Abstract. Abundant production of organic matter that decomposes slowly under anaerobic conditions can result in substantial accumulation of soil organic matter in wetlands. Tedious means for estimating production and decomposition of plant material, especially roots, hampers our understanding of organic matter dynamics in such systems. In this paper, I describe a study that amended typical estimates for both production and decomposition of organic matter by measuring net flux of carbon dioxide (CO$_2$) over the peat surface within a conifer swamp, a sedge-dominated marsh, and a bog in the Appalachian Mountain region of West Virginia and western Maryland, USA. The sites are relatively productive, with net primary production (NPP) of 30 to 82.5 mol C m$^{-2}$ yr$^{-1}$, but peat deposits are shallow with an average depth of about 1 m. In summer, all three sites showed net CO$_2$ flux from the atmosphere to the peat during the daytime (-20.0 to -30.5 mmol m$^{-2}$ d$^{-1}$), supported by net photosynthesis, which was less than net CO$_2$ flux from the peat into the atmosphere at nighttime (39.2 to 84.5 mmol m$^{-2}$ d$^{-1}$), supported by ecosystem respiration. The imbalance between these estimates suggests a net loss of carbon (C) from these ecosystems. The positive net CO$_2$ flux seems to be so high because organic matter decomposition occurs throughout the peat deposit -- and as a result concentrations of dissolved inorganic carbon (DIC) in peat pore waters reached 4,000 $\mu$mol L$^{-1}$ by late November, and concentrations of dissolved organic carbon (DOC) in peat pore waters reached 12,000 $\mu$mol L$^{-1}$. Comparing different approaches revealed several features of organic matter dynamics: (i) peat accretion in the top 30 cm of the peat deposit results in a C accumulation rate of about 15 mmol m$^{-2}$ d$^{-1}$; however, (ii) the entire peat deposit has a negative C balance losing about 20 mmol m$^{-2}$ d$^{-1}$.

1. Introduction

In peatland ecosystems, the accumulation of partially decomposed organic matter (née peat) is the foundation of the structure and function of the system. However, describing the dynamics of this material presents several problems. One traditional approach tries to measure the balance between the production and decomposition of organic matter, resulting in peat accumulation (Brinson et al., 1981 and references cited therein). A different approach tries to measure the accretion rate of peat by dating deposition of successive layers in the profile (cf., Craft and Richardson, 1993). I suggest in this paper that one can significantly improve their understanding of organic matter dynamics in peatlands by studying net flux of CO$_2$ over the peat surface which integrates independent production measurements (assimilation of CO$_2$ by net photosynthesis) with decomposition measurements (remineralization of organic matter to CO$_2$ by respiration).

There are inherent limitations in any measurement of organic matter dynamics. For example, measurements of organic matter production that rely on allometric relationships derived from destructive harvests have an annual time scale at best and are difficult to relate to estimates of organic matter decomposition that rely on mass loss of litter samples confined in mesh bags for a much shorter period of time (Brock and Bregman, 1989;

Another serious limitation involves the role played by plant roots in organic matter dynamics. Production estimates require frequent sampling and arduous work counting very small roots (Wallen, 1986; Finer, 1989; Conlin and Lieffers, 1993), while one could argue that confining roots in litter bags is so unrealistic that an estimate of decomposition is meaningless (Fahey, 1992). In contrast, measurements of peat accretion require accurate dates for different depth intervals and a thorough understanding of peat compaction with increasing depth in the peat (Johnson et al., 1990; Malmer and Wallen, 1993). These considerations are not trivial, and misconceptions and short-cuts help fuel controversy about organic matter dynamics in peatlands (cf., Gorham, 1991).

One can amend some of these limitations by measuring net flux of CO2 over the peat surface. Such a measurement integrates CO2 flux between the atmosphere and vegetation (both aboveground and belowground) plus soil. Daytime measurements represent the following equation:

$$\text{Net flux of CO}_2 = \phi_{\text{peat}} + (R_{\text{plant}} - A)$$

where

- $\phi_{\text{peat}} = \text{CO}_2 \text{ flux between peat and the atmosphere (supported by root and microbial respiration),}$
- $R_{\text{plant}} = \text{plant respiration of aboveground components}$
- $A = \text{assimilation of CO}_2 \text{ by photosynthesis.}$

Positive values indicate that respiration exceeds assimilation of CO2, and negative values indicate that assimilation of CO2 exceeds respiration. Nighttime measurements represent the following equation:

$$\text{Net flux of CO}_2 = \phi_{\text{peat}} + R_{\text{plant}}$$

and estimate net ecosystem respiration for both aboveground and belowground components of the ecosystem.

In addition, one also should include the change (d) in storage of peat CO2. One actually measures the change in dissolved inorganic carbon (dDIC) that accounts for the pH-dependent reaction of dissolved CO2 with water forming bicarbonate ($\text{HCO}_3^-$) or carbonate ($\text{CO}_3^{2-}$). The DIC represents a significant pool for CO2 when respiration rates are high and water flux out of the wetland is slow.

Wieder et al. (1990) investigated organic matter dynamics in peatlands of the Appalachian Mountain region of West Virginia and western Maryland and suggested a net annual loss of C from the peat of these systems to the atmosphere despite seemingly high rates of organic matter production. Yavitt et al. (1993) measured net flux of CO2 in a portion of one peatland, dominated by a weakly minerotrophic bog, that also suggested an annual loss of C to the atmosphere.
The purpose of the present study is to provide additional insight into organic matter dynamics by measuring net flux of CO2 in a conifer swamp, a marsh, and an ombrotrophic bog that commonly occur within Appalachian peatlands. The results suggest that these Appalachian peatlands do release more CO2 into the atmosphere than they assimilate on an annual basis.

2. Methods

2.1. STUDY AREA

The research was carried out in two Appalachian peatlands, Big Run Bog, West Virginia (39°07'N, 79°35'W), and Buckle's Bog, Maryland (39°35'N, 79°22'W). Peatlands in this region of Appalachia are similar to more northern (>45°N) counterparts, with ground cover of *Sphagnum* spp. mosses and ericaceous shrubs such as *Andromeda glaucophylla* and *Kalmia latifolia*.

Mean annual temperature of the region is 7.9°C, with a minimum monthly mean of -3.2°C in January and maximum monthly mean of 18.3°C in July. The average frost-free season (number of days between 0°C) is 97. Mean annual precipitation averages 133 cm, with a fairly even distribution throughout the year. Annual snowfall averages 305 cm, and at least 2.5 cm of snow is on the ground for an average of 70 days. The peat deposit rarely freezes in winter, but it will freeze when there is a marginal snowpack. On an annual basis, precipitation exceeds potential evapotranspiration. However, it is likely that any month between April and October might experience a water deficit (i.e., potential evapotranspiration exceeds precipitation). In such months, water table levels may drop as low as 20 cm below the peat surface, before returning to the surface by winter.

Big Run Bog is physiographically a minerotrophic fen (sensu Sjors, 1950), receiving water and nutrients in runoff from the 276-ha watershed dominated by both deciduous and coniferous species (Wieder, 1985). Some parts of Big Run Bog receive more minerotrophic water than other parts that result in a mosaic of plant communities. I sampled in two of the more minerotrophic sites (Table 1). One site was a forested fen (referred to hereafter as the swamp site) in which *Sphagnum girgensohnii* covered 90% of the peat surface, with an open canopy of red spruce (*Picea rubens*) and a dense understory of *Rhododendron maximum*. The second site was a marsh (referred to hereafter as the marsh site) in which a sedge (*Carex canescens*) covered about 85% of the peat surface and mosses covered less than 5% of the surface.

Buckle's Bog is a reasonable example of a true ombrotrophic bog (sensu Sjors, 1950), with a domed central region isolated from water and nutrients in runoff from the surrounding forested watershed. This region of the bog also has microtopography typical of many northern wetlands, with raised hummocks covered by *Sphagnum magellanicum* and deeper hollows dominated by *Sphagnum fallax*. (This study site is referred to hereafter as the bog site.)
<table>
<thead>
<tr>
<th>Site</th>
<th>swamp</th>
<th>Site</th>
<th>marsh</th>
<th>bog</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant plants</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>vascular</td>
<td>red spruce,</td>
<td>Carex</td>
<td>ericaceous</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rhododendron</td>
<td>canescens</td>
<td>shrubs</td>
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</tr>
<tr>
<td></td>
<td>S. girgensohnii</td>
<td>none</td>
<td>S. fallax,</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>S. magellanicum</td>
<td></td>
</tr>
<tr>
<td>non vascular</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peat depth (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>0.35</td>
<td>0.35</td>
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</tr>
<tr>
<td>maximum</td>
<td>0.70</td>
<td>0.55</td>
<td>2.5</td>
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<tr>
<td>Bulk density (g cm^{-3})</td>
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<tr>
<td>0-5 cm depth</td>
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<td>0.01</td>
<td>0.05</td>
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<tr>
<td>Organic matter (%)</td>
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<td></td>
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<tr>
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<tr>
<td>30-35 cm depth</td>
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</tr>
<tr>
<td>0-5 cm depth</td>
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<td>3.8</td>
<td>4.4</td>
<td></td>
</tr>
<tr>
<td>30-35 cm depth</td>
<td>6.8</td>
<td>6.3</td>
<td>4.6</td>
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<tr>
<td>Ca^{2+} (μmol L^{-1})</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5 cm depth</td>
<td>22.8</td>
<td>26.1</td>
<td>20.2</td>
<td></td>
</tr>
<tr>
<td>30-35 cm depth</td>
<td>16.9</td>
<td>25.4</td>
<td>18.1</td>
<td></td>
</tr>
<tr>
<td>K^{+} (μmol L^{-1})</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5 cm depth</td>
<td>6.8</td>
<td>12.1</td>
<td>6.2</td>
<td></td>
</tr>
<tr>
<td>30-35 cm depth</td>
<td>6.4</td>
<td>13.1</td>
<td>15.5</td>
<td></td>
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<tr>
<td>SO_{4}^{2-} (μmol L^{-1})</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>0-5 cm depth</td>
<td>167</td>
<td>242</td>
<td>137</td>
<td></td>
</tr>
<tr>
<td>30-35 cm depth</td>
<td>126</td>
<td>131</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

A more complete description of the study sites is given in Yavitt et al. (1988) and in Wieder et al. (1990).

2.2. METHODOLOGICAL CONSIDERATIONS

There is a fair amount of literature that deals with approaches for measuring net flux of CO_{2} between terrestrial ecosystems and the atmosphere (Denmead, 1991, and references cited therein). Undoubtedly, micrometeorological techniques -- e.g., eddy correlation that measures vertical CO_{2} transport in the atmosphere caused by eddy motion.
-- are preferred because they are nondestructive and nonevasive. However, micrometeorological techniques require relatively large study areas, thereby precluding their use in such small peatlands studied here.

An alternative approach uses relatively small, open-bottom chambers made of clear plastic (cf., Vourlitis et al., 1993). Net flux of CO2 is estimated by measuring the change in CO2 concentration within the chamber headspace upon placing the chamber on the ground and periodically thereafter. Because clear plastic is used, daytime measurements reflect the balance between assimilation of atmospheric CO2 (by photosynthesis) and release of CO2 to the atmosphere (supported by respiration). As mentioned in the introduction section, positive values indicate that respiration exceeds assimilation of CO2 and negative values indicate that assimilation of CO2 exceeds respiration.

Chambers do have their own host of problems, however. For example, chambers change the microclimate (temperature, wind, evapotranspiration rate) within the chamber headspace, leading to better -- or in some cases worse -- growing conditions. Moreover, small pressure differences inside versus outside the chamber can cause an extremely large error in the flux measurement. It is possible to minimize this error by venting the chamber headspace with outside air to maintain pressure equilibrium. Furthermore, daytime measurements must be as short as possible, since a rapid photosynthetic rate can reduce CO2 concentration within the chamber to low enough levels that would limit further photosynthesis. Such short-term measurements inevitably present their own problem of scaling-up repeated measurements to an hourly or longer time scale. Nevertheless, chambers offer relatively inexpensive means for estimating net flux of CO2 in the absence of any other estimate.

2.3. MEASUREMENT OF NET FLUX OF CO2

Net flux of CO2 was estimated at each of the three sites using open-bottom, clear plastic chambers (125-L volume, covering 0.25 m2). The chambers were tall enough to cover all of the vegetation in the marsh and in the bog sites. At the swamp site, however, the chambers were obviously too small to include the aboveground portions of trees and shrubs -- and thus the CO2 flux measurements represent the balance between respiration in the peat, respiration by mosses on the peat surface, and photosynthesis by mosses.

Sampling consisted of four chambers per site, placed about 3 m from each other, with measurements made at midday (1000 to 1300 EST) at least monthly from August 1987 to March 1989. The procedure in the field involved placing a chamber over the peat surface as carefully as possible without disturbing the peat surface, turning on a radial fan to mix the chamber headspace, then collecting five gas samples from the chamber headspace consecutively at 3-min intervals, allowing ambient air to replace the volume of air sampled to equalize pressure. The CO2 concentration of ambient air also was sampled to correct for the addition to the headspace of the chamber. On three sampling dates in 1988 measurements were carried out at 2 hr intervals from 0800 to 1800 (EST) to estimate net flux of CO2 throughout the course of a day.
I also monitored air temperature, relative humidity and solar irradiance both inside and outside each chamber as well as wind speed and peat temperature at 2 and 15 cm depths for each measurement period.

2.4. MEASUREMENT OF DIC AND DOC

Two (replicate) equilibrators (sensu Hesslein, 1976) were used per site to sample concentrations of DIC and DOC in peat pore water seven times in 1988. Each equilibrator had nine rows of wells at 5-cm vertical intervals. The wells were filled with degassed, deionized water and covered with a sheet of 0.45 μm-pore-size membrane filter. Each equilibrator placed in the peat remained for a 10-day period. Within 10 min after retrieval, the water from each well was removed using a 30-mL syringe, acidified, and DIC was stripped into 10 mL of air by shaking vigorously for 2 min. The acidified water sample was saved for analysis of DOC.

2.5. ANALYTICAL MEASUREMENTS

The concentration of CO₂ in air samples was determined by gas chromatography using a thermal conductivity detector and a Poropak column (2 m X 3 mm) maintained at 35°C with He carrier gas (30 mL min⁻¹). I quantified gas concentrations by comparing peak area for samples and standards. Certified standards (286 to 10,000 μL L⁻¹ of CO₂ in N₂) bracketed every 10-15 samples. Analytical precision was <0.2% and accuracy was within 2% of each standard.

The concentration of DOC in water samples was determined using a dedicated total organic carbon analyzer.

3. Results

3.1. DAYTIME MEASUREMENTS OF NET CO₂ FLUX

Daytime measurements of net CO₂ flux varied considerably among the three sites sampled (Figure 1). The bog site had a mean net CO₂ flux of -2.60 mmol m⁻² hr⁻¹ or about 2-times greater than the mean CO₂ flux of -1.26 mmol m⁻² hr⁻¹ at the swamp site and 3-times greater the mean CO₂ flux of -0.86 mmol m⁻² hr⁻¹ at the marsh site. These values represent mean fluxes made in the daytime across all sampling dates. The range of individual values was a maximal negative net CO₂ flux of -26 mmol m⁻² hr⁻¹ at the swamp site and a maximal positive net CO₂ flux of 16.5 mmol m⁻² hr⁻¹ at the marsh site.

Net CO₂ flux in daytime at all three sites was always positive for measurements made in December through February. Otherwise, negative values for net CO₂ flux occurred as early as March at all three sites, predominantly between May and September, and still
Fig. 1. Seasonal trend in midday measurements of net CO$_2$ flux in three different Appalachian peatland sites. Means for four replicate chambers ± 1 SE.

sporadically at all three sites in October and November. Positive values for net CO$_2$ flux in the daytime were <10% of the individual estimates made between May and September.
TABLE II
Net CO₂ flux (mmol m⁻² hr⁻¹) during nighttime (2300 and 0300 EST) within three Appalachian peatland sites. Values are the mean of four replicate chambers per sampling date ± one standard error.

<table>
<thead>
<tr>
<th>Site</th>
<th>swamp</th>
<th>marsh</th>
<th>bog</th>
</tr>
</thead>
<tbody>
<tr>
<td>February</td>
<td>0.0 ± 0.0</td>
<td>0.1 ± 0.0</td>
<td>0.1 ± 0.0</td>
</tr>
<tr>
<td>April</td>
<td>2.1 ± 1.0</td>
<td>0.7 ± 0.5</td>
<td>1.0 ± 0.3</td>
</tr>
<tr>
<td>June</td>
<td>10.6 ± 4.6</td>
<td>14.2 ± 8.1</td>
<td>2.4 ± 1.0</td>
</tr>
<tr>
<td>August</td>
<td>21.6 ± 10.0</td>
<td>6.0 ± 3.2</td>
<td>1.1 ± 0.2</td>
</tr>
<tr>
<td>October</td>
<td>2.1 ± 0.6</td>
<td>2.1 ± 1.1</td>
<td>10.4 ± 2.0</td>
</tr>
<tr>
<td>November</td>
<td>0.4 ± 0.2</td>
<td>0.4 ± 0.2</td>
<td>1.3 ± 0.5</td>
</tr>
</tbody>
</table>

The Bog site showed less variation among the four chamber measurements per sampling date, with a standard error about 40-60% of the mean, compared to the variation among measurements at the other two sites where the standard error was often 100% of the mean.

3.2. NIGHTTIME MEASUREMENTS OF NET CO₂ FLUX

At all three sites, net CO₂ flux at nighttime was measured in February, April, June, August, October and November (Table II) and always showed positive values as expected. The swamp site had the highest mean net CO₂ flux of 6.13 mmol m⁻² hr⁻¹ or about 56% higher than the mean CO₂ flux of 3.92 mmol m⁻² hr⁻¹ at the marsh site and 125% higher than the mean CO₂ flux of 2.72 mmol m⁻² hr⁻¹ at the bog site. The range of individual values for net CO₂ flux at nighttime was 0.1 to 32 mmol m⁻² hr⁻¹.

Net CO₂ flux at nighttime was lowest in February at each site (less respiration) and increased during the growing season. The highest flux occurred at different times of the year among the three sites, with the highest values occurring in June at the Marsh site, in August at the swamp site, and in October at the Bog site.

3.3. DAILY RATES OF NET CO₂ FLUX

Measurements of net CO₂ flux were made repeatedly throughout the day at all three sites on three dates in 1988. At all three sites, net CO₂ flux was positive at nighttime and negative soon after sunrise, with a maximal value being reached at noon before declining steadily after that (Figure 2). The set of measurements made on 14 June for a mostly clear day (photosynthetic photon flux [PPFD] > 1500 μmol m⁻² s⁻¹ throughout midday) showed a relatively similar daily pattern as that for a partly cloudy day on August 13 (PPFD as low as 500 μmol m⁻² s⁻¹ during cloudcover of 10 to 30 min), except that
negative net CO₂ flux at midday was not as low (less assimilation of CO₂) as that on the sunny day.

3.4. DIC AND DOC IN PEAT PORE WATER

Vertical profiles of DIC concentrations in peat pore water showed considerable variation within site per sampling date (Figure 3). The swamp site developed the highest DIC concentrations of nearly 3,000 μmol L⁻¹ at the 15 to 25 cm depths, whereas concentrations at the marsh and bog sites seemed to increase with increasing depth but did not exceed 2,500 μmol L⁻¹. At the swamp site concentrations of DIC were lowest early in the season and increased significantly (p < .05 repeated measures analysis of
Fig. 3. Seasonal trends in dissolved inorganic carbon concentrations (DIC) in peat beneath three different Appalachian peatland sites.

variance [ANOVA]) throughout the depth profile to maximal concentrations in August, before declining to still moderate DIC concentrations of 500 μmol L⁻¹ in November. At
Fig. 4. Seasonal trends in dissolved organic carbon concentrations (DOC) in peat beneath three different Appalachian peatland sites.

the marsh site, concentrations also were lowest early in the season and increased significantly (p < .05 repeated measures ANOVA) to maximal concentrations in July and
August but decreased to low concentrations by November. At the bog site, concentrations fluctuated from one date to the next -- but not significantly (p > .05 repeated measures ANOVA).

Relatively similar patterns were noted for DOC concentrations in peat pore waters (Figure 4). Vertical profiles of DOC concentrations at the swamp and marsh sites showed the highest concentrations of >12,000 μmol L⁻¹ in July and August, in particular at depths >20 cm below the peat surface. In contrast, DOC concentrations at the Bog site were quite variable among sampling dates and with depth on any given sampling.

4. Discussion

I am not aware of any daytime measurements of net CO₂ flux in conifer-dominated swamps that consider only the peat and low-growing vegetation to compare the results reported here. For the other two study sites, however, daytime measurements of net CO₂ flux are relatively low (i.e., less negative) compared to previous findings in more northern peatlands. For example, midsummer measurements of daytime net CO₂ flux in the marsh site of 0 to -7 mmol m⁻² hr⁻¹ are less negative than findings for other sedge-dominated sites of -11.4 mmol m⁻² hr⁻¹ in western Alaska reported by Whiting et al. (1992) and -8.2 and -13.1 mmol m⁻² hr⁻¹ in two sites in the Hudson Bay lowlands of Canada reported by Whiting (1994). Both of those studies used clear plastic chambers, making the results comparable to results reported here. Others using chamberless, aerodynamic methods have reported daytime net CO₂ fluxes of -9.0 to -18.0 mmol m⁻² hr⁻¹ for sedge-dominated peatlands near Barrow, Alaska (Coyne and Kelley, 1975), and -8.2 mmol m⁻² hr⁻¹ for sedge-dominated peatlands in western Alaska (Fan et al., 1992).

Likewise, the bog site with daytime net CO₂ flux in midsummer of -3 to -8 mmol m⁻² hr⁻¹ had a relatively low negative flux compared to a mean flux of -6.8 mmol m⁻² hr⁻¹ in southern Finland reported by Silvola and Heikkinen (1979) and mean fluxes of -8.8 to -28.6 mmol m⁻² hr⁻¹ for two sites in the Hudson Bay lowlands of Canada reported by Whiting (1994). Neumann et al. (1994) used a chamberless, aerodynamic method and found mean daytime net CO₂ fluxes in midsummer of -2.4 to -14.7 mmol m⁻² hr⁻¹ for a bog in the Hudson Bay lowlands.

On the other hand, Grulke et al. (1990) reported a maximum daytime net CO₂ flux of -0.42 mmol m⁻² hr⁻¹ for tussock tundra (mix sedge, shrub, and moss) in northern Alaska. The relatively low negative values of net CO₂ flux in the daytime for the Appalachian sites suggest less assimilation of atmospheric CO₂, which is notable in light of the presumption that NPP in Sphagnum-dominated peatlands increases with decreasing latitude (Wieder and Lang, 1983).

In contrast, nighttime measurements of net CO₂ flux in these Appalachian peatlands are near the high (i.e., more positive) end of previous findings for more northern peatlands. For example, net CO₂ flux at nighttime in the swamp site of 21.6 mmol m⁻² hr⁻¹ in August is at least 73% higher than the nighttime flux of 4.7 mmol m⁻² hr⁻¹ in a
forested bog in Alaska reported by Luken and Billings (1985) and 12.5 mmol m\(^{-2}\) hr\(^{-1}\) in a black spruce stand established on peat in Alaska reported by Schlentner and Van Cleve (1985).

Likewise, net CO\(_2\) flux at nighttime in the marsh site of 14.2 mmol m\(^{-2}\) hr\(^{-1}\) in June is at least 80% higher than nighttime flux of 1.6 to 7.9 mmol m\(^{-2}\) hr\(^{-1}\) measured in several sedge-dominated sites in Alaska (Billings et al., 1977; Luken and Billings, 1985; Giblin et al., 1991) and 2.8 mmol m\(^{-2}\) hr\(^{-1}\) in a sedge-dominated fen in subarctic Canada (Moore, 1986). Net CO\(_2\) flux at nighttime in the bog site of 10.4 mmol m\(^{-2}\) hr\(^{-1}\) in October is at least 37% higher than nighttime flux of 2.4 mmol m\(^{-2}\) hr\(^{-1}\) measured in a bog in Sweden (Svennson, 1980) and 7.6 mmol m\(^{-2}\) hr\(^{-1}\) measured in a bog in Alaska (Luken and Billings, 1985). Kim and Verma (1992) did report net CO\(_2\) flux at nighttime of 2.8 to 17 mmol m\(^{-2}\) hr\(^{-1}\) for a *Sphagnum*-dominated peatland in Minnesota. It also is notable that the Appalachian sites have positive net CO\(_2\) flux during the winter which agrees with net CO\(_2\) fluxes of 0.2 to 2.0 mmol m\(^{-2}\) hr\(^{-1}\) reported Zimov et al. (1993) for unfrozen peat above the permafrost in Siberian tundra in winter.

In addition to the biosphere-atmosphere exchange of CO\(_2\), some CO\(_2\) accumulates as DIC in peat pore water of peatlands. The DIC concentrations reported here are somewhat lower than CO\(_2\) concentrations of peat pore water reported by Nilsson and Bohlin (1993) for several peatlands in Sweden (970 to 6,500 \(\mu\)mol L\(^{-1}\)) and by Benstead and Lloyd (1994) for a peatland in Scotland (up to 4,500 \(\mu\)mol L\(^{-1}\)). The lower concentrations in Appalachian peatlands might result from preferential flux of CO\(_2\) to the atmosphere rather than accumulation in peat pore water. For example, the data in Table II and in Figure 4 suggest that seasonal patterns in nighttime measurements of net CO\(_2\) flux matched subtle differences in the vertical profiles of DIC concentration in peat pore water. Accordingly, the highest values for net CO\(_2\) flux in the swamp site occurred in August at the same time DIC concentration in peat pore water reached a maximum. Likewise, the marsh site showed maximal net CO\(_2\) flux and DIC concentration in June, whereas the bog site had the highest net CO\(_2\) flux and DIC concentrations in November.

I did find a lower mean DIC concentration in the marsh site (844 \(\mu\)mol L\(^{-1}\)), dominated by *Carex*, than in the swamp (1,226 \(\mu\)mol L\(^{-1}\)) and bog (1,602 \(\mu\)mol L\(^{-1}\)) sites, dominated by *Sphagnum*, as confirmed by Nilsson and Bohlin (1993). The reason for this difference in DIC concentrations among peat types is not clear and could relate to different rates of organic matter decomposition or hydrologic regimes (Nilsson and Bohlin, 1993).

The DOC concentrations in peat pore water found here are much higher than mean concentrations of 2,000 to 4,900 \(\mu\)mol L\(^{-1}\) commonly reported for other peatlands (McKnight et al., 1985; Moore, 1987; Marin et al., 1990; Dalva and Moore, 1991). Such high DOC concentrations in these Appalachian peatlands probably result from relatively incomplete decomposition of organic matter, producing soluble organic matter, compared to that in the other northern peatlands. Moreover, lower mean concentration of DOC in the marsh site (6,346 \(\mu\)mol L\(^{-1}\)) than in the swamp (7,228 \(\mu\)mol L\(^{-1}\)) and bog (6,936
The measurements reported here provide the basis for ecosystem C budgets. Such budgets indicate whether each site is presently accumulating or losing C (i.e., net sink or source for atmospheric CO$_2$). This is a pertinent question for Appalachian peatlands such as Big Run Bog and Buckle’s Bog that formed under a much cooler climate 13,000 years ago than their present climate (Maxwell and Davis, 1972; Watts, 1979). While persistence of these peatlands in the present-day temperate climate is obvious, persistence does not mean that they still accumulate C. They could be losing C because assimilation of C by photosynthesis and release of C by respiration have different responses to increasing temperature (cf., Townsend et al., 1992). Respiration rates increase with increasing temperature, whereas photosynthetic rates have an asymptotic relationship with increasing temperature. Thus, it is possible that peat deposited in Appalachian peatlands in the past is no longer accumulating C but rather is being mobilized to CO$_2$ (and CH$_4$; Yavitt et al., 1993).

For example, these Appalachian peatlands release CO$_2$ to the atmosphere from December to early April despite being snow covered. To estimate the amount of CO$_2$ lost from each site during the winter (1 December to 15 April) I developed linear relationships between peat temperature (2 cm depth) and positive net flux of CO$_2$, then used daily peat temperatures for the region (National Oceanic and Atmospheric Administration, 1988) to estimate total CO$_2$ flux to the atmosphere. It is notable that such equations (not shown) described only 40 to 50% of the variation in nighttime net CO$_2$ flux; including data on peat moisture content (i.e., water table depth; cf., Kim and Verma, 1992) did not improve their predictive capability. Nevertheless, I estimated CO$_2$ release to the atmosphere of 2.9 mol m$^{-2}$ from the swamp site, 1.4 mol m$^{-2}$ from the marsh site, and 3.1 mol m$^{-2}$ from the bog site during the winter, representing roughly 3.5% of the C in annual NPP in the swamp site and 5% of the C in annual NPP in the marsh and bog sites (Wieder et al., 1989).

During the snow-free season (15 April to 30 November), the swamp site was the only site where the highest nighttime net CO$_2$ flux coincided with the highest peat temperature (19$^\circ$C at 2 cm depth) in August. In contrast, the nighttime net CO$_2$ flux reached its maximal value before the warmest time of the year in June in the Marsh site (12$^\circ$C at 2 cm depth) and in autumn in the Bog site (8$^\circ$C at 2 cm depth). This disparity between maximal nighttime net CO$_2$ flux and peat temperature among the different sites makes scaling-up the limited number of measurements reported here to seasonal -- or annual -- estimates unrealistic.

Scaling-up the daytime measurements of net CO$_2$ flux reported here to estimate C balance is even more problematic because it requires more than just temperature as the
TABLE III
Summary of C fluxes for three Appalachian peatland sites. Negative values indicate assimilation of atmospheric CO₂, and positive numbers indicate release of CO₂ to the atmosphere. See text for assumptions and derivations of estimated values.

<table>
<thead>
<tr>
<th></th>
<th>swamp</th>
<th>Site marsh</th>
<th>bog</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Net CO₂ flux (mmol m⁻² d⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>daytime</td>
<td>-30</td>
<td>-20</td>
<td>-27</td>
</tr>
<tr>
<td>nighttime</td>
<td>83</td>
<td>53</td>
<td>39</td>
</tr>
<tr>
<td>daily-integrated</td>
<td>53</td>
<td>33</td>
<td>12</td>
</tr>
<tr>
<td><strong>dDIC (mmol m⁻² d⁻¹)</strong></td>
<td>11</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>(June to August)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>dDOC (mmol m⁻² d⁻¹)</strong></td>
<td>-66</td>
<td>-116</td>
<td>-23</td>
</tr>
<tr>
<td>(June to August)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>NPP (mol m⁻² yr⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aboveground</td>
<td>-61</td>
<td>-15</td>
<td>-39</td>
</tr>
<tr>
<td>belowground</td>
<td>-21</td>
<td>-15</td>
<td>-22</td>
</tr>
<tr>
<td>total</td>
<td>-82</td>
<td>-30</td>
<td>-61</td>
</tr>
<tr>
<td><strong>Peat accretion (mol m⁻² yr⁻¹)</strong></td>
<td>-5</td>
<td>-5</td>
<td>-5</td>
</tr>
</tbody>
</table>

independent variable in a simple model; i.e., photosynthetic rates vary in response to changes in irradiance, temperature, humidity, CO₂ concentration (Nobel, 1983), as well as water table level in peatlands. In this regard, I previously found poor correlations (r < .40) for net CO₂ flux and a suite of environmental factors for other sites within Big Run Bog (Yavitt et al., 1993). Therefore, I did not repeat the correlations with the data set presented here because I expected equally poor results. Rather, I realize that more studies, possibly experimental in nature, are required to explain the patterns in daytime net CO₂ flux reported here.

For three sampling dates, I did have several daytime measurements of net CO₂ flux to estimate separate daytime- and nighttime-integrated net CO₂ fluxes. A surprising outcome of these measurements was that negative CO₂ flux in the daytime did not account for the positive net CO₂ flux at nighttime at all three sites (Table III). As a result, the daily-integrated net CO₂ flux was positive, suggesting a net loss of CO₂ to the atmosphere from each site. Oechel et al. (1993) also reported that arctic tundra in Alaska was a net CO₂ source at rates of 2.8 to 18 mmol m⁻² d⁻¹.
A partial explanation for this outcome is the relatively low negative values for net CO$_2$ flux in the daytime. It is notable that measurements made both in June (clear sky and PPFD of about 1500 µmol m$^{-2}$ s$^{-1}$) as well as those made in August (partly cloudy sky and PPFD of about 500 µmol m$^{-2}$ s$^{-1}$) showed the maximal value at noon, with the assimilation of CO$_2$ declining steadily after that. Others (Grulke et al., 1990; Whiting, 1994) have found much more negative values for net CO$_2$ flux after noon on clear days than on partly cloudy days, suggesting that assimilation of CO$_2$ closely tracks levels of PPFD. The daytime patterns in net CO$_2$ flux in these Appalachian peatlands are more like those in upland situations on well-drained soil, where midday water stress lowers net CO$_2$ flux in late afternoon on clear days by reducing stomatal conductance and limiting CO$_2$ assimilation.

A different -- and certainly plausible -- explanation for the relatively low negative values for net CO$_2$ flux in the daytime at these sites is that the plants are taking up CO$_2$ emitted from the peat surface in addition to the uptake of atmospheric CO$_2$ (cf., Sternberg, 1989). This phenomenon would lower the amount of atmospheric CO$_2$ taken up to support photosynthesis, without limiting production of organic matter. Certainly more study is need to document this explanation -- but it seems likely nonetheless.

A net C balance close to -- and possibly less than -- zero is a reasonable assumption for these Appalachian peatlands. While these systems seem to have relatively high NPP, they maintain shallow peat deposits, suggesting rapid decomposition of the annual production. For example, data on NPP for the three study sites are incomplete but relevant. Wieder et al. (1989) reported that aboveground production (on a C basis) in the bog site of 39 mol m$^{-2}$ yr$^{-1}$. That study did not specifically measure belowground production but speculated that it could be 22 mol m$^{-2}$ yr$^{-1}$ on the basis of equal production aboveground and belowground by the vascular plants at the site. The same approach for the marsh site yields 30 mol m$^{-2}$ yr$^{-1}$, with half of that aboveground and the other half belowground.

An estimate of NPP at the swamp site is more problematic. I estimated shrub, herb and moss production on the basis of the same approach as that for the bog site, except correcting for differences in species composition between the sites (Walbridge, 1982). No data are presently available for the tree component. However, Grigal et al. (1985) estimated annual tree production (aboveground plus belowground) of 27 mol m$^{-2}$ yr$^{-1}$ for a similar spruce-dominated peatland in Minnesota. Using this value for the swamp site results in annual NPP of 82.5 mol m$^{-2}$ yr$^{-1}$.

On the other hand, Wieder et al. (199x) measured the rate of peat accretion in the top 35 cm of the peat deposit at Big Run Bog -- and at four other peatlands in the eastern U.S.A. -- but unfortunately those studies did not consider the sites in this study. Nevertheless, the results suggest that peat accretion as measured by $^{210}$Pb dates of peat at 2-intervals is equal to a C accumulation rate of only 5.5 mol m$^{-2}$ yr$^{-1}$ among the study sites ranging from northern Minnesota to the Pocono Mountains of Pennsylvania to Big Run Bog and Cranesville Swamp in West Virginia. Assuming this accumulation rate
applies to the three sites I studied, then C accretion in the surface peat is only 6 to 18% of the NPP (Table III).

The results of the studies reported here show that organic matter decomposition occurs throughout the year in the peat deposit at each site, resulting in (i) CO₂ that largely escapes to the atmosphere even in winter, and (ii) partial decomposition products that accumulate as DOC. Through the combination of approaches, it appears the three sites are net sources of atmospheric CO₂. Certainly, more rigorous measurements are necessary to prove this conclusion. Nevertheless, C cycling is quite active in these Appalachian ecosystems, relying on large inputs and loss of CO₂. Consequently environmental changes including improper management that affect one -- or more -- aspect of C cycling could alter the overall dynamics of these ecosystems. I encourage others to use these methods to help understand the biogeochemistry of C in a wide range of Appalachian peatlands.

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