Sensitivity of Northern Peatland Carbon Dynamics to Holocene Climate Change

Zicheng Yu,1 David W. Beilman,2,3 and Miriam C. Jones1

In this paper, we evaluate the long-term climate sensitivity and global carbon (C) cycle implications of northern peatland C dynamics by synthesizing available data and providing a conceptual framework for understanding the dominant controls, processes, and interactions of peatland initiation and C accumulation. Northern peatlands are distributed throughout the climate domain of the boreal forest/taiga biome, but important differences between peatland regions are evident in annual temperature vs. precipitation (T-P) space, suggesting complex hydroclimatic controls through various seasonal thermal-moisture associations. Of 2380 available basal peat dates from northern peatlands, nearly half show initiation before 8000 calendar years (cal years) B.P. Peat-core data from sites spanning peatland T-P space show large variations in apparent C accumulation rates during the Holocene, ranging from 8.4 in the Arctic to 38.0 g C m⁻² a⁻¹ in west Siberia, with an overall time-weighted average rate of 18.6 g C m⁻² a⁻¹. Sites with multiple age determinations show millennial-scale variations, with the highest C accumulation generally at 11,000–8000 cal years B.P. The early Holocene was likely a period of rapid peatland expansion and C accumulation. For example, maximum peat expansion and accumulation in Alaska occurred at this time when climate was warmest and possibly driest, suggesting the dominant role of productivity over decomposition processes or a difference in precipitation seasonality. Northern peatland C dynamics contributed to the peak in atmospheric CH₄ and the decrease in CO₂ concentrations in the early Holocene. This synthesis of data, processes, and ideas provides baselines for understanding the sensitivity of these C-rich ecosystems in a changing climate.

1. INTRODUCTION

Northern peatland ecosystems have cycled and stored substantial amounts of global land carbon (C) over the Holocene (the last 11,700 years). Today, peatlands are one of the largest terrestrial biosphere C pools and are the largest natural source of methane (CH₄) in the northern hemisphere. Owing to their large accumulated C mass and dynamic greenhouse gas fluxes, these ecosystems have been an important component of the high-latitude C cycle for thousands of years.

Peatland ecosystems and their C-rich peat archives have been studied for several decades, mostly for reconstructing past climate [Charman, 2002], and have been central
to early ideas about recurrent climate changes [Sernander, 1908]. Over recent decades, attention has also turned to carbon cycling and the implications of long-term peatland ecosystem dynamics and climate sensitivity [Clymo, 1984; Gorham, 1991; Rydin and Jeglum, 2006]. Peat C accumulation is determined by the balance of biological inputs (plant growth and litter production) and outputs (organic matter decomposition); both of these processes are sensitive to climate change and climate variability or are indirectly affected by climate through related processes.

In this chapter, we provide a conceptual framework for understanding the dominant controls, processes, and interactions of northern peatland initiation and long-term peat C accumulation and dynamics using climate data and peat-core data. We use modern instrumental climate data to explore the climate envelope of today’s northern peatland distribution. We synthesize spatial and temporal patterns of peat C accumulation rates during the Holocene in different regions and discuss climatic and autogenic influences. We also discuss the implications of peatland dynamics for the global carbon cycle. Understanding the causal connection between peat C dynamics and past climate would provide insight into the possible future response of these C-rich ecosystems to climate change in different regions and over different timescales.

2. CLIMATE CONTROLS OVER DISTRIBUTION, INITIATION, AND EXPANSION OF NORTHERN PEATLANDS

Northern peatlands occur mostly in boreal and subarctic regions in the northern hemisphere. A cool climate, low evaporation rates, and high effective moisture (precipitation minus evaporation) are essential for the formation and development of northern peatlands on suitable substrates and in suitable topographic settings. Despite the generally short summer seasons at high latitudes and the moderate net primary production (NPP) of peatland vegetation, peatlands accumulate excess organic matter as peat owing to depressed decomposition in waterlogged and anoxic conditions and the chemical recalcitrance of some peatland plant tissues. Extensive development of northern peatland ecosystems has occurred in west Siberia, central Canada, northwest Europe, and Alaska (Plate 1). Due to different regional climate and deglaciation histories, the timing of peatland initiation varies greatly from region to region [Kuhry and Turunen, 2006], but the majority of today’s peatlands first expanded in the early and mid-Holocene [MacDonald et al., 2006; Gorham et al., 2007] (Plate 1).

To explore the climate domain of northern peatlands, particularly in relation to the boreal forest/taiga ecoregion [Olson et al., 2001], we compared the distribution of peatlands [MacDonald et al., 2006] to gridded instrumental climate data (0.5° × 0.5° grids) for land north of 45°N (1960–1990 [Rawlins and Willmott, 1999]). Northern peatlands typically occur where mean annual temperatures are between −12° and 5°C and mean annual precipitation is between 200 and 1000 mm. This distribution spans most of the climate domain of the boreal ecoregion (Plate 2). Peatlands are often abundant in regions that receive <500 mm of mean annual precipitation, which is a broader climate range than suggested by previous analyses [Gignac and Vitt, 1994; Wieder et al., 2006]. This wide range in annual temperature versus precipitation (T-P) space contrasts with the uneven geographic distribution of northern peatlands (Plate 1), including broad regions of cold East Siberia taiga with relatively few peatlands. This contrast indicates that climate seasonality and local factors, such as topography and geologic substrate (parent material), have probably exerted critical secondary controls on Holocene peatland expansion and C accumulation.

Although peatland regions display considerable overlap in annual T-P space, many important regional differences are evident (Plate 2). For example, and considering the largest wetland regions, peatlands of the West Siberia Lowland (WSL) and Mackenzie River Basin (MRB) include peatland areas with mean annual temperatures about 7°C colder than those of the Hudson Bay Lowland (HBL). In contrast, the warmer peatlands in these three regions (between −2° and 2°C) receive highly variable annual precipitation, and many HBL peatlands receive twice as much precipitation as those in the WSL or MRB (900 versus 400 mm), owing to the climatic influence of Hudson Bay. Peatlands in Alaska span a similar range in mean annual temperature as those in the HBL, but span a very broad precipitation range from 150 to >1500 mm, owing to coastal and orographic influences. The distinct character of the peatland regions in modern T-P space suggests that the maintenance of peatland hydrology suitable for long-term peat C accumulation is the result of various thermal-moisture associations and precipitation seasonality. In the same way, climate histories and temperature and precipitation associations in the past were likely also very different between regions. As a result, a regional perspective would be most informative in understanding and projecting C cycling responses to climate change. In particular, peatlands located in regions near the limits of peatland climate space may be the first to experience expansion and shrinkage under changing regional climates.

Preliminary results from similar analysis of relative humidity (RH) show that northern peatlands have high annual RH values ranging from 65 to 95%. Peatlands with the highest RH occur in regions with a mean annual temperature around −10°C. A surprising pattern is that peatlands with the highest RH (and also a wide range of RH) tend to oc-
cur at low annual precipitation of <550 mm. Further analysis of seasonal patterns of climate parameters, including temperature, precipitation, and relative humidity, would provide additional insights into understanding climate controls of peatland distribution.

At the hemispheric scale, northern peatlands expanded rapidly following the last glacial termination, in response to changes in large-scale boundary conditions and climate controls. These include ice retreats and availability of new land surface [Dyke et al., 2004], large increases in summer insolation [Berger and Loutre, 1991], increases in greenhouse gases [Brook et al., 2000; Monnin et al., 2004], deglacial warming [Kaufman et al., 2004], and possibly increasing moisture conditions [Wolf et al., 2000]. At the regional scale, peatland initiation and expansion, either by means of paludification (formation or expansion onto non-wetland terrestrial ecosystems) or terrestrialization (lake-infilling) processes [Kuhry and Turunen, 2006], followed regional climate changes. For example, Holocene thermal maximum (HTM) conditions in the early Holocene might have promoted peatland initiation and expansion in south-central Alaska (see sections 3 and 5 below). In eastern Canada, including the HBL and Labrador, the deglaciation and subsequent climate warming occurred much later during the mid-Holocene, resulting in peatland expansion later in time (Plate 1). At the basin scale, regional and local factors interact to control peatland dynamics. Local expansion is highly nonlinear as a function of both local terrain and regional climate [Korhola et al., 1996; Bauer et al., 2003]. Therefore, climate sensitivity of peatland expansion to Holocene climate change needs to be evaluated on different spatial scales.

3. SPATIAL AND TEMPORAL PATTERNS OF CARBON ACCUMULATION DURING THE HOLOCENE

Overall peat accumulation patterns, i.e., convex versus concave peat mass versus age curves, show long-term trajectories of peatland changes that do not necessarily re-
veal peatland sensitivity to climate changes at millennial or Holocene scales. However, different trajectories imply different underlying fundamental processes [Yu, 2006a], which may relate to persistent climatic or ecological controls. For example, a concave accumulation pattern, with increasing long-term apparent accumulation rates over time, indicates that cumulative decomposition is the dominant control on net peat accumulation, i.e., more recent peat yields high apparent accumulation rates as less time has elapsed for decomposition. This concave pattern is often observed in oceanic raised bogs [Clymo, 1984]. In contrast, a convex pattern, with decreasing accumulation rates over time, suggests that either allogetic (e.g., directional change in climate) or autogenic (e.g., peatland height growth) factors have played a major role. This convex pattern is often observed in continental climates, especially in fens [Yu, 2006b]. Several conceptual models show that the trajectory of peatland development is controlled by initial conditions, external influences, and internal processes [Belyea and Baird, 2006]. Any deviations from an overall trajectory are at least partly the result of the direct or indirect influence of climate variability.

Numerous studies have presented C accumulation data from northern peatlands at the site or regional scale. We compiled available data to examine the variability of apparent C accumulation rates within and between sites during the Holocene (Plate 3). Peatland development is affected not only by climate but also by local edaphic and autogenic factors [Kuhry and Turunen, 2006] (Plate 4), which may explain the spatial heterogeneity of peatland C accumulation rates across the boreal biome and within a region (Plate 3b). We calculated time-weighted average C accumulation rates for each site using multiple calibrated 14C ages and bulk

Plate 2. The climate space of mean annual temperature and precipitation (T-P space) of total land area north of 45°N latitude (dark gray), the boreal/taiga biome (light gray), and northern peatland regions based on 0.5° × 0.5°-gridded instrumental climate data for the period 1960–1990 [Rawlins and Willmott, 1999]. The location in climate space of C accumulation sites is shown by yellow triangles (site numbers as in Table 1).
Plate 3. Variation in long-term apparent C accumulation rates from 33 northern peatland sites with bulk density and C measurements and multiple radiocarbon or tephra dates (Table 1). (a) Box plot of C rates in 1000-year bins from 33 sites. The horizontal lines within boxes indicate the medians. Numbers below the panel indicate the number of sites used in each bin. (b) Variations in C accumulation rates from selected sites with the highest number of dates across five peatland regions (site numbers as in Table 1).

density measurements. We then averaged the rates from all sites within each region, also considering the time lengths of peat accumulation at individual sites. These reconstructed rates of peat C accumulation are apparent rates in that they typically underestimate the true rate of past carbon uptake (net ecosystem production), since often many thousands of years of deep C decomposition have occurred. Thus, reconstructed C accumulation rates necessitate a careful interpretation relative to modern C flux measurements from eddy flux tower and chamber techniques [e.g., Roulet et al., 2007] despite being reported in the same measurement units (g C m\(^{-2}\) a\(^{-1}\)). The highest apparent C accumulation rates over the Holocene are observed in west Siberia (38.0 g C m\(^{-2}\) a\(^{-1}\); \(n=4\)) followed by western Canada (20.3 g C m\(^{-2}\) a\(^{-1}\); \(n=7\)), and the lowest rates are found in the High Arctic (8.4 g C m\(^{-2}\) a\(^{-1}\); \(n=5\)). The overall time-weighted average rate is 18.6 g C m\(^{-2}\) a\(^{-1}\) during the Holocene based on 33 sites (Table 1). Peatland regions showing high C accumulation rates appear to occur in the intermediate ranges of annual T-P space (Plates 2 and 3), such as in west Siberia and western Canada, in particular around 0° to 2.5°C of mean annual temperature and 450–550 mm of annual precipitation. In other words, these climate conditions may be optimal in producing a balance between primary production and decomposition that strongly promotes C accumulation. On the other hand, the regions showing low C accumulation rates appear to be located either at the extreme cold end of climate space, e.g., sites in the Arctic (Plate 2, Table 1) or at high temperature and high precipitation locations, e.g., sites in eastern Canada and perhaps also in Finland (Plates 2 and 3). This
observation suggests that high total precipitation does not necessarily lead to high C accumulation, as high precipitation may be offset by increased evaporation under high temperatures, or the seasonal precipitation regime may be such that the site is quite dry during the growing season, thereby reducing NPP and increasing decomposition.

The temporal pattern of peatland initiation across the boreal region is not uniform. For the most part, peatlands older than 12,000 cal years B.P. are found in Alaska, southern parts of central and eastern North America, and the Pacific coast that remained unglaciated during the last glacial maximum (Plate 1) [MacDonald et al., 2006; Gorham et al., 2007]. The highest C accumulation rates in Alaska occurred at 11,000–9000 cal years B.P. (Plates 3b and 5d) during the period of Holocene thermal maximum (HTM) conditions in Alaska (Plate 5a) [Kaufman et al., 2004]. The HTM, with warm summers and strong climate seasonality, was caused by increased summer insolation in the early Holocene [Berger and Loutre, 1991]. The C accumulation peaks occurred later in other regions, due to either delayed deglaciation, different timing of the HTM, or other climate factors. For example, warm summer conditions were delayed in eastern North America owing to the presence and cooling effect of the remnant Laurentide ice sheet, so high C accumulation rates in eastern Canada at 5000–3000 cal years B.P. (Plate 3b) were likely caused by a warm and humid climate as the result of shifting atmospheric circulation [Kaufman et al., 2004]. In western Canada, peak C accumulation occurred in the mid-Holocene, which could be due to a warm climate at that time [Schweger and Hickman, 1989] or the dominance of fen peatlands that were nutrient-rich at young ages. Across northern Siberia, warm Holocene conditions persisted until 5000 cal years B.P. as reflected by the northern expansion of the tree line [MacDonald et al., 2008]. An overall slowdown of carbon accumulation seems to have occurred after ~4000 cal years B.P. across many sites, especially in west Siberia and in western Canada (Plate 3b). The decline in C accumulation has been attributed to neoglacial climate cooling and permafrost development [Zoltai, 1993; Peteet et al., 1998; Vitt et al., 2000; Beilman et al., 2009]. Relatively high C accumulation rates in the late Holocene are partly attributable to younger peat that has experienced less decomposition. Averaging across all 33 sites, apparent C accumulation rates are highest in the early Holocene, a pattern that holds when only averaging the 20 oldest sites with basal ages of 10,000 cal years B.P.
Table 1. Peat Carbon Accumulation Sites From Northern Peatlands

<table>
<thead>
<tr>
<th>Site</th>
<th>Site Name</th>
<th>Location</th>
<th>Peatland Type&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Dating Method&lt;sup&gt;b&lt;/sup&gt;</th>
<th>No. of Dates</th>
<th>Basal Age (cal years B.P.)</th>
<th>Time-Weighted Holocene Accumulation Rates (g C m&lt;sup&gt;-2&lt;/sup&gt; a&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Salym-Gyugan Mire, site 3</td>
<td>West Siberia, Russia</td>
<td>bog</td>
<td>60°10'N</td>
<td>72°50'E</td>
<td>conventional</td>
<td>6</td>
<td>10,500</td>
<td>21.9</td>
<td>Turunen et al. [2001]</td>
</tr>
<tr>
<td>2</td>
<td>Salym-Gyugan Mire, site 4</td>
<td>West Siberia, Russia</td>
<td>bog</td>
<td>60°10'N</td>
<td>72°50'E</td>
<td>conventional</td>
<td>4</td>
<td>11,000</td>
<td>24.4</td>
<td>Turunen et al. [2001]</td>
</tr>
<tr>
<td>3</td>
<td>Vasyugan V21</td>
<td>West Siberia, Russia</td>
<td>bog</td>
<td>56°50'N</td>
<td>78°25'E</td>
<td>conventional</td>
<td>11</td>
<td>9710</td>
<td>42.6</td>
<td>Borren et al. [2004]</td>
</tr>
<tr>
<td>4</td>
<td>86-Kvartal Zh0</td>
<td>West Siberia, Russia</td>
<td>fen</td>
<td>56°20'N</td>
<td>84°35'E</td>
<td>conventional</td>
<td>9</td>
<td>8700</td>
<td>70.6</td>
<td>Borren et al. [2004]</td>
</tr>
<tr>
<td>5</td>
<td>Kenai Gasfield</td>
<td>Alaska, USA</td>
<td>fen</td>
<td>60°27'N</td>
<td>151°14'W</td>
<td>AMS</td>
<td>12</td>
<td>11,408</td>
<td>13.1</td>
<td>Z. C. Yu (unpublished data, 2008)</td>
</tr>
<tr>
<td>6</td>
<td>No Name Creek</td>
<td>Alaska, USA</td>
<td>fen</td>
<td>60°38'N</td>
<td>151°04'W</td>
<td>AMS</td>
<td>11</td>
<td>11,526</td>
<td>12.3</td>
<td>Z. C. Yu (unpublished data, 2008)</td>
</tr>
<tr>
<td>7</td>
<td>Horsetrail fen</td>
<td>Alaska, USA</td>
<td>rich fen</td>
<td>60°25'N</td>
<td>150°54'W</td>
<td>AMS</td>
<td>10</td>
<td>13,614</td>
<td>10.7</td>
<td>Jones [2008]</td>
</tr>
<tr>
<td>8</td>
<td>Swanson fen</td>
<td>Alaska, USA</td>
<td>poor fen</td>
<td>60°47'N</td>
<td>150°49'W</td>
<td>AMS</td>
<td>9</td>
<td>14,225</td>
<td>5.7</td>
<td>Jones [2008]</td>
</tr>
<tr>
<td>9</td>
<td>Fairbanks</td>
<td>Alaska, USA</td>
<td>taiga bog</td>
<td>64°52'N</td>
<td>147°46'W</td>
<td>conventional</td>
<td>4</td>
<td>5509</td>
<td>24.1</td>
<td>Billings [1987]</td>
</tr>
<tr>
<td>10</td>
<td>Diana Lake bog</td>
<td>British Columbia, Canada</td>
<td>slope bog</td>
<td>54°09'N</td>
<td>130°15'W</td>
<td>AMS</td>
<td>5</td>
<td>8500</td>
<td>8.6</td>
<td>Turunen and Turunen [2003]</td>
</tr>
<tr>
<td>11</td>
<td>Upper Pinto Creek</td>
<td>Alberta, Canada</td>
<td>rich fen</td>
<td>53°35'N</td>
<td>118°01'W</td>
<td>AMS</td>
<td>20</td>
<td>7600</td>
<td>30.6</td>
<td>Yu et al. [2003a]</td>
</tr>
<tr>
<td>12</td>
<td>Goldyee Lake fen</td>
<td>Alberta, Canada</td>
<td>fen</td>
<td>52°27'N</td>
<td>116°12'W</td>
<td>AMS</td>
<td>6</td>
<td>10,000</td>
<td>31.7</td>
<td>Yu [2006b]</td>
</tr>
<tr>
<td>13</td>
<td>Slave Lake bog</td>
<td>Alberta, Canada</td>
<td>bog</td>
<td>55°01'N</td>
<td>114°09'W</td>
<td>conventional</td>
<td>6</td>
<td>10,200</td>
<td>22.4</td>
<td>Kuhry and Vitt [1996]</td>
</tr>
<tr>
<td>14</td>
<td>Martin River peatland</td>
<td>NWT, Canada</td>
<td>permafrost</td>
<td>61°48'N</td>
<td>121°24'W</td>
<td>conventional/AMS/tephra</td>
<td>7</td>
<td>8010</td>
<td>18.3</td>
<td>Robinson [2006]</td>
</tr>
<tr>
<td>15</td>
<td>CC-P, Campbelt Ck peatland</td>
<td>Nunavut, Canada</td>
<td>fen</td>
<td>68°17'N</td>
<td>133°15'W</td>
<td>conventional/AMS/tephra</td>
<td>4</td>
<td>10,050</td>
<td>6.1</td>
<td>Vardy et al. [2000]</td>
</tr>
<tr>
<td>16</td>
<td>KJ-B, Kuk/Juk peatland</td>
<td>Nunavut, Canada</td>
<td>fen</td>
<td>69°29'N</td>
<td>132°40'W</td>
<td>AMS</td>
<td>4</td>
<td>8000</td>
<td>3.4</td>
<td>Vardy et al. [2000]</td>
</tr>
<tr>
<td>17</td>
<td>Patuanak</td>
<td>Saskatchewan, Canada</td>
<td>permafrost</td>
<td>55°51'N</td>
<td>107°41'W</td>
<td>AMS</td>
<td>11</td>
<td>9050</td>
<td>15.6</td>
<td>D. W. Beilman and Z. C. Yu (unpublished data, 2008)</td>
</tr>
<tr>
<td>18</td>
<td>BB1</td>
<td>Nunavut, Canada</td>
<td>fen</td>
<td>64°43'N</td>
<td>105°34'W</td>
<td>AMS</td>
<td>2</td>
<td>7720</td>
<td>8.4</td>
<td>Vardy et al. [2000]</td>
</tr>
<tr>
<td>19</td>
<td>TK1P2</td>
<td>Nunavut, Canada</td>
<td>fen</td>
<td>66°27'N</td>
<td>104°50'W</td>
<td>AMS</td>
<td>2</td>
<td>6700</td>
<td>12.5</td>
<td>Vardy et al. [2000]</td>
</tr>
<tr>
<td>20</td>
<td>Selwyn Lake (SL1)</td>
<td>Saskatchewan, Canada</td>
<td>permafrost/bog</td>
<td>59°53'N</td>
<td>104°12'W</td>
<td>AMS</td>
<td>13</td>
<td>6690</td>
<td>12.1</td>
<td>Sannel and Kuhry [2009]</td>
</tr>
</tbody>
</table>
### Table 1. (continued)

<table>
<thead>
<tr>
<th>Site</th>
<th>Site Name</th>
<th>Location</th>
<th>Peatland Type(^a)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Dating Method(^b)</th>
<th>No. of Dates</th>
<th>Basal Age (cal year B.P.)</th>
<th>Time-Weighted Holocene Accumulation Rates (g C m(^{-2}) a(^{-1}))</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>21</td>
<td>Mirabel Bog (average of 7 cores)</td>
<td>Québec, Canada</td>
<td>bog</td>
<td>45°41'N</td>
<td>74°02'W</td>
<td>conventional/AMS</td>
<td>2–7</td>
<td>10,000</td>
<td>7.0</td>
<td>Muller et al. [2003]</td>
</tr>
<tr>
<td>22</td>
<td>Ellesmere Island (average of 4 cores)</td>
<td>Canada</td>
<td>rich fen</td>
<td>82°N</td>
<td>68°W</td>
<td>conventional/AMS</td>
<td>3</td>
<td>7507</td>
<td>12.9</td>
<td>LaFarge-England et al. [1991]</td>
</tr>
<tr>
<td>23</td>
<td>Miscou</td>
<td>New Brunswick, Canada</td>
<td>N/A</td>
<td>47°56'N</td>
<td>64°30'W</td>
<td>AMS</td>
<td>7</td>
<td>9000</td>
<td>30.6</td>
<td>Gorham et al. [2003]</td>
</tr>
<tr>
<td>24</td>
<td>Fourchou</td>
<td>Nova Scotia, Canada</td>
<td>N/A</td>
<td>45°56'N</td>
<td>60°16'W</td>
<td>AMS</td>
<td>8</td>
<td>11,200</td>
<td>18.7</td>
<td>Gorham et al. [2003]</td>
</tr>
<tr>
<td>25</td>
<td>The Glen Carron bog</td>
<td>Scotland</td>
<td>bog</td>
<td>57°31'N</td>
<td>5°09'W</td>
<td>conventional</td>
<td>6</td>
<td>10,140</td>
<td>10.5</td>
<td>Anderson [2002]</td>
</tr>
<tr>
<td>26</td>
<td>The Glen Torridon bog</td>
<td>Scotland</td>
<td>bog</td>
<td>57°34'N</td>
<td>5°22'W</td>
<td>conventional</td>
<td>7</td>
<td>9490</td>
<td>20.5</td>
<td>Anderson [2002]</td>
</tr>
<tr>
<td>27</td>
<td>The Eilean Subbainn bog</td>
<td>Scotland</td>
<td>bog</td>
<td>57°41'N</td>
<td>5°41'W</td>
<td>conventional</td>
<td>4</td>
<td>8550</td>
<td>17.7</td>
<td>Anderson [2002]</td>
</tr>
<tr>
<td>28</td>
<td>Hanhjänkä</td>
<td>Finland</td>
<td>palsa mire</td>
<td>68°24'N</td>
<td>23°33'E</td>
<td>conventional</td>
<td>7</td>
<td>9800</td>
<td>12.4</td>
<td>Mäkilä and Moisanen [2007]</td>
</tr>
<tr>
<td>29</td>
<td>Luovuoma (average of 3 center cores)</td>
<td>Finland</td>
<td>fen</td>
<td>68°24'N</td>
<td>23°33'E</td>
<td>conventional</td>
<td>5–6</td>
<td>9800</td>
<td>13.7</td>
<td>Mäkilä and Moisanen [2007]</td>
</tr>
<tr>
<td>30</td>
<td>S. Haukkasuo, (average of 3 cores)</td>
<td>Finland</td>
<td>raised bog</td>
<td>60°49'N</td>
<td>26°57'E</td>
<td>conventional</td>
<td>5–13</td>
<td>9500</td>
<td>22.5</td>
<td>Mäkilä [1997]</td>
</tr>
<tr>
<td>31</td>
<td>Ruosuo P8</td>
<td>Finland</td>
<td>aapa mire</td>
<td>65°39'N</td>
<td>27°19'E</td>
<td>conventional</td>
<td>7</td>
<td>9500</td>
<td>12.9</td>
<td>Mäkilä et al. [2001]</td>
</tr>
<tr>
<td>32</td>
<td>Ruosuo P20</td>
<td>Finland</td>
<td>aapa mire</td>
<td>65°39'N</td>
<td>27°19'E</td>
<td>conventional</td>
<td>9</td>
<td>9500</td>
<td>16.2</td>
<td>Mäkilä et al. [2001]</td>
</tr>
<tr>
<td>33</td>
<td>Saarisuo B8</td>
<td>Finland</td>
<td>fen</td>
<td>65°39'N</td>
<td>27°19'E</td>
<td>conventional</td>
<td>11</td>
<td>9600</td>
<td>22.4</td>
<td>Mäkilä et al. [2001]</td>
</tr>
</tbody>
</table>

\(^a\)N/A, not available.
\(^b\)AMS, accelerator mass spectrometry.
Plate 5. Case study of peatland carbon-climate connections during the Holocene from the Kenai Peninsula, Alaska. (a) Summer insolation [Berger and Loutre, 1991] and general Holocene climate history [Edwards et al., 2001; Kaufman et al., 2004]; (b) Non-wetland vegetation history [Anderson et al., 2006; Jones, 2008]; (c) Basal peat ages from the Kenai (n = 29; black bars [Reger et al., 2007], with additions) and across Alaska (n = 190; gray bars; Plate 1); (d) Carbon accumulation rates at four peatland sites on the Kenai Peninsula, Alaska (Swanson Fen and Horse Trail [Jones, 2008]; No Name Creek and Kenai Gas Field [Z. C. Yu, unpublished, 2008]). HTM, Holocene Thermal Maximum.

4. CONCEPTUAL MODEL OF LONG-TERM CARBON ACCUMULATION IN NORTHERN PEATLANDS

Peat initiation, persistence, and accumulation are controlled directly by the balance of production and decomposition (Plate 4). NPP of peatland vegetation and the decomposition of plant litter and soil organic matter are two key ecosystem processes, and are affected by numerous physical and biological factors. In common with all other soil types, the formation and development of peat, as organic soils (histosols), can be conceptually organized around five state factors [Jenny, 1941], i.e., parent material (geologic mineral substrate), topography, climate, potential biota, and time [Gorham, 1957; Amundson and Jenny, 1997; Chapin et al., 2002]. These factors affect the two key processes (production and decomposition) either directly or through additional intermediate processes. Some state factors are more important during peatland initiation and the onset of C accumulation processes and less important after the peatland ecosystem is established. For example, topography and geologic substrate (parent material) can promote or prevent peatland initiation through their effects on porosity and permeability, and the supply and flow of nutrients [Gorham, 1957].

In a number of fundamental respects, peatland soils are different from mineral soils. These important differences include the presence of a stable water table and the resulting two-layer structure of peat [Ivanov, 1981], the lack, or secondary role, of organo-mineral molecular interactions and the physical aggregate structure of mineral soils [Sollins et al., 1996], and the strong feedbacks between biological and physical processes [Belyea and Clymo, 2001], including interactions between fast biological and slow peat-forming processes [Belyea and Baird, 2006]. The upper layer of peat above the water table (called the “acrotelm”) is often aerated and contains many plant roots, while the lower layer (the “catotelm”) is permanently waterlogged [Ivanov, 1981]. The acrotelm contains recent plant litter inputs and less-decomposed organic matter, which promotes a higher hydraulic conductivity and the lateral movement of water in near-surface peat layers. Also, most microbial activity occurs in the acrotelm, where aerobic decomposition rates can be orders of magnitude higher than the anaerobic decomposition
in the catotelm [Clymo, 1984]. The proportion of peat entering the catotelm depends on the burial rate and residence time of litter and organic matter in the acrotelm, which is controlled by plant productivity and water table dynamics. Slow processes in deep peat can be as important as fast processes near the peatland surface for long-term peatland development [Belyea and Baird, 2006]. Compared to dry upland mineral soils, peatlands experience stronger internal interactions and feedbacks between hydrology and plant production and C accumulation. For example, as a peatland grows and the groundwater mound within it develops, the peatland surface can become progressively isolated from the surrounding mineral-rich water, slowing down plant production and peatland growth due to reduced nutrient input (Plate 4) [Damman, 1979; Yu et al., 2003a; Belyea and Baird, 2006]. Also, the peatland may experience drying conditions, if the growth of the groundwater mound does not keep pace with the increase in height of the peatland surface. On the other hand, highly humified deep catotelm peat with low hydraulic conductivity can buffer short-term climate variations by maintaining a relatively high and stable water table in an otherwise dry climate period.

Climate affects both primary production and decomposition processes, either directly or indirectly through vegetation and hydrology. Both the annual character and the seasonality of temperature and precipitation are important in determining peatland water balances. Increases in summer temperatures may directly stimulate photosynthesis and NPP. For example, in a metadata analysis, temperature has been identified as the single most important factor controlling Sphagnum production [Gunnarsson, 2005]. Climate also affects plant productivity through its influence on hydrology and resultant vegetation and peatland types (e.g., ombrotrophic Sphagnum-dominated bogs versus minerotrophic fens dominated by brown mosses or sedges). Even within a peatland type, climate can affect the relative dominance of plant functional types (e.g., vascular plants versus mosses) that have different NPP [Campbell et al., 2000a].

Less studied and discussed is the indirect influence of temperature on productivity through its influences on decomposition and peatland nutrient availability. Temperature has direct impact on organic matter decomposition, owing to the inherent temperature mediation of microbial activity and biochemical reactions, though the temperature sensitivity of soil decomposition is debatable [Trumbore et al., 1996; Davidson and Janssens, 2006]. The characteristic waterlogging of peat soils, which makes belowground processes distinct from non-wetland terrestrial ecosystems, is affected by state factors of climate, topography, and parent material (geologic substrate; Plate 4). Low oxygen content under waterlogged conditions, together with acidic waters partly related to cation exchange by the Sphagnum plants, limit microbial activity and decomposition [van Breemen, 1995]. Different peatland plant litter types and litter chemistry are important factors that affect the inherent decomposability of organic matter [Moore and Basiliko, 2006; Turetsky et al., 2008]. Climate change may also shift interactions between vegetation and plant parasites (fungi) in peatland ecosystems [Wiedermann et al., 2007], which may affect plant communities, NPP, and C balances. Changes in seasonality, especially the seasonal association of thermal and moisture conditions, would affect growing season lengths and water...
Postglacial initiation, expansion, and subsequent variation in C accumulation of northern peatlands have responded to global climate change. At hemispheric and regional scales, northern peatlands show rapid expansion during the initial warming of the last deglaciation, especially in the early Holocene (Plate 6c) [MacDonald et al., 2006]. Our synthesis of peatland initiation and C accumulation data in northern peatlands consistently shows the highest initiation and C accumulation rates at 11,000–8000 cal years B.P. (Plates 6c and 6d). In western continental Canada, one of the best-studied peatland regions [Fitt et al., 2000], 71 basal dates from paludified peatlands show regular millennial-scale variation in peatland initiation [Campbell et al., 2000b], which is also corroborated by a detailed peat C accumulation analysis during the mid- and late Holocene [Yu et al., 2003b]. These oscillations in peatland expansion and C accumulation appear to correlate with millennial-scale climate variations in the Holocene [Bond et al., 2001].

As a case study, four fen sites from the Kenai Peninsula, Alaska show a remarkably similar pattern in C accumulation over the Holocene, with a peak C accumulation at 11,000–9000 cal years B.P. (Plate 5d). There is good evidence to indicate that a warm climate in south-central Alaska prevailed during the early Holocene, but the moisture conditions are less clear (Plate 5a) [Kaufman et al., 2004]. Widespread Populus-dominated deciduous forests (Plate 5b) and low levels of some lakes at that time [Anderson et al., 2006] suggest dry non-wetland soils where potential evaporation was greater than precipitation. On the basis of the evidence for a warm climate, dry forests, and rapid peat C accumulation in the early Holocene, we suggest that moisture conditions could have been different for non-wetland ecosystems than for peatlands. Enhanced climate seasonality in the early Holocene, especially different seasonal associations between temperature and precipitation, could have resulted in contrasting moisture conditions on peatlands and non-wetland terrestrial ecosystems. For example, droughts in late summer are major constraints for growing season lengths and vegetation production on peatlands [Aurela et al., 2007], while upland soil moisture and lake hydrology are mostly controlled by winter snowfall and snow melt recharge in springs [Shuman and Donnelly, 2006]. Here, we speculate that high summer temperatures in the early Holocene promoted greater vapor transport from surrounding warmer oceans, resulting in significant increases in summer precipitation in Alaska. High summer precipitation would prevent summer droughts often experienced by peatlands, facilitating a longer growing season and greater vegetation production, but the decrease in winter and spring precipitation under cold winters would cause lower lake levels and dry upland soils, even during the summer season. Therefore, greater NPP has more likely controlled high C accumulation than low decomposition in these peatlands during the early Holocene.

Similar to the overall pattern in northern peatlands (Plate 6c), peatland initiation was widespread across Alaska in the early Holocene, including the Kenai Peninsula (Plate 5e). A sustained and widespread peak in fern (Polypodiaceae) spores in Kenai lakes and peats during this time (Plate 5b) [Ager, 2000; Anderson et al., 2006; Jones, 2008] suggests extensive peatland expansion during the first two millennia of the Holocene because we have observed abundant fern growth around expanding peatland margins today in south-central Alaska. A climate shift associated with the establishment of boreal forest on the Kenai in the early mid-Holocene [Anderson et al., 2006] is associated with a decrease in C accumulation in all four sites (Plate 5d) and a decline in peatland initiation (Plate 5c). An increase in C accumulation around 6000–4000 cal years B.P. is a robust signal across sites (Plate 5d) that might have been in response to a cool and moist climate beginning ~6000 cal years B.P. [Mann and Hamilton, 1995]. In contrast, peatland expansion appears to have slowed at this time (Plate 5c), suggesting that optimal climate conditions for peatland initiation are not exactly the same as those conditions that promote C accumulation in extant peatlands, which may be related to state factor interactions.

Peatland C dynamics have, in turn, had an influence on the global carbon cycle during the Holocene. Ice core records from Greenland and Antarctica show a dramatic increase and sustained peak in atmospheric CH4 concentration between 11,500 and 8000 cal years B.P. (Plate 6a) [Chappellaz et al., 1997; Brook et al., 2000]. Ice core 13C values and trends show that this early Holocene CH4 increase was strongly influenced by 13C-enriched CH4 emissions, suggesting a number of biosphere sources rather than catastrophic or sustained marine clathrate dissociation [Schaefer et al., 2006]. Changes in the interstellar CO2 gradient suggest a dominant tropical source, but also an increase in northern sources at
this time [Brook et al., 2000]. This sharp rise is coincident with the rapid expansion of many northern peatlands (Plate 6c) [MacDonald et al., 2006], particularly across western North America and Eurasia (Plate 1). Also, the prevalence of northern peatlands and their sequestered terrestrial C would favor methanogenic microbial activity in warm summers during the HTM (see section 3). Thus, northern peatlands were a likely and substantial CH₄ source that contributed to the early Holocene atmospheric CH₄ rise.

The large C pools in northern peatlands may have also affected past changes in atmospheric CO₂ concentration. While CH₄ concentration rose sharply and remained high in the early Holocene, CO₂ concentration decreased by several parts per million between 11,000 and 8000 cal years B.P., equivalent to an uptake of about 100 Pg C [Indermühle et al., 1999]. Simple terrestrial ecosystem models suggest that a similar mass of new C was sequestered as biomass and soil C during the re-growth of northern forests [Joos et al., 2004; Kohler et al., 2005]. In addition to non-wetland ecosystems, the C sequestered by northern peatlands was a further, possibly substantial, contribution to this postglacial land C buildup. An estimate of the northern peatland C pool at 8000 cal years B.P. is possible on the basis of our data synthesis. Of the ¹⁴C basal peat ages north of 45°N from available land area at that time (not covered by the Laurentide ice sheet; Plate 1), 975 (out of a total of 2173) are older than 8000 cal years B.P. (Plate 1). Assuming that the Holocene expansion of peatlands to their modern extent (about 4 million km²) was roughly proportional to the cumulative frequency of peat basal ages, northern peatlands may have covered 1.8 million km² of land area by that time. The mean of apparent C accumulation rates for the 12,000–8000 cal years B.P. period from the available sites is 23.1 ± 3.4 g C m⁻² a⁻¹ (n = 5 – 26; Plate 3; Table 1), a value that likely underestimates the true early Holocene C uptake rate (see section 3). The combination of these conservative approximations suggests that the northern peatland C pool at 8000 cal years B.P. was 73–98 Pg C, an estimate that is similar to or greater than previous estimates [29–58 Pg C by MacDonald et al. [2006] and 92 Pg C by Adams and Faure [1998]].

6. CONCLUDING REMARKS: OUTSTANDING ISSUES AND FUTURE DIRECTIONS

Carbon dynamics of northern peatlands have shown sensitive responses to changes in boundary conditions and climate and have had noticeable influence on the global carbon cycle during the Holocene. Our synthesis and analysis of climate-peatland distributions and peat-core data provide a framework for understanding the dominant controls of peatland C dynamics and climate sensitivity. We emphasize that primary productivity and decomposition are two ecosystem processes that have direct controls over carbon accumulation in peatlands. These key controls are, in turn, affected by intermediate processes (i.e., hydrology and vegetation) and ultimately by broader state factors. Our spatial analysis of climate data and northern peatland distributions shows that most peatlands occur within a mean annual air temperature range of –12° to 5°C and a mean annual precipitation range of 200 to 1000 mm, which spans the climate space of the boreal/taiga ecoregion. Also, peatlands in different regions show a distinct regional character in annual T-P space, suggesting the complex control of regional effective moisture and resultant peatland water budgets.

About a half of northern peatlands initiated before 8000 cal years B.P. in the early Holocene on the basis of >2000 basal peat dates from the northern hemisphere. Also, peat C accumulation appears to have been highest in the first few millennia of the Holocene, especially in regions that experienced Holocene thermal maximum conditions at that time. We observe that peatlands having high C accumulation rates tend to occur in regions with intermediate temperature and precipitation. These regions have the largest peatland areas in the world, including west Siberia and western Canada. On the other hand, high precipitation may not necessarily result in high C accumulation, e.g., in eastern Canada and British Columbia, suggesting that water budgets and carbon balance between production and decomposition are key to net C accumulation.

The early Holocene peatland expansion and C accumulation contributed to the peak in global CH₄ concentration and the decline in CO₂ concentration at this time. Also, the estimates on the basis of our synthesis of the largest available data sets show that, in the early Holocene before 8000 cal years B.P., northern peatlands alone may have sequestered about 100 Pg of atmospheric carbon.

This synthesis of data and ideas has identified some major outstanding issues and key future research directions.

1. Our data compilation and synthesis show major data gaps for peatland initiation and carbon accumulation histories in the Russian Far East, East Siberia, and the Hudson Bay Lowland (Plate 1). These regions represent geographic locations of intermediate temperatures and high precipitation in modern climate space (Plate 2), where peat-core data are lacking. Therefore, filling these gaps will further inform our understanding of the climate sensitivity of peatland C dynamics.

2. Further refined analysis of the large data sets of available basal peat ages could provide useful information for understanding climate control and sensitivity of peatland expansion, including separation of paludified and terrestrial-
ized peatlands since these peatland formation pathways have very different climate controls.

3. There is a need to develop and integrate process-based peatland dynamic models that take into account interactions and feedbacks of local and regional factors as well as fast and slow processes affecting production and decomposition to determine net peat C accumulation.

4. Developing novel peat-based proxies will facilitate our understanding of climate sensitivity of specific ecosystem processes, including independent proxies for productivity and decomposition. Also, new proxies to indicate hydrological and permafrost dynamics would improve our understanding of these important processes.

Acknowledgments. We thank Andy Baird and an anonymous reviewer for their constructive comments, and Daniel Brosseau and Julie Loisel for assistance with data analysis. Yu and Jones were supported by the United States National Science Foundation (NSF)—Biocomplexity in the Environment: Carbon and Water in the Earth System Program (ATM 0628455) for their peatland research in Alaska. Beilman was supported by the Marie Curie Incoming International Fellow Program of the European Commission (MC IIF 40974). We acknowledge the stimulating discussions and ideas presented at the NSF-supported PeatNet workshop in March 2008, which were part of the impetus for this paper.

REFERENCES


Indermühle, A., et al. (1999), Holocene carbon-cycle dynamics
Gunnarsson, U. (2005), Global patterns of
Gorham, E. (1957), The development of peat lands,
Edwards, M. E., C. J. Mock, B. P. Finney, V. A. Barber, and P. J.
Kuhry, P., and J. Turunen (2006), The postglacial development of
Kuhry, P., and D. H. Vitt (1996), Fossil carbon/nitrogen ratios as a
MacDonald, G. M., D. W. Beilman, K. V. Kremenetski, Y. W.
Sheng, L. C. Smith, and A. A. Velichko (2006), Rapid early
development of circumarctic peatlands and atmospheric CH4 and
MacDonald, G. M., K. V. Kremenetski, and D. W. Beilman (2008),
Climate change and the northern Russian treeline zone, 
Mäkilä, M. (1997), Holocene lateral expansion, peat growth and
accumulation on Haukkasuo, a raised bog in southeastern
Finland, Boreas, 26, 1–14.
Mäkilä, M., and M. Moisanen (2007), Holocene lateral expansion and
carbon accumulation of Luovuoma, a northern fen in Finnish
Mäkilä, M., M. Saarnisto, and T. Kankainen (2001), Aapa mires as a
carbon sink and source during the Holocene, J. Ecol., 89, 589–599.
Mann, D. H., and T. D. Hamilton (1995), Late Pleistocene and
Holocene paleoenvironments of the North Pacific coast, 
Monnin, E., et al. (2004), Evidence for substantial accumulation rate variability in Antarctica during the Holocene, through
synchronization of CO2 in the Taylor Dome, Dome C and DML ice
Muller, S. D., P. H. Richard, and A. C. Larouche (2003), Holocene development of a peatland (southern Québec): A
spatio-temporal reconstruction based on pachymetry, sedimentology, microfossils and macrofossils, Holocene, 13, 649–664.


---

D. W. Beilman, Department of Geography, University of Hawai‘i at Manoa, 2424 Maille Way, Honolulu, HI 96822, USA. (beilman@hawaii.edu)

M. C. Jones and Z. Yu, Department of Earth and Environmental Sciences, Lehigh University, 31 Williams Drive, Bethlehem, PA 18015, USA. (mcj208@lehigh.edu; ziy2@lehigh.edu)