Holocene carbon flux histories of the world’s peatlands: Global carbon-cycle implications

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Introduction

Peatlands store a large amount of organic carbon (C) at the Earth’s surface only a few meters from the atmosphere. Recently, global C cycle research communities have recognized the importance of peatlands in affecting the Holocene C cycle, and there have been efforts to incorporate peatlands into global vegetation models and global climate–carbon cycle models (e.g. Frolking et al., 2009; Kleinen et al., 2010; Wang et al., 2009; Wania et al., 2009). A recent synthesis of peat-core data from global peatlands has provided the observed C stores from northern, tropical and southern peatlands and their changes over time since the last glacial maximum (Yu et al., 2010). However, there has been no attempt to analyze or separate two important C flux processes (C uptake and C release) from the observed peat C data. These decomposed C flux terms as derived from peat-core data are directly relevant to the global C cycle because of their effect on atmospheric carbon dioxide (CO2) concentrations and δ13CO2 values over the Holocene. The analysis of global peatland data described here allows us to evaluate the role of peatlands in affecting the late-Holocene rises in CO2 and CH4 concentrations, and in testing the early anthropogenic hypothesis (Ruddiman, 2007; Ruddiman et al., 2011, this issue). Also, a quantitative understanding of these fluxes over the Holocene will help us project the trajectories of the large C pool in the world’s peatlands in a changing future climate and their possible feedback to climate change (Arneth et al., 2010; McGuire et al., 2009).

Here I present a new approach (‘Super Peatland’ approach) to analyzing and modeling the observed peatland data and separating the C uptake and release terms over time from the peat C pool data. The data are based on recent large-scale and global syntheses (MacDonald et al., 2006; Yu et al., 2009, 2010). The objectives of this paper are (1) to describe the C flux decomposition approach and its underlying assumptions; (2) to provide a global-scale assessment of the roles of peatlands in affecting the Holocene C cycle; and (3) to discuss the contributions to the rises of CO2 and CH4 in the late Holocene. Based on these analyses, I found that global peatlands, especially the predominant northern (boreal and subarctic) peatlands, have played a very important role in affecting Holocene CO2 concentrations, more so than previously recognized. Over the entire Holocene, peatlands have served as C sinks (net C uptake/burial) at a mean rate of 44 GtC/kyr (or 44 TgC/yr); however, they captured C from the atmosphere at a rate twice that in the early Holocene but only half that in the late Holocene. As a consequence, the cumulative net C pool...
of 612 GtC as observed in global peatlands (Yu et al., 2010) has had differential impacts on the global C cycle throughout the Holocene, mostly owing to the slow and delayed decay of prior-deposited peat C.

Data sources and the ‘Super Peatland’ approach

Data sources

The data sets used in the analysis are from a global peatland data synthesis using the approaches as described for northern peatlands in Yu et al. (2009). We now have data for global peatlands, including northern peatlands (boreal and subarctic), tropical peatlands and southern peatlands in the high-latitude Southern Hemisphere (Figure 1; Yu et al., 2010). Although the data sets represent the most comprehensive compilation of the available peatland data, I caution that the data base is still incomplete for the tropics and is perhaps biased toward small peatlands for some large peatland areas in North America, especially in the Hudson Bay lowlands. Except the Hudson Bay lowlands and the Far East of Russia (see Yu et al., 2009), the data base of basal ages and C accumulation records we used for northern peatlands is the most extensive (MacDonald et al., 2006; Yu et al., 2009). Thus, the analysis presented in this paper is a first approximation of C flux reconstructions of global peatlands using the best available data.

The data used include peat basal dates and C accumulation rate histories for each of these three major peatland types/regions. The compilation method of basal peat dates was described earlier (Campbell et al., 2000; Yu et al., 2009). Frequencies of basal initiation dates were used as a proxy of peatland area change over time, assuming that the peatland area increases linearly with the rate of peat initiation (i.e., increase in the number of individual peatlands) over time. However, the rates of peatland area increase are likely different and non-linear at different times. For example, in Alaska most peatlands initiated during the early Holocene (11–8 ka; 1 ka = 1000 cal. yr BP) and C accumulation rates were several fold higher at that time (Jones and Yu, 2010; Yu et al., 2009). Thus, presumably the rates of peatland area expansion of individual existing peatlands would be much higher at that time than the rest of the Holocene in these regions, assuming that the conditions causing peatland initiation, expansion and accumulation were similar. As a result, the linear-expansion-rate assumption used here would underestimate the total amount of C accumulated in the early Holocene for Alaska and many other northern peatland regions (Yu et al., 2009). On the other hand, some of the largest peatlands, including the Hudson Bay lowlands and in the proglacial Lake Agassiz basin, were formed after 8 ka (Glaser et al., 2004). However, owing to the lack of detail on peatland expansion data at individual peatland sites (but see Korhola et al., 2010), I argue that the linear-expansion-rate assumption represents the best first approximation of peatland area change over time during the Holocene at a global scale.

Peat C accumulation rates were derived from detailed dating, bulk density and C content analysis from many sites in each of these three regions. These data were presented at 1000 year binned intervals. The product of peatland area change over time and the average C accumulation at 1000 year intervals was used to generate net peat C pools at 1000 year bins, which can be summed to produce the cumulative peat C pool for each of three peatland regions. These are the observed patterns from peat-core data. The basal age and C accumulation data sets used here represent the most comprehensive coverage of global peatlands (see Supplement Information in Yu et al., 2010, for details about the sites used for global peatland data synthesis).

General idea of ‘Super Peatland’ approach

Below I describe how I used and decomposed the observed data to model and calculate the C uptake and release flux terms. For each of these three peatland regions (northern, tropical and southern peatlands), I analyzed the data from individual sites as if they were from a single large continental-scale peatland, a transcontinental-scale ‘Super Peatland’. The idea is analogous to the ‘Big Leaf’ model used in global ecosystem and land–atmosphere exchange studies (Sellers et al., 1996), though it is different in terms of the processes involved. The observed time histories of C pools during the Holocene (or the last 25 ka for tropical and southern peatlands) were calculated by multiplying the overall peatland area as derived from basal date frequency and mean C accumulation rates at 1000 year binned intervals (Figure 1; see above and Yu et al., 2010). Clymo et al. (1998) and Gorham (1991) applied a similar idea of pooling data from individual sites in a region as if from a single peatland to assess the climate impact on peat-addition and decay rates for Finland and to estimate average C accumulation rates and ages of peat deposits in North America, respectively. However, no previous studies have been carried out to reconstruct time-dependent C flux histories using large-scale data bases over the Holocene.

An accurate accounting of net uptake/burial of peat C must consider two factors: The amount initially deposited and the subsequent decomposition (analyzed here in 1000 year bins). For example, some of the peat initially deposited between 8000 and 7000 years ago decomposes in subsequent millennia. As a result, the amount of buried peat observed today for that earlier millennium will be smaller than the amount that was initially deposited. Furthermore, the decomposition process emits CO2 and reduces net carbon burial during subsequent intervals. For example, net C uptake by peatlands during the interval from 7000 to 6000 years ago will be reduced by decomposition of peat originally deposited 8000–7000 years ago (and in all previous intervals). Reconstructing the combined effects of initial deposition (uptake) and subsequent decomposition (release) for all 1000 year intervals in the Holocene requires working backward from the amounts preserved and observed at the present, using equations that estimate rates of peat decomposition under certain assumptions.

Decay models

For each region, a decomposition model (Clymo, 1984) was used to derive peat-addition rate to the catotelm (the anaerobic layer below water-table for long-term accumulation) and peat decomposition rate from the cumulative C pool data. The single exponential decomposition model with a constant decay coefficient has the form of

\[
\frac{dM}{dt} = p - \alpha * M
\]  

(1)

which has the analytical solution of

\[
M = \left(\frac{P}{\alpha}\right) \left(1 - e^{-\alpha t}\right)
\]  

(2)
In both equations, \( M \) is the cumulative peat C and \( t \) is time. The peat-addition rate (PAR; \( p \)) determines the general slope of the cumulative peat mass versus age curve, and the decomposition coefficient (a), or ‘fractional mass loss rate due to decomposition’, determines the curvature (Clymo, 1984).

In addition to the constant decay coefficient used here, I also explored and tested the suitability of other decay rules, including linear and quadratic decay functions as described in Clymo et al. (1998). I found that the constant decay rule provided the best fit to the pooled data on the basis of the \( R^2 \) values and visual examinations of the fitted curves. Clymo et al. (1998) found no difference between these different decay functions in fitting their pooled data from Finland, which could be partly due to the high noise in their data than our binned data. Therefore, I only presented results from the simplest constant decay rule in my analysis. It would be interesting to explore other decay functions in future analysis, if the added complexity would still make C flux reconstructions tractable analytically.

**Figure 1.** Global peatland data synthesis. (A) Atmospheric CH\(_4\) concentrations from ice core in Greenland (curve; Brook et al., 2000) and inter-polar gradient between Greenland and Antarctica (dots with error bars; Chappellaz et al., 1997). Peat basal age frequency histograms (bars), cumulative percentage and peatland areas (curves) from (B) northern peatlands (\( n=1516 \); MacDonald et al., 2006), (D) tropical peatlands (\( n=116 \); Yu et al., 2010) and (F) Patagonia peatlands (\( n=54 \); Yu et al., 2010). Observed apparent C accumulation rates (mean and standard errors of the means) from (C) northern peatlands (\( n=33 \); Yu et al., 2009), (E) tropical peatlands (\( n=26 \); Yu et al., 2010), and (G) southern (Patagonia) peatlands (\( n=17 \); Yu et al., 2010).
The “Super Peatland” approach for regional carbon flux reconstructions using peat-core data

![Flowchart showing the logical steps and procedure for the 'Super Peatland Approach' in modeling peat C flux (uptake and release) terms from observed peat-core data. The top three boxes are input data, the highlighted cumulative C pool (CCP) is the term for peat C pool estimates, and net C balance (NCB) is the C flux term that directly affects atmospheric CO₂ concentrations. See Table 1 for explanation of these terms used in the paper.](Image)

Reconstructing carbon fluxes

The modeled decomposition rate was used to decompose the cumulative C pools into cumulative C uptake and release terms over the Holocene. These data were used to partition time histories of net C release and net C uptake at 1000 year intervals. The net C uptake (NCU) represents the C input during each 1 kyr time period, assuming that all C was added at the beginning of that interval. Net C release (NCR) includes decomposition over each 1 kyr interval of all existing (older) peat cohorts. I generated and presented another C release curve, the cumulative cohort C release (CCCR), to keep track of the lifetime decomposition of every 1 kyr peat cohort. As a final product of the analysis, the modeled net C balance (NCB) can be used to analyze the peat C impacts on atmospheric CO₂ concentrations and δ¹³C values. The flowchart in Figure 2 illustrates the procedure and logical steps used in the observed peat-core data to reconstruct net C flux terms over the peatland histories. See Table 1 for a definition and explanation of the terms used in this approach. The Super Peatland approach can be used for individual peatlands as well as for peatland data from larger regions, such as the entire northern peatlands, as long as the peatland area and C accumulation rate data can be regarded as representative.

The observed net C pool (NCP), along with modeled decomposition coefficient (α; Figure 3), can be used to calculate net C uptake (NCU) for each 1 kyr interval by considering NCU as initial mass (C) and NCP as mass (C) remaining after time t as commonly used in ‘litterbag’ decomposition studies. The equation has the following form,

\[ NCU_t = \frac{NCP_t}{e^{-\alpha t}} \]

The net C release (NCR) represents the total C release by the entire peatland at a particular 1 kyr period. So the NCR at time t is the sum of C release during that period of all peat cohorts older than time t. The C release during the 1 kyr period at time t can be calculated by the difference of potential NCU’s at time t and time t−1. Remember that NCU is added at the beginning of each 1 kyr period. This is a mathematical trick for keeping track of decomposition of peat cohorts at various time intervals, as the terms themselves, such as NCU/t calculated for time intervals other than time t, have no real ecological meanings. The equation is,

\[ NCR_t = \sum_{k=1}^{\text{initiation}} \left( \frac{NCP_k}{e^{-\alpha t}} - \frac{NCP_k}{e^{-\alpha (t-1)}} \right) \]

Table 1. Explanation of terms used for peatland carbon dynamics

<table>
<thead>
<tr>
<th>Term</th>
<th>Unit</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed Net C Pool (NCP)</td>
<td>GtC/kyr</td>
<td>C pool observed from peat-core data at the present (derived from multiplying the calculated C accumulation rates and estimated peatland areas) at each time interval (e.g. 1000 yr binned interval in this study)</td>
</tr>
<tr>
<td>Cumulative Pool (CCP)</td>
<td>GtC</td>
<td>Cumulative C store as observed at the present and as calculated from Net C Pool (NCP) above</td>
</tr>
<tr>
<td>Modelled Net C Uptake (NCU)</td>
<td>GtC/kyr</td>
<td>Modeled C uptake from observed Net C Pool (NCP) by considering and adding total C release/loss since the formation of the 1000 yr peat cohort using the modeled decomposition (fractional mass loss) rate</td>
</tr>
<tr>
<td>Net C Release (NCR)</td>
<td>GtC/kyr</td>
<td>Total C release from the entire peatland at every 1000 yr interval</td>
</tr>
<tr>
<td>Cumulative Cohort C Release (CCCR)</td>
<td>GtC</td>
<td>Total C release from a 1000 yr cohort peat since its formation; the difference between Net C Uptake (NCU) and Net C Pool (NCP)</td>
</tr>
<tr>
<td>Cumulative C Uptake (CCU)</td>
<td>GtC</td>
<td>Cumulative Net C Uptake (NCU) over time for the entire peatland</td>
</tr>
<tr>
<td>Cumulative C Release (CCR)</td>
<td>GtC</td>
<td>Cumulative Net C Release (NCR) over time, or the sum of Cumulative Cohort C Release (CCCR) for all peatland cohorts</td>
</tr>
<tr>
<td>Net C Balance (NCB)</td>
<td>GtC/kyr</td>
<td>Difference between Net C Uptake (NCU) and Net C Release (NCR); equivalent to the term of net ecosystem C balance (NECB) as proposed and used for describing ecosystem C balance (Chapin et al., 2006)</td>
</tr>
</tbody>
</table>
where $k$ is the peat cohort ID to track all peat cohorts older than time $t$ since the initiation of the peatland. For example, $k = 1$ means the peat cohort of the last 1000 years.

The net C balance ($NCB$) was calculated as the difference between $NCU$ and $NCR$ as derived above,

$$NCB = NCU - NCR \quad (5)$$

Other flux terms and relationships can be expressed below. The cumulative cohort C release (CCCR) for peat cohort $k$ can be calculated in two ways:

$$CCCR = NCU - NCP \quad (6)$$

or

$$CCCR_k = \sum_{i=1}^{k} \left( \frac{NCP_i}{e^{-\alpha t_i}} - \frac{NCP_i}{e^{-\alpha t_i(t-i)}} \right) \quad (7)$$

For a super peatland, the cumulative C uptake (CCU) and the cumulative C release (CCR) are just the sum of $NCU$ and $NCR$ or $CCCR$. They can be expressed as below,

$$CCU = \sum (NCU) \quad (8)$$

and

$$CCR = \sum (NCR) = \sum (CCCR). \quad (9)$$

The cumulative C pool ($CCP$; the total C pool size) is the sum of observed NCP for each 1 kyr interval. $CCP$ can also be calculated using the following relationship at $t = 0$ (at present),

$$CCP = CCU - CCR \quad (10)$$

This relation is only applicable for the present-day inventory of the total cumulative C uptake and release (Figure 4). For time periods in the past, the relation would have been different because the observed cumulative C pool at that time has already taken into account the C release since that time.

The NCP and NCB should have the same ‘cumulative’ value (i.e. the same total area below these curves as in Figure 5), representing the eventual total cumulative peat C pool as in Figure 4; however, NCP represents the C pool observed at the present while NCB indicates the modeled net C flux at each 1 kyr interval that we would have observed at that time. By the same argument, NCR and CCCR have the same cumulative values (the cumulative C release) but account for decomposition in different ways (tracing the entire peatland over time (NCR) versus tracing the individual 1 kyr cohorts since its formation (CCCR)). If a peatland grows very deep and accumulates a large amount of C, then the cumulative C release may balance the C uptake and, as a result, it may reach ‘its limit of bog growth’ (the term $(\rho/\alpha)$ in Eq. (2); Belyea and Baird, 2006; Clymo, 1984). In that case, NCB would reach zero at the present time. After reaching the growth limit, the peatland still grows at the surface, but it has zero C balance as a whole, owing to the delayed effect of peat C decomposition of a large amount of previously accumulated (‘old’) peat.

Figure 3. Observed net C pools (NCP) at 1000 yr intervals and errors based on S.E. of mean C accumulation rates (A), and cumulative peat C–age relationships and decomposition modeling results for northern peatlands (B), tropical peatlands (C) and southern peatlands (D). The decay rate for tropical peatlands is more than three-fold greater than the ones from high-latitude (northern and southern) peatlands, showed as different curvatures.
Decomposition of all previously buried peat is occurring at every point in time, although at decreasing rates. As a result, some C flux and pool terms are a snapshot in time that will change as additional decomposition occurs over time. For example, both NCP and CCCR will continue to change in the future. However, NCU and NCR histories do not change over time, as both are calculated for that time and are independent from what happens after their realization. Thus, the NCB as calculated from NCU and NCR is a fixed snapshot of net C uptake at a particular time during the Holocene, which will not change after that. NCB is the best term to assess the net C removal by peatlands from the atmosphere for each 1 kyr interval – its impact on the atmospheric CO₂ concentrations has been preserved in the ice cores or other archives. The robustness of this assessment depends on the limitations of the assumptions used in this approach and reliability of the available data used.

**Results**

Peatlands from three major regions show different patterns of initiation and C accumulation rates (Figure 1 and Table 2; Yu et al., 2010). Northern peatlands mostly developed during the Holocene as indicated by >1500 basal peat dates (MacDonald...
et al., 2006), with <10% of the peatlands formed before 12 ka (Figure 1B). Also, maximum peatland formation and initiation appeared to occur during the early Holocene at 11–8.5 ka, a time when most northern high-latitude regions experienced the strongest seasonality in insolation and climate (Jones and Yu, 2010; Yu et al., 2009, 2010). Apparent peat C accumulation rates were also highest in the early Holocene (Figure 1C). Tropical peatlands between 30°S and 30°N latitudes began to form during the last glaciation at >25 ka (Page et al., 2004), but only about 35% of the basal dates are pre-Holocene in age (>12 ka) (Figure 1D). Tropical peatlands show a peak in initiation during the mid Holocene around 8–4 ka and a small accumulation peak around 5 ka. Most southern peatlands (70% in Patagonia) were initiated before the Holocene (Figure 1F), probably because of land availability or a warm climate following local deglaciation. The C accumulation trend from sites in Patagonia shows a long-term gradual increase (Figure 1G).

Total peat C pools are 547 GtC, 50 GtC, 15 GtC for northern, tropical and southern peatlands, respectively (Figure 3, Table 2; Yu et al., 2010), with a global peat C pool of 612 GtC. Long-term decomposition rates (fractional mass loss rates) for these regions were 0.0000855 per yr, 0.000238 per yr, 0.0000978 per yr, respectively. Based on these decomposition constants, I calculated mean residence times of peat C of about 7400 years for northern peatlands and 4200 years for tropical peatlands. The modeled peat C addition rates (‘C sequestration rate’) are 74.8 TgC/yr, 11.9 TgC/yr, 1.6 TgC/yr for northern, tropical and southern peatlands, respectively. On the basis of the observed cumulative C pool (CCP) and modeled decomposition rates, I derived a cumulative C uptake (CCU) of 884 GtC and a cumulative C release (CCR) of 340 GtC for northern peatlands, 268 GtC and 218 GtC for tropical peatlands, and 42 GtC and 27 GtC for southern peatlands (Figure 4). The difference (CCP) between CCU and CCR pertain only for the present time, as described above.

For northern peatlands, the net C balance (NCB) has a mean value of 41.8 GtC/kyr (or 41.8 TgC/yr) during the Holocene. NCB reached the highest value of 83.1 TgC/yr in the early Holocene around 9 ka and then declined to 21.5 TgC/yr around 2 ka, mostly owing to the delayed long-term decay of previously accumulated peat C (Figure 5A). The NCB from tropical peatlands fluctuated between slightly >10 (C sinks) and <−5 GtC (C sources), and became a C source at ~10 ka, 6 ka and 2 ka (Figure 5B). This pattern is mostly determined by the net C uptake (NCU). Southern peatlands have a low (0.2 TgC/yr) and relatively constant NCB during the Holocene (Figure 5C).

### Discussion

#### Comparison of C pools and fluxes in northern, tropical and southern peatlands

There is about an order of magnitude difference in peat C pools in decreasing order from northern, to tropical, to southern peatland regions. As northern peatlands represent about 90% of the global peatland C pool (612 GtC), they have played a dominant role as the largest biosphere C reservoir. This is also reflected in the much larger peat C addition rate (C sequestration rate) in northern peatlands than in other peatland regions. The catotelm decomposition rates reported in this paper for high-latitude (northern and southern) peatlands are similar to the rates of about 0.0001 per yr in the literature (Clymo, 1984; Clymo et al., 1998; Yu et al., 2001). However, the rates from tropical peatlands are a factor of three higher (Figure 3C), presumably owing to the higher temperature and longer decomposition season. As a result, a much higher C uptake rate and high primary productivity than in high-latitude peatlands would be needed to accumulate the observed C pools under the high decomposition rates in tropical peatlands. For example, net C uptake in tropical peatlands is five times more than their total remaining cumulative C pool (Figure 4B), while for high-latitude peatlands the ratio of net C uptake to cumulative C pool is about 2.

Previous estimates of northern and tropical peatland C pools were mostly based on estimates of peatland area, bulk density and carbon content, and mean peat depth (e.g. Gorham, 1991; Page et al., 2009; Turunen et al., 2002). The product of these three terms generated estimates of total peat C pools for these two major peatland regions. The large range of 275–455 GtC for northern peatlands from previous estimates was attributed to uncertainties in peat depth and bulk density values (Turunen et al., 2002). Our estimate of a mean C pool of 547 GtC for northern peatlands used in this paper was based on an entirely different approach using detailed data from dated individual peat profiles (Yu et al., 2010). We used the basal peat ages as the basis for estimating peatland area change over time and C accumulation rates for every 1000 yr bin to calculate the total peat C pool. The assumptions in this approach are that: (1) peatland area increases linearly with the rate of peatland initiation after the formation of individual peatlands, so the area change over time can be represented by cumulative basal peat ages (see Korhola et al., 2010 for the availability of multiple dates from some individual peatlands); and (2) the available sites with 14C-dated C accumulation rates (33 sites from northern peatlands, 26 sites from tropical peatlands, and 17 sites from Patagonian peatlands) are representative of C accumulation.
rates in those three major regions. These assumptions can be tested in the future with better understanding of peatland expansion processes and with more extensive data coverage.

Our peat C pool estimate for northern peatlands has a range of ~150 GtC (from 473 to 621 GtC), which represents a minimum uncertainty that considers only errors in mean C accumulation rates. Given the limitations and uncertainties of all these estimates (Gorham 1991; Yu et al., 2010), we perhaps have confidence to only one significant figure (e.g. Davidson and Janssens, 2006), so our estimate of 547 GtC (Yu et al., 2010) is only slightly higher than the most widely cited C pool size of 455 GtC by Gorham (1991). Based on the new estimates, northern peatlands likely have a C pool of ~500–600 GtC, while other (tropical and southern) peatlands have ~100 GtC.

For northern peatlands, our estimated mean C accumulation rate of 18.6 gC/m² per yr on an areal basis (Yu et al., 2009) is much lower than the 23–29 gC/m² per yr estimated by Gorham (1991). Overall ‘net C accumulation rate’ based on peat-addition rate of 75 TgC/yr in this study is similar to the lower end of Gorham’s (1991) estimated rates of 76–96 TgC/yr. However, our Holocene average net C balance (NCB) of 42 TgC/yr is about half of the C sequestration rate estimated by Gorham (1991). These differences reflect the different approaches that have been used in these estimates as well as differences in the flux terms and their ecological meanings. I argue that the NCB better reflects the long-term average as well as the contemporary net C sequestration capacity of peatlands during specific intervals in the Holocene, as it takes into consideration of later decomposition of previously deposited peat. Also, the NCB would allow more meaningful comparison between the past C accumulation rates, derived from peat cores, and the contemporary C balance, measured from eddy covariance, flux chamber and other techniques (see the first such comparison study using conventional peat-core C accumulation analysis by Roulet et al., 2007).

The time histories of peatland C dynamics as presented in this paper are different from previous studies. The modeled NCB from all three major peatland domains (‘Super Peatlands’) shows a decreasing trend during most parts of the Holocene, likely caused by the delayed effects of C release from old peat deposited millennia ago. The net C balance and C sequestration capacity of northern peatlands were highest during the early Holocene at 9–8 ka, which is supported by recent regional and hemispheric syntheses (e.g. Jones and Yu, 2010; MacDonald et al., 2006; Smith et al., 2004; Yu et al., 2009, 2010) but is significantly different from earlier synthesis studies (e.g. Gajewski et al., 2001; Gorham, 1991; Harden et al., 1992).

Gorham (1991) concluded that northern peatlands expanded and accumulated more rapidly in the later half of the Holocene, based on site-specific and regional studies and on the calculated average age of peat deposition. However, the 2664 basal peat ages, from the combined data bases in MacDonald et al. (2006) and Gorham et al. (2007) after removing duplicates, have an average age of 7300 years, which is much older than the average age of 4600 years estimated by Gorham (1991). Using soil chronosequence data and empirical models, Harden et al. (1992) indicated that the greatest peatland expansion in glaciated North America occurred at 8–4 ka, several millennia after the peak ice retreat period. Gajewski et al. (2001) proposed a reconstruction of Sphagnum (peat moss) peatland extent in northern peatlands during the last 21 000 years based on Sphagnum spores in the global pollen data base. They concluded that peatland C accumulation greatly increased during the past 5000 years. As Gajewski et al. (2001) used peat moss spores to infer the presence of mosses and then the extent of peatlands, their approach likely greatly underestimates the extent of peatlands dominated by non-Sphagnum plants during the early Holocene, such as rich fens that are known to be dominant types of peatlands early in their development stages, and overestimates Sphagnum-dominated bogs and poor fens in the late Holocene. Also, Gajewski et al. (2001) did not generate an independent estimate of the peatland C pool, as they calibrated their empirical model to match the best-known and most widely cited C pool estimate of 455 GtC in Gorham (1991). It appears counter-intuitive that rapid peatland growth and great C sequestration occurred during the early Holocene, a time period corresponding to the Holocene thermal maximum in many high northern latitude regions. However, this pattern has been documented by observational data (not model simulations) from West Siberia (Smith et al., 2004), Alaska (Jones and Yu, 2010) and hemispheric syntheses (MacDonald et al., 2006; Yu et al., 2009). The early-Holocene maxima in peatland expansion and accumulation are attributed to increased productivity in warmer summers and reduced decomposition in colder winters as induced by the strongest insolation seasonality at that time (Jones and Yu, 2010).

To reduce uncertainties and improve the estimates of peatland C pools and fluxes, I suggest that future research should focus on the following three areas: (1) increasing data coverage and representation, (2) better understanding of peatland expansion processes, and (3) progress in methodologies. For example, there is a significant data gap in some largest peatlands, including the Hudson Bay lowlands and East Siberia, and this lack of data may introduce biases in the derived peatland initiation histories and total C pool estimates. Further analysis of the valuable multidate data sets, such as the one synthesized in Korhola et al. (2010), would significantly improve our understanding of peatland lateral expansion processes under different climatic and topographic conditions. The C flux history as presented in this paper has only considered limited uncertainties and errors, and a more systematic approach and methodology would be to generate ensembles of C flux histories that are constrained by the observed data and by all the associated uncertainties (see Frank et al., 2010).

Global peatlands and Holocene CH₄ concentration history

The roles of wetlands in determining Holocene CH₄ budgets and atmospheric CH₄ concentrations have long been assessed using a top-down approach based on ice-core records of CH₄ concentrations and δ¹³CH₄ and dD of CH₄ (Brook et al., 2000, 2008; Chappellaz et al., 1997; Sowers, 2010). Our data synthesis of global peatlands (Yu et al., 2010) provides the first bottom-up assessment of the global peatland contribution to Holocene CH₄ dynamics. Regional and global CH₄ emissions from wetlands are mostly controlled by the total area of peatlands and the rates of emissions per unit wetland area. The rates of CH₄ emissions are controlled by peatland types (minerotrophic fens versus oligotrophic bogs; Laine and Vasander, 1996), and environmental conditions (temperature and moisture; Büber et al., 1995; Moore and Roulet, 1993).

The rate of peatland area increase as inferred from basal peat dates (Figure 1) provides the first approximation of peatland impacts on the atmospheric CH₄ budget. The fast rate of area
increase in northern peatlands during the early Holocene (Figure 1B) apparently contributed to the peak CH\textsubscript{4} concentration and the large North–South inter-polar gradient derived from ice-core records in Greenland and Antarctica (Figure 1A; Brook et al., 2000). This interpretation is in agreement with conclusions from northern peatlands and thermokarst lakes (e.g. Jones and Yu, 2010; MacDonald et al., 2006; Smith et al., 2004; Walter et al., 2007; Yu et al., 2010), as well as with peat-based paleoecological reconstructions showing that most peatlands were minerotrophic CH\textsubscript{4}-emitting fens during this period. However, it differs somewhat from the inferences of dominant tropical or low-latitude CH\textsubscript{4} sources, using the top-down approach from ice cores (Brook et al., 2000), based on the insolation-driven monsoon hypothesis (COHMAP Members, 1988; Kutzbach, 1981; Ruddiman, 2008), and from speleothem isotope evidence for monsoon intensities for the East Asian and Indian monsoon regions (Fleitmann et al., 2003; Wang et al., 2005). If the tropics were the dominant CH\textsubscript{4} source in the early Holocene, then tropical peatlands were obviously not this source based on our data synthesis, which shows low area expansion rates during this period (Figure 1D). Alternative sources of CH\textsubscript{4} are non-peat wetlands and seasonally flooded areas in tropical and subtropical regions, including possibly vast wetland regions across southern Asia (India) and East Asia (China). However, we do not have robust empirical data to document and support the presence of these wetlands or flooded areas, except the lake-level records from subtropical northern Africa. Furthermore, Southeast Asia, the most dominant tropical peatland region, appeared to show a different timing for the monsoon maximum as predicted by summer insolation. For example, Griffiths et al. (2009) showed that the maximum monsoon occurred after 7 ka in Kalimantan, Indonesia, as a result of a closer moisture source after the sea level rose and was stabilized. Thus, our data support a more important role of northern peatlands in contributing to the early-Holocene CH\textsubscript{4} peak.

In the mid Holocene, around 8–4 ka, the highest rate of area increase in tropical peatlands (Figure 1D), in particular in Southeast Asia (Yu et al., 2010), contributed to the lowest North–South CH\textsubscript{4} gradient at 6 ka (Brook et al., 2000). The subsequent decrease in peatland expansion rate from both northern and tropical peatlands coincides with the lowest CH\textsubscript{4} concentration around 5 ka (Figure 1A), which suggests that CH\textsubscript{4} emissions from both peatland regions were reduced. This is supported by the top-down interpretations as from ice-core data. The decreasing rate of peatland area increase in the last 5 ka was mostly caused by climate change in these regions with the neoglacial cooling in high northern latitudes and weakening monsoons in low latitudes during the later half of the Holocene.

Over the last 5000 years, the global CH\textsubscript{4} rise derived from ice cores coincides with a general decrease in the North–South inter-polar CH\textsubscript{4} gradient (Brook et al., 2000, 2008; Chappellaz et al., 1997). This suggests that tropical sources were likely responsible for this post-5 ka rise in CH\textsubscript{4} concentrations. However, the peatland area expansion (Figure 1D) decreased because of the weakening monsoon in SE Asia (Griffiths et al., 2009) and elsewhere in monsoon regions (COHMAP Members, 1988; Wang et al., 2005). In addition, the more intense and frequent El Niños (Moy et al., 2002) have induced droughts in SE Asia, a major tropical peatland region, reinforcing the interpretation of a reduced contribution of tropical peatlands as CH\textsubscript{4} sources. Other CH\textsubscript{4} sources could include natural non-peat-forming wetlands in the tropics during the late Holocene, but presumably these wetlands should have expanded or shrunk in a similar fashion as peatlands did in responding to climatic conditions. This indicates that the source of CH\textsubscript{4} during the late Holocene is most likely from non-natural sources, including agriculture and irrigation activities, as proposed by Ruddiman (2007). Our global peatland data support the CH\textsubscript{4} part of the early anthropogenic hypothesis.

### Peatlands as a long-term regulator of the global carbon cycle during the Holocene

The term of net C balance (NCB) derived from peat-core data and used here is equivalent to the concept of net ecosystem C balance (NECB) in the ecosystem ecology literature (Chapin et al., 2006), reflecting long-term C accumulation in ecosystems. The N(E)CB represents the net C exchange between the atmosphere and peatlands, after considering all the important C fluxes, such as net ecosystem exchange (NEE), CH\textsubscript{4}, and dissolved organic carbon (DOC), explicitly in most NECB studies and implicitly in peatland NCB analysis. Thus, the NCB is a term that represents direct impact of these ecosystems on the atmospheric CO\textsubscript{2} concentration. To my knowledge, this is the first time that a time-dependent net C balance has been derived from peat-core data for the Holocene.

During the Holocene, global (northern, tropical and southern) peatlands had a mean NCB of 44 GtC per 1000 years (i.e. 44 TgC/yr), so peatlands have consistently been a C sink during the Holocene. As a result, the net effect of peatlands would have been to reduce atmospheric CO\textsubscript{2} concentrations during the last 12,000 years. However, the NCB derived from peat-data modeling varied from a maximum rate of 87.9 TgC/yr in the early Holocene at 9–8 ka to a minimum value of 16.3 TgC/yr in the late Holocene at 3–2 ka (Figure 6). This differential effect of peatland NCB on atmospheric CO\textsubscript{2} concentration is mostly due to the delayed effect of decomposition of old peat, even under the assumption of constant plant primary production and peat-addition rates. Therefore, if everything else (other terrestrial biomes and ocean C exchanges with the atmosphere) has been equal, the total of 612 GtC stored in global peatlands at the present served as a stronger C sink in the early Holocene than in the late Holocene. The maximum NCB in global (mostly northern) peatlands in the early Holocene might have contributed significantly to the 5 ppm decrease in CO\textsubscript{2} concentration from 11 to 7 ka (Figure 7B and Table 3). This decrease has been attributed to the re-establishment of vegetation and soil in the northern high-latitude regions following the last deglaciation (Elsig et al., 2009; Indermühle et al., 1999). I argue that peatlands might have been a dominant player in that CO\textsubscript{2} decrease, as the total cumulative net C removal (‘burial’) by peatlands from 12 to 7 ka (5 kyr period) is 289 GtC. Considered alone, the net C storage should have been 289 GtC. Considered alone, the net C storage should have been a factor of 4.

Here I explore the role of peatlands as a persistent but variable C sink in the context of the global C system and in affecting the CO\textsubscript{2} concentration during the last 7 ka. The 20 ppm increase in CO\textsubscript{2} over the last 7 ka has been variously attributed to carbonate compensation in oceans responding to earlier land biosphere C uptake (Broecker et al., 2001), coral reef buildup (Ridgwell et al., 2003), emissions from natural terrestrial sources (Brovkin et al., 2002;
Figure 6. Net C balance (NCB) of global peatlands. (A) NCB from northern, tropical, southern peatlands and global total. (B) NCB from northern peatlands with estimated upper and lower limits based on different average C accumulation rates. (C) Global NCB with ranges of estimates (error bars) and cumulative global NCB during the Holocene.

Table 3. Impacts of the world’s peatlands on the global carbon cycle during the Holocene

<table>
<thead>
<tr>
<th>Holocene period (ka)</th>
<th>Peatland total NCB (GtC)</th>
<th>NCB rate (TgC/yr)</th>
<th>Change in CO₂ (ppm)a</th>
<th>Change in δ¹³CO₂ (%)b</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>4–0</td>
<td>116</td>
<td>29</td>
<td>+7</td>
<td>−0.05</td>
<td>Peatlands still served as C sink (decreasing CO₂ rise), but perhaps had reduced influence on δ¹³CO₂; ocean carbonate compensation C release at reduced rate; other biomes and possible anthropogenic deforestation balance the difference between ocean C release and peatland C uptake</td>
</tr>
<tr>
<td>7–4</td>
<td>151</td>
<td>50</td>
<td>+13</td>
<td></td>
<td>Slight decrease Rapid and strong initial response from ocean (carbonate compensation mechanism), causing steep increase in CO₂ but no secular change in δ¹³CO₂; C uptake by peatlands at Holocene mean rate; peatland uptake balanced other biome C release?</td>
</tr>
<tr>
<td>11–7</td>
<td>272</td>
<td>68</td>
<td>−5</td>
<td>+0.25</td>
<td>Deglacial long-term land biospheric C uptake, mostly by peatlands; peatlands served as a perturbation to the global C system</td>
</tr>
</tbody>
</table>

aCO₂ data from Flückiger et al. (2002) and Monnin et al. (2001).
bδ¹³CO₂ data from Elsig et al. (2009).
Figure 7. Impacts of global peatlands on the global carbon cycle during the Holocene. (A) NCB from global (northern, tropical, southern) peatlands (error bars showing the ranges of estimates), showing cumulative net C uptake of 272 GtC at 11–7 ka, 151 GtC at 7–4 ka and 116 GtC during the last 4 ka. (B) Atmospheric CO₂ concentration from EPICA Dome C in Antarctica (Flückiger et al., 2002; Monnin et al., 2001, 2004), showing the same three-phase pattern with 5 ppm decrease at 11–7 ka, a rapid increase of 13 ppm at 7–4 ka and slow increase of 7 ppm in the last 4 ka. (C) δ¹³CO₂ from EPICA Dome C in Antarctica (Elsig et al., 2009), showing an increase of 0.25‰ at 11–7 ka, a slight decrease at 7–4 ka, and a decrease of 0.05‰ over the last 4 ka. The straight lines for the three phases in CO₂ (B) or δ¹³CO₂ (C) were from linear regression only using data points in each of these three periods, and the rates of change were slopes of regression lines (with $r^2$ values).

Indermühle et al., 1999; Joos et al., 2004) and releases from anthropogenic terrestrial sources (Ruddiman, 2003, 2007). The net amount of C released from the land biosphere (natural or anthropogenic) is constrained by high-resolution δ¹³CO₂ data from atmospheric CO₂ from ice cores (Elsig et al., 2009), which show a slight decrease of 0.05‰ over the last 7 ka (Figure 7C). This small decrease in δ¹³CO₂ led Elsig et al. (2009) to conclude that the later Holocene CO₂ rise is most likely explained by contributions from ocean carbonate compensation and from coral reef formation, with only a minor contribution from land-biosphere C release.
Our peatland synthesis data and C flux reconstructions show that peatlands have taken up about 267 GtC (cumulative NCB) over the last 7 ka, a number that is significantly higher than the 40 GtC uptake estimated from the top-down approach based on ice-core data (Elsig et al., 2009). The 267 GtC of peat C ‘burial’ would alone cause a 19 ppm decrease in CO₂, about the same amplitude as the change observed in ice cores, but opposite in direction (Figure 7B). This large amount of ‘C burial’ in peatlands during the last 7 ka would need to be balanced by C release from other land biosphere sources, natural or anthropogenic, to meet the constraints from the small decrease in δ¹³CO₂ (Elsig et al., 2009). On the basis of this isotope-mass balance argument, Ruddiman et al. (2011, this issue) proposes that deforestation and almost flat δ¹³CO₂ during Phase II may represent the oceanic buffering response (carbonate compensation mechanism) to earlier C uptake by the land biosphere (mostly in peatlands). During Phase III, the land biosphere again became a dominant factor, along with reduced carbonate compensation and reef formation effects, in controlling CO₂ and δ¹³CO₂ with slower C uptake by peatlands balanced by increased C release from other biomes, including from anthropogenic deforestation.

(4) The approach used in this study has not only generated a first approximation of C flux histories of global peatlands in the Holocene but also provides a framework that can be used in the future for updating the C pool and flux estimates, with more comprehensive and representative data sets and improved process understanding.

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References


