net annual carbon flux. Q^* is net radiation; T is temperature; P is precipitation; E is evapotranspiration; and SMD is soil moisture deficit for the months June–September inclusive.

Year	C_{NET} (g Cm ² per year)	Q^* (Wm ⁻²)	T (°C)	P (mm)	E (mm)	SMD (mm)
Average (1965–99)		106	9.0	220	271	-65
1994	-55	102	10.7	169	236	-116
1996	23.1	108	10.8	209	290	-64
1997	-23.9	108	10.8	324	291	-36
1998	22.5	108	11.0	259	271	-31
1999	-28.3	129	10.4	202	300	-42
5 Yr Mean	-12.3	111	10.7	233	278	-58
4 Yr Mean	-1.6	113	10.7	249	288	-44

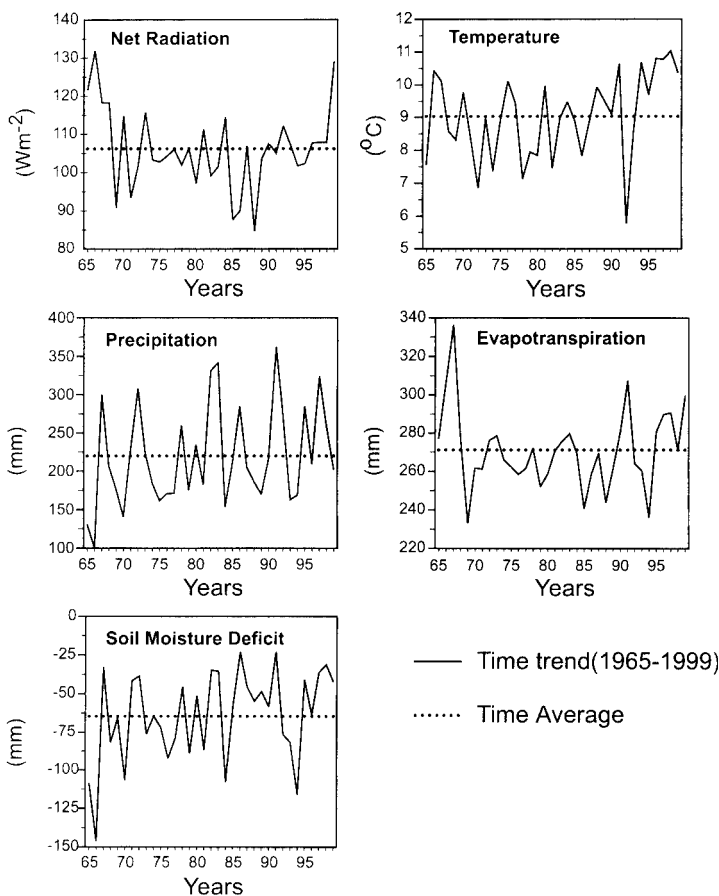


FIG. 3. Time series of environmental parameters over a 35-year period (1965–99) derived from a water balance model developed by Rouse (1998). The data apply to the period June to September inclusive.

indices, then the estimates are quite similar (Table 5). As in the fen, and for the same reasons, some difference may be attributable to error. In the three-year period, the forest experienced growing-season temperatures almost 2°C warmer than the 53-year average and precipitation totals that were a little less than average (Table 4).

It appears likely that the high-latitude carbon budgets of different wetlands, such as the fen and the forest, respond differently to climate forcing (Joiner et al., 1999; Lafleur,

TABLE 5. Average annual carbon budget of fen and forest as calculated from long-term organic soil accumulation and shorter-term fluxes. Positive values indicate a carbon uptake and negative values a carbon loss. The number for forest flux estimates (in parentheses) assumes that two-thirds of the uptake results in tree growth and one-third goes into organic soil accumulation.

	Soil Accumulation Estimates (g Cm ² per year)	Flux Estimates (g Cm ² per year)
FEN	-0.58	-14.2
FOREST	13.41	52.7 (17.6)

1999; Lafleur et al., 2001). One of the most important differences is in the pre-growing season period. Warm and moist conditions favour the vigorous development of root structures and shoots in the fen, leading to subsequent large carbon dioxide uptake. Such conditions also favour the forest by allowing a rapid onset of photosynthesis by evergreen spruce trees and the early leafing of deciduous larch trees and understory deciduous shrubs. Even with favourable growing season conditions, as in 1998, the forest has a net carbon uptake about three times larger than the fen (Table 1). It is a floristically richer system with a leaf area index of more than 2.0 (compared to about 0.4 for the fen), which allows it to photosynthesize more vigorously during the growing season. Also, the growing season is longer, since the evergreen spruce trees extend the photosynthetic period into fall (Lafleur et al., 2001). Warm and dry conditions in the early season are much more deleterious to wetland fens than to forests, as was apparent in 1999, when the fen displayed a substantial negative carbon budget, whereas the forest had its greatest uptake in the three years of flux measurement (Table 1). This difference may be attributable to the deeper rooting system of the forest trees, thicker moss and lichen layers that conserve soil moisture, a deeper peat layer in the forest, or probably a combination of these factors.

There are many unknowns in these complex natural systems. The nutrient status is important. The fen is known as a “poor fen” because it is nutrient-deficient, especially

in nitrogen. The element of temporal evolution must be an important factor in comparisons of fen to forest. Over time, the forest trees have grown, presumably making them more effective in the photosynthesizing of CO₂. Over a time span of 53 years, the hummocky terrain of the fen appears to have increased in relief, probably making it less effective in the photosynthesizing of CO₂, especially during dry conditions. When the hollows dry completely, the brown moss, *Scorpidium turgescens*, senesces until it becomes rewetted (Schreuder et al., 1998). As shown by Rouse (1998), such drying out is a normal occurrence for a short period each summer, and in some years it can persist during much of the growing season. Thus there appear to be legitimate reasons for suggesting that the results indicated in Table 5 are indicative of reality in this example of carbon budget differences at the Arctic tree line.

CONCLUSIONS

In this study of a wetland system at the Arctic tree line, estimates obtained using two different methodologies over different time frames both offer clear evidence that the carbon budgets of fen and forest systems can differ substantially. Long-term measurements of organic soil accumulation or loss during the last half-century indicate that, on average, the fen has been a source of atmospheric carbon, but the forest has been a sink for larger amounts of atmospheric carbon dioxide. These longer-term data are supported by shorter-term flux measurements and estimates. However, the shorter-term data indicate that during 1994–99, the fen was losing and the forest was possibly gaining carbon dioxide at increased rates relative to the 53-year average. Most of the carbon loss from the fen during this period is attributable to one particularly dry year. Such dry conditions have occurred more than 10% of the time in the last 35 years of the hydrological record. Two primary factors appear to be controlling these different rates of carbon exchange in the two ecosystems. The first is the enhanced development in the fen of a hummock-hollow landscape, which we suggest inhibits photosynthesis. The second relates to warmer and drier than average growing season conditions, which inhibit carbon dioxide uptake in the fen and enhance it in the forest.

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