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Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America

Dan J. Charman [a, *], Matthew J. Amesbury [a], William Hinchliffe [a], Paul D.M. Hughes [b], Gunnar Mallon [c], William H. Blake [d], Tim J. Daley [d], Angela V. Gallego-Sala [a], Dmitri Mauquoy [e]

[a] Geography, College of Life and Environmental Sciences, University of Exeter, Amory Building, Rennes Drive, Exeter, EX4 4RJ, UK
[b] Geography and Environment, University of Southampton, University Road, Highfield, Southampton, Hampshire, SO17 1BJ, UK
[c] Department of Geography, University of Sheffield, Sheffield, S10 2TN, UK
[d] School of Geography, Earth and Environmental Sciences, Plymouth University, Drake Circus, Plymouth, Devon, PL4 8AA, UK
[e] School of Geosciences, University of Aberdeen, St. Mary's Building, Elphinstone Road, Aberdeen, AB24 3UF, UK

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ABSTRACT

Peatlands are an important component of the Holocene global carbon (C) cycle and the rate of C sequestration and storage is driven by the balance between net primary productivity and decay. A number of studies now suggest that climate is a key driver of peatland C accumulation at large spatial scales and over long timescales, with warmer conditions associated with higher rates of C accumulation. However, other factors are also likely to play a significant role in determining local carbon accumulation rates and these may modify past, present and future peatland carbon sequestration. Here, we test the importance of climate as a driver of C accumulation, compared with hydrological change, fire, nitrogen content and vegetation type, from records of C accumulation at three sites in northeastern North America, across the N–S climate gradient of raised bog distribution. Radiocarbon age models, bulk density values and %C measurements from each site are used to construct C accumulation histories commencing between 11,200 and 8000 cal. years BP. The relationship between C accumulation and environmental variables (past water table depth, fire, peat forming vegetation and nitrogen content) is assessed with linear and multivariate regression analyses. Differences in long-term rates of carbon accumulation between sites support the contention that a warmer climate with longer growing seasons results in faster rates of long-term carbon accumulation. However, mid-late Holocene accumulation rates show divergent trends, decreasing in the north but rising in the south. We hypothesise that sites close to the moisture threshold for raised bog distribution increased their growth rate in response to a cooler climate with lower evapotranspiration in the late Holocene, but net primary productivity declined over the same period in northern areas causing a decrease in C accumulation. There was no clear relationship between C accumulation and hydrological change, vegetation, nitrogen content or fire, but early successional stages of peatland growth had faster rates of C accumulation even though temperatures were probably lower at the time. We conclude that climate is the most important driver of peatland accumulation rates over millennial timescales, but that successional vegetation change is a significant additional influence. Whilst the majority of northern peatlands are likely to increase C accumulation rates under future warmer climates, those at the southern limit of distribution may show reduced rates. However, early succession peatlands that develop under future warming at the northern limits of peatland distribution are likely to have high rates of C accumulation and will compensate for some of the losses elsewhere.

1. Introduction

Peatlands play a significant role in the global carbon cycle and may become either enhanced carbon sinks or sources under future

* Corresponding author.
E-mail address: d.j.charman@exeter.ac.uk (D.J. Charman).

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climate change. They store approximately one third of the global organic soil carbon pool (Gorham, 1991; Batjes, 1996) with 500 ± 100 Gt C stored in northern peatlands (Gorham et al., 2012; Yu, 2012). Despite this, peatland carbon accumulation is not currently represented in global climate models (Limpens et al., 2008) and there is uncertainty over the direction of any potential carbon cycle feedback under future climate scenarios (Bergeron et al., 2010; Frolking et al., 2011). Recent research suggests a small negative feedback from northern peatlands in response to enhanced net primary productivity (NPP; Charman et al., 2013), in contrast to the view that higher temperatures may enhance decay and lead to a positive feedback (Dorrepaal et al., 2009). Changes in Holocene peatland carbon accumulation also support the contention that temperature drives carbon accumulation rates at millennial timescales over northern peatlands as a whole (Yu et al., 2009, 2010; Loisel et al., 2014; Yu et al., 2014a) and at regional scales (e.g. Jones and Yu, 2010; Garneau et al., 2014; Zhao et al., 2014). On sub-millennial timescales, the Medieval Climate Anomaly and Little Ice Age also appear to have affected peatland carbon accumulation rates (e.g. Loisel and Garneau, 2010; Charman et al., 2013), although these higher frequency changes are not easily detectable due to dating resolution and the effect of incomplete decay in very recent peat deposits.

Higher temperatures may lead to greater NPP and enhanced peat accumulation. However, it is not simply annual average temperature which controls NPP, but growing season length (Lund et al., 2010), photosynthetically active radiation (PAR) and cloudiness (Loisel et al., 2012; Charman et al., 2013). In addition, the NPP of peatland plants can be affected and limited by a range of autogenic and allogenic factors including hydrological conditions, nutrient availability, fire and the mix of plant species present (e.g. van Bellen et al., 2011), all of which may affect future carbon accumulation.

Projections of 21st century precipitation are less certain than those for temperature (Bergeron et al., 2010), but increased precipitation is expected over large areas of the northern peatland domain (Kirtman et al., 2013). Consequent changes in hydrological conditions may lead to increased carbon accumulation when moisture stresses are a limiting factor, but where moisture conditions are adequate for plant growth and the suppression of decay, further increases in wetness are likely to be of secondary importance to temperature and PAR over the growing season (Bubier et al., 2003; Charman et al., 2013).

Nutrient availability can be a major limiting factor on plant NPP and decay. Nitrogen deposition rates have risen sharply during the last century and are likely to remain high in the near future due to industrial and agricultural activities (Bragazza et al., 2006). *Sphagnum* mosses are effective at utilizing available nutrients and restricting mineralization, limiting the ability of vascular plants to compete (Malmer and Wallen, 2004). However, high nitrogen deposition can remove nutrient limitations on the growth of vascular plants allowing them to successfully compete with *Sphagnum*, resulting in increased decay rates (Bragazza et al., 2006, 2012). Nitrogen content in peat reflects a combination of dominant source plant material, nutrient status and atmospheric nitrogen deposition.

Fire occurrence is projected to increase in boreal regions over the next century (Pitkänen et al., 1999; Bergeron et al., 2010). Frequent or more severe fire events could lead to a decline in carbon accumulation (Kuhry, 1994; Pitkänen et al., 1999; Wieder et al., 2009), though van Bellen et al. (2012) did not find a clear correlation between Holocene peatland fire regimes and carbon accumulation in Québec. Fire events can also affect carbon accumulation by providing the circumstances for vegetation change if different species rapidly colonise a site following a fire, replacing pre-existing species (Pitkänen et al., 1999).

Dominant plant types are largely determined by climate but major changes in vegetation type may produce significant changes in carbon accumulation rates (e.g. van Bellen et al., 2011; Loisel and Yu, 2013). However, potential differences in rates of peatland carbon accumulation driven by changes in species composition have received relatively little attention, excepting the broad consensus that there is likely to be a contrast between *Sphagnum* and vascular plants, with lower bulk density, lower C content and higher C:N ratios in *Sphagnum* peat (e.g. Loisel et al., 2014). More intensive research on the interactions between climate, local environmental change and species composition is needed (e.g. Hughes et al., 2013). If factors such as enhanced nitrogen deposition or changing hydrological conditions led to a competitive advantage for other vegetation types at the expense of *Sphagnum*, then future carbon accumulation rates could be significantly affected.

The interaction of environmental factors with changing climate will determine future peatland carbon accumulation rates and the strength of any peatland carbon source or sink. Determining the roles and relative strength of each of these variables remains an important research goal. Here, we investigate the relationship between peat carbon accumulation rates and climate, water table depth (WTD), nitrogen content, fire occurrence and plant species composition at three well-dated raised bogs in eastern North America, providing an assessment of the relative roles of autogenic and allogenic factors on rates of peatland carbon accumulation.

2. Study sites and methods

Cores were taken from three undisturbed lowland ombrotrophic bogs: Burnt Village Bog, Newfoundland (BVB); Petite Bog, Nova Scotia (PTB) and Sidney Bog, Maine (SYB) (Fig. 1, Table 1). These sites represent the extremes of raised bog distribution in eastern North America, from the southern limit in Maine to the northern limit in northern Newfoundland. Mean summer (JJA) temperatures range from 11.4 °C at BVB to 17.9 °C at SYB, whereas total summer precipitation is more consistent across sites with the highest value of 101 mm at SYB (Table 1).

Contiguous samples of known volume (4 cm^3) were extracted from the cores at 2 cm resolution, freeze-dried and re-weighed to enable calculation of bulk density. Percentage carbon and nitrogen content by mass were measured on homogeneous ground and weighed sub-samples of 4–5 mg. Repeat measurements were taken for some bulk density ($n = 117$) and C/N ($n = 122$) samples and the difference between them used to provide an observational error interval within which 95% of samples fell. Age-depth models for all cores (Fig. 2) were constructed using the R package BACON (Blaauw and Christen, 2011), with approximately 30 radiocarbon dates per site (Supplementary Table 1). Hand-picked and cleaned *Sphagnum* stems and leaves were dated wherever possible, with other samples consisting of above-ground ericaceous or monocotyledon plant remains. In addition, recent peat accumulation was modelled using short-lived radioisotopes ^{210}Pb and ^{137}Cs (Supplementary Table 2), using gamma spectrometry and a constant rate of supply (CRS) model (Appleby and Oldfield, 1978). Ages from the CRS models were also included in the BACON age-depth modelling. Carbon accumulation histories for each site were constructed using the weighted mean dates from each model based on millions of iterations, with >1000 iterations remaining in the final models in each case.

Testate amoeba-based reconstructed depth to water table profiles were produced at 4 cm resolution using the regional transfer function of Amesbury et al. (2013). Estimates of vegetation species composition and fire histories were produced for the same depths using standard techniques (Barber et al., 1994). Only a subset of these data was used here; plant macrofossils were grouped into

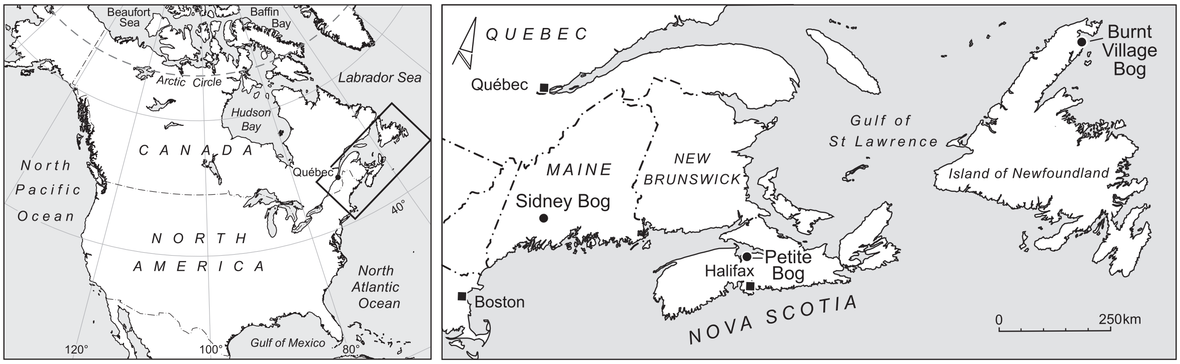

Fig. 1. Site location map.

Table 1

Site data. Total core depth includes non-peat basal sediments. Basal age is the weighted mean age from the output of the BACON age-depth model, rounded to the nearest 10 years with depth of the dated sample in cm in parentheses. Climate data is extracted from the relevant 0.5 × 0.5° grid cell of the CLIMATE 2.2 dataset (Kaplan et al., 2003). PAR0, GDD0 and the P/Eq moisture index are calculated *sensu* Charman et al. (2013).

Site name	Location	Latitude (°N)	Longitude (°W)	Elevation (m)	Total core depth (cm)	Number of ^{14}C dates	Peat basal age (cal. years BP)	Mean JJA temp (°C)	JJA precip. (mm)	PAR0	GDD0	P/Eq moisture index
Burnt Village Bog	Newfoundland, Canada	51° 7.562	55° 55.645	28	575	26	8240 (545)	11.4	90	5370	1602	2.63
Petite Bog	Nova Scotia, Canada	45° 8.659	63° 56.219	50	868	32	11,280 (856)	17.2	93	7369	2880	2.04
Sidney Bog	Maine, USA	44° 23.274	69° 47.260	24	750	31	9540 (725)	17.9	101	8079	2956	1.68

major peatland vegetation types; Ericaceae, monocotyledons and bryophytes (almost entirely *Sphagnum*) to estimate percentage abundances for each vegetation component. Percentage occurrence of charred remains at SYB and charred remains and charcoal at PTB were used to estimate relative changes in fire, but no equivalent data were available for BVB.

The pollen-based record of North American July temperature anomalies of Viau et al. (2006) was used to provide a regional climate record. The continental scale of this record means it will not necessarily reflect local temperature changes, but it does permit comparison between major changes in temperature and carbon accumulation over millennial timescales. It is more robust than individual local records, although in practice the long terms trends are very similar (e.g. Muller et al., 2003; Hausmann *et al.*, 2011). As a record of summer temperature it is likely to be correlated with growing season length but does not reflect changes in PAR, which has recently been suggested to be an important climatic driver determining peatland carbon accumulation (Loisel et al., 2012; Charman et al., 2013). A further assessment of climate effects on accumulation was made by comparing the differences between sites in relation to their different climatic settings (Table 1).

Linear regression analyses of the relationships between carbon accumulation and site-specific palaeoenvironmental data were carried out on individual sample intervals to test the relative importance of each variable in determining carbon accumulation. To ensure a statistically robust approach, we then used R (R Development Core Team, 2011) to build multivariate linear models using stepwise regression (using the Akaike Information Criterion to choose the most parsimonious model) for the dataset as a whole and by site, for both individual sample intervals and over 500 year averages. Two sample, two tailed t-tests were carried out using the carbon accumulation data corresponding to the extreme quartiles for each variable to further test the relationship between different environmental extremes and carbon accumulation rates.

3. Results

3.1. Carbon accumulation at individual sites

Bulk density and carbon content varied moderately between the sites (Figs. 3–5 A and B). BVB had the highest average bulk density (0.14 g cm^{-3}, SD = 0.297) but the lowest mean carbon content (45.97%, SD = 9.17). SYB had the highest mean carbon content (48.96%, SD = 8.3) and mean bulk density of 0.12 g cm^{-3} (SD = 0.146). PTB had a similar mean carbon content (48.76%, SD = 1.92) but a distinctly lower mean bulk density (0.065 g cm^{-3}, SD = 0.019). Carbon accumulation rates vary down core but are within the range generally observed in northern peatlands (e.g. Loisel et al., 2014, Figs. 3 and 4E). Average carbon accumulation rate over the entire profile was highest at SYB (45 ± 3.2 g cm^{-2} yr^{-1} (95% confidence interval)), followed by PTB (31 ± 1.5 g cm^{-2} yr^{-1}) and BVB (28.5 ± 1.6 g cm^{-2} yr^{-1}), generally higher than the mean for northern peatlands of 22.9 g cm^{-2} yr^{-1} (Loisel et al., 2014).

To summarise longer-term patterns of carbon accumulation we summed 500 year periods for each site (Fig. 6). At SYB, carbon accumulation peaked in the early Holocene around 9000 cal. BP then declined gradually until around 5000 cal. BP. Since then, carbon accumulation has gradually increased with notable peaks around 3700 cal. BP, 2500 cal. BP, 750 cal. BP and over the past 200 years (Fig. 5E). At PTB, peat formation began over 11,000 cal years BP. There was an early Holocene peak in carbon accumulation around 10,000–9000 cal. BP before it declined to a minimum around 8000 cal. BP. Carbon accumulation recovered to higher values after approximately 6000 cal. BP with a long-term peak at around 3000 cal. BP, before declining again to a new minimum around 2000 cal. BP. Higher carbon accumulation over the past 1500 years included prominent peaks around 1400 cal. BP and 600 cal. BP. There has been a local increase in carbon accumulation over the past century (Fig. 4E). At BVB, long-term carbon accumulation also peaked in the early stages of development around 8000 to 7000 cal. BP, followed by a steady decline until around 3000 cal.

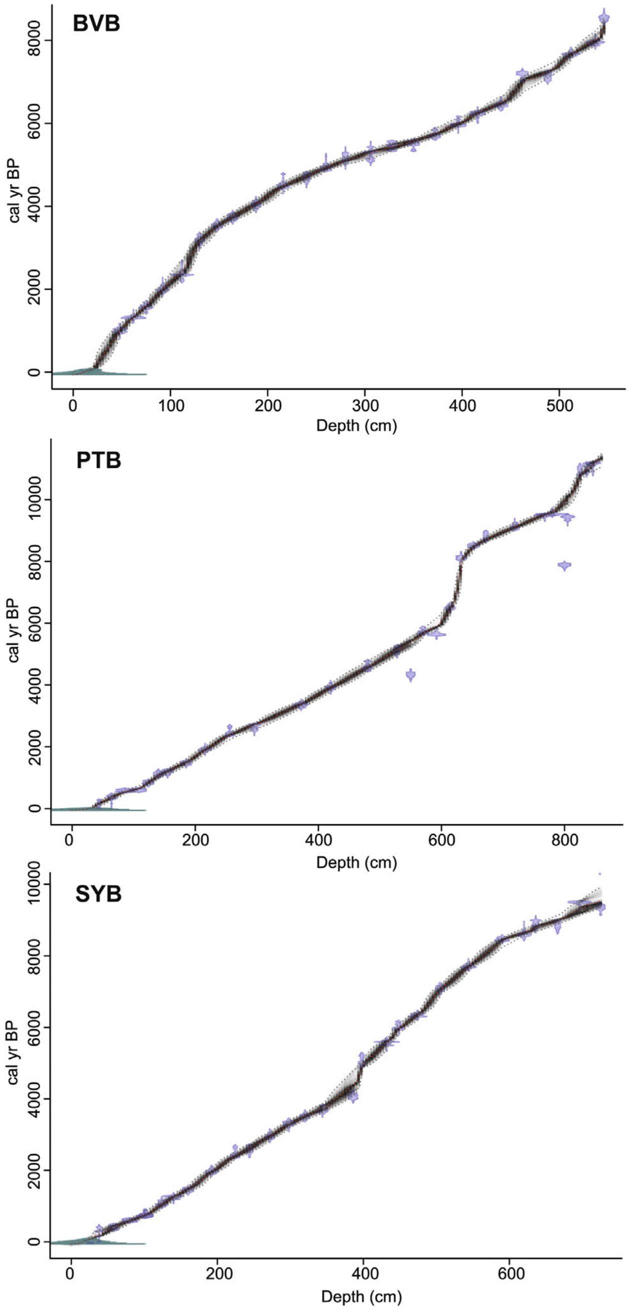

Fig. 2. Age-depth models for all sites, constructed using the R package, Bacon. See Section 2 for further details. L–R: Burnt Village Bog, Newfoundland; Petite Bog, Nova Scotia; Sidney Bog, Maine.

BP. Since then carbon accumulation has recovered somewhat with an increase over the last century, but this does not reach the values recorded in the first half of the Holocene (Fig. 3E).

To examine long-term total carbon accumulation across the spatial climate gradient, we calculated total carbon accumulation for the past 2000, 4000, 6000 and 8000 years, the time intervals for which data were available at all the sites (Table 2). Results show that SYB is the largest carbon store over the past 8000 years with a total of 296.9 kg cm^{-2}, compared to 188.6 and 192 kg cm^{-2} for PTB and BVB respectively. However, there is a much more consistent north – south gradient evident for the last 4000 years, such that SYB > PTB > BVB for this whole period and for both sub periods, with more than three times the C accumulation at SYB than BVB over the last 2000 years. The total 8000 year C accumulation at PTB is significantly reduced by the very slow accumulation in the period 8000–6000 cal. BP, and BVB accumulated as fast or faster than the more southern sites between 8000 and 4000 cal years BP, but more slowly in the last 4000 years.

3.2. Carbon accumulation and Holocene temperature change

There are no clear and consistent relationships between the temperature reconstruction of Viau et al. (2006) and C accumulation at all three sites (Table 3), though significant weak negative correlations are observed with C accumulation at BVB and SYB. However, at all sites there were significant ($p < 0.05$) differences between C accumulation values corresponding to the extreme quartiles of the temperature reconstruction, with lower C accumulation corresponding to the higher temperature quartile (Table 4). The highest rates of C accumulation are observed in the early Holocene at SYB and PTB, before the Holocene Thermal Maximum. The rates at both these sites decline rapidly after 9000 cal yr BP, before rising again after 6500 cal yr BP (PTB) and 5000 cal yr BP (SYB). Meanwhile, BVB shows rapid initial accumulation from 8000 cal yr BP, followed by a gradual decline over the mid Holocene. The long-term trends are divergent for the mid-late Holocene since around 5000 cal yr BP, when temperature declined steadily. There is a downward trend in accumulation at BVB and an upward trend in SYB over this period, perhaps reflecting a differential regional response at these sites at opposite ends of the spatial climate gradient.

3.3. Carbon accumulation and environmental variables

Summary proxy data are shown in Figs. 3–5, shown as reconstructed depth to water table and relative proportions of major plant macrofossil groups. The discussion below focuses on the relationship between these variables and carbon accumulation (Tables 3 and 4).

3.3.1. Water table depth

There was a weak but significant positive correlations between WTD and C accumulation at SYB (Table 3), suggesting faster C accumulation during drier than wetter periods. At all sites, there were no significant differences between C accumulation values associated with the upper and lower quartiles of WTD values (Table 4).

3.3.2. Nitrogen

There was a weak but significant positive correlation between % N and C accumulation at BVB, but no statistically significant relationships at other sites (Table 3). Furthermore, at BVB and SYB, C accumulation rates associated with the extreme quartiles of %N values were significantly different (at BVB $p < 0.001$; at SYB $p = 0.04$, Table 4). However, short-term changes often appear to suggest contradictory relationships. At BVB an increase in carbon accumulation rates at *ca.* 3000 cal. BP occurs synchronously with increasing nitrogen levels (Fig. 3) whereas at PTB a period of low C accumulation from *ca.* 8000–6000 cal. BP saw a rise in nitrogen levels (Fig. 4).

3.3.3. Fire

There was a weak positive but significant correlation between charred remains and C accumulation per year at PTB (Table 3). A two-tailed, two-sample t-test of C accumulation values corresponding to the extreme quartiles for charred remains at SYB was not significant (Table 4). However, due to the nature of the charred remains and charcoal records at PTB, which were dominated by

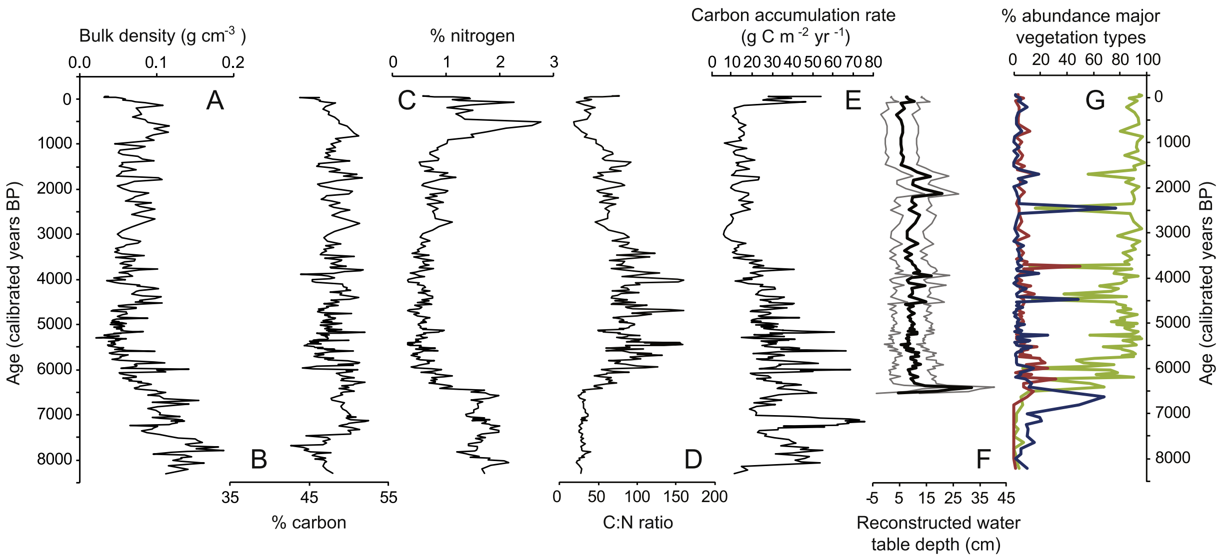

Fig. 3. Physical properties and proxy data for Burnt Village Bog, Newfoundland. L–R: Bulk density; %C; %N; C:N ratio; C accumulation rate per year; testate-amoeba reconstructed depth to water table; summary plant macrofossil composition (red = Ericaceae, blue = monocots, green = bryophytes). See Section 2 for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

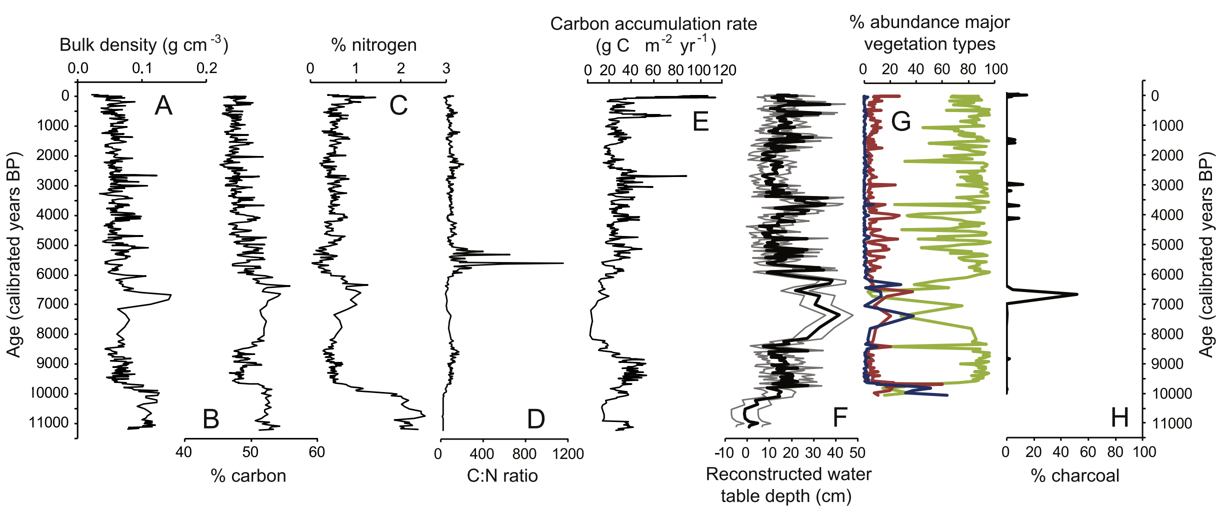

Fig. 4. Physical properties and proxy data for Petite Bog, Nova Scotia. L–R: Bulk density; %C; %N; C:N ratio; C accumulation rate per year; testate-amoeba reconstructed depth to water table; summary plant macrofossil composition (red = Ericaceae, blue = monocots, green = bryophytes); % charcoal. See Section 2 for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

zero values with infrequent peaks of fire activity (an average of only 6% of samples had an occurrence of charred remains/charcoal, Fig. 4), upper and lower quartiles both calculated as 0 and so t-tests were not carried out on these data.

3.3.4. Vegetation type

There were statistically significant correlations between C accumulation and vegetation type at BVB and PTB. At BVB, bryophyte cover was significantly negatively correlated with C accumulation ($r = -0.473$, $p = 0.001$) and at PTB, there was a weak but significant positive correlation between Ericaceae and C accumulation ($r = 0.141$, $p = 0.041$). Both of these relationships were supported by two-sample, two-tailed t-tests of C accumulation values for the upper and lower quartiles of vegetation cover (Table 4). At BVB, low bryophyte cover was associated with significantly higher accumulation rates (mean 38.6 g cm^{-2} yr^{-1}) than high bryophyte cover (mean 21.6 g cm^{-2} yr^{-1}, $p < 0.001$). This effect is likely related to the switch from fen to bog vegetation that occurred around 6500 cal. BP (Fig. 3), with higher C accumulation rates occurring in the first 1500 years of the BVB record (Fig. 6). At PTB, low Ericaceae cover was associated with significantly lower C accumulation rates (mean 27.8 g cm^{-2} yr^{-1}) than high Ericaceae cover (mean 35.4 g cm^{-2} yr^{-1}, $p = 0.01$). In addition, there was a significant difference between C accumulation rates associated with the extreme quartiles of monocot cover at BVB (Table 4), but this was not supported by a significant correlation between the two time series (Table 3).

3.3.5. Multivariate modelling

The often weak and sometimes contradictory relationships between individual variables and C accumulation suggest that there is no single over-riding environmental factor that is driving peat accumulation at the sites throughout the Holocene. The relationships are therefore presumably multivariate or not captured by the

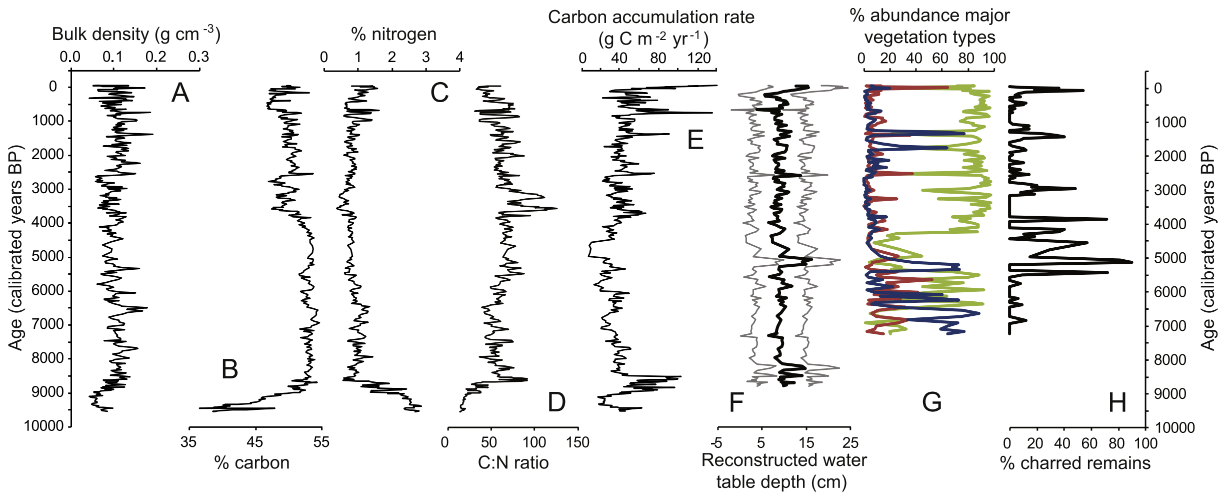

Fig. 5. Physical properties and proxy data for Sidney Bog, Maine. L–R: Bulk density; %C; %N; C:N ratio; C accumulation rate per year; testate-amoeba reconstructed depth to water table; summary plant macrofossil composition (red = Ericaceae, blue = monocots, green = bryophytes); % charred remains. See Section 2 for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

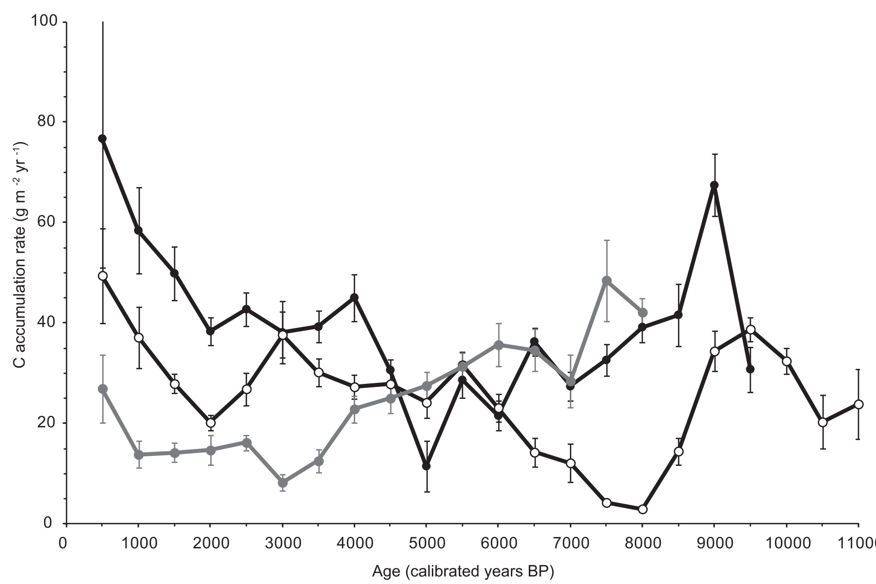

Fig. 6. Long-term carbon accumulation rates (500 year mean values) for all three sites with ±95% confidence intervals. Grey line = Burnt Village Bog, Newfoundland; Black line with open circles = Petite Bog, Nova Scotia; black line with closed circles = Sidney Bog, Maine.

data collected. Multivariate modelling was therefore carried out on the carbon accumulation data for individual sites and for all site data combined. In addition, broad scale patterns of C accumulation were explored with the same approach to data binned in 500 year intervals (Table 5). The variation in carbon accumulation per year across all sites was best described by a linear model that combined the variables Ericaceae ($p = 0.0001$), temperature ($p = 0.0004$), bryophytes ($p = 0.007$) and %N ($p = 0.08$), but which had an adjusted R^2 of only 0.14 ($p < 0.001$). When the data were subdivided by site, only %N emerged as an explanatory variable at all sites, but was often non-significant (Table 5). The variation in 500 year averaged C accumulation was best described by a linear model with an adjusted R^2 of 0.18 ($p = 0.005$) that combined the variables of water table depth ($p < 0.001$), Ericaceae ($p = 0.05$) and %N ($p = 0.06$). When the 500 year averaged data was divided by site, bryophyte cover and water table depth were explanatory variables

Table 2
Total carbon accumulation (Kg cm^{-2}) for all three sites for 2000 year intervals and cumulative C over the past 8000 years.

	Burnt Village bog		Petite bog		Sidney bog	
	Cumulative	2000 yr Interval	Cumulative	2000 yr Interval	Cumulative	2000 yr Interval
Past 2000 years	31.1	31.1	58.6	58.6	103.6	103.6
Past 4000 years	60.3	29.1	118.7	60.2	184.9	81.3
Past 6000 years	120.3	60.1	171.7	53	229.8	44.9
Past 8000 years	192	71.7	188.6	16.8	296.9	67.2

Table 3
Correlation coefficients (r values) between carbon accumulation per year and climate/environmental variables for all sites. All p values <0.1 are shown in parentheses, with significant relationships with p values (<0.05) also shown in bold.

Site name	North American summer temperature	Reconstructed water table	% N	Bryophytes	Ericaceae	Monocots	Charred remains	Charcoal
Burnt Village Bog	**−0.225 (0.009)**	0.128	**0.276 (0.001)**	**−0.473 (0.001)**	0.007	0.153 (0.075)	–	–
Petite Bog	−0.056	−0.027	−0.021	0.100	**0.141 (0.041)**	−0.122 (0.076)	**0.178 (0.009)**	0.040
Sidney Bog	**−0.177 (0.019)**	**0.170 (0.032)**	0.011	0.098	0.020	−0.083	−0.097	–

Table 4
Low (L) and high (H) mean carbon accumulation rates (g cm^{-2} yr^{-1}) associated with the extreme quartiles of climate/environmental variables. All significant p values <0.05 from two-tailed, two-sample t-tests assuming homoscedasticity are shown in parentheses are shown in bold. No test for charred remains and charcoal values was possible at PTB, due to a high proportion of zero values.

Site name	North American summer temperature	Reconstructed water table	% N	Bryophytes	Ericaceae	Monocots	Charred remains	Charcoal
Burnt Village Bog	**L 31.7, H 24.6 (0.02)**	L 21.8, H 26.3	**L 26.3, H 36.9 (<0.001)**	**L 38.6, H 21.6 (<0.001)**	L 35.9, H 30.7	**L 24.3, H 35.4 (0.001)**	–	–
Petite Bog	**L 32.2, H 28.1 (0.04)**	L 27, H 27.8	L 28.9, H 30.4	L 28.1, H 28.7	**L 27.8, H 35.4 (0.01)**	L 33.2, H 29.2	–	–
Sidney Bog	**L 47.8, H 37 (0.007)**	L 44.6, H 58.7	**L 42.2, H 51.1 (0.04)**	L 38.8, H 42.3	L 42.2, H 50.3	L 40, H 38.8	L 45.9, H 37.7	–

for all sites, although inter-site differences existed for all models and the direction of the relationships with significant variables also differed between sites (Table 5).

4. Discussion

Determining the relationship between climate variability and carbon accumulation is a key problem in understanding the Holocene terrestrial carbon cycle and in predicting changes in northern peatland carbon sequestration and storage under future climate scenarios. Whilst a number of models suggest decreased accumulation rates due to increased decay rates driven by rising temperatures (Ise et al. 2008; Dorrepaal et al. 2009), empirical data on centennial–millennial scale peatland carbon accumulation now suggest that periods of warmer climate generally led to higher rates of carbon accumulation, presumably due to higher NPP more than compensating for increased decay (Yu, 2012). This appears to be the case for northern peatlands at a broad geographical scale in response to precession-driven multi-millennial climate change during the Holocene (Yu et al., 2010; Loisel et al., 2014) and also over shorter sub-millennial periods such as the Medieval Climate Anomaly to Little Ice Age transition in the last millennium (Charman et al., 2013). It is also likely that the most important influence of temperature is through mean summer and maximum summer temperature and growing season length, rather than through annual average temperature, because during the months when temperatures are below zero, both productivity and decay are likely to be negligible compared to the main growing season. Furthermore, relationships with broad temperature trends probably incorporate and are modified by other climate variables, particularly PAR as a key driver of NPP (Loisel et al., 2012; Charman et al., 2013). The data presented here provide two tests of the temperature-peat accumulation hypotheses via; 1) spatial comparisons of total accumulated carbon, and 2) temporal trends in C

Table 5
Summary of results from multivariate linear modelling of relationships between carbon accumulation and environmental variables for all sites combined and for individual sites.

Carbon accumulation per year					Carbon accumulation 500 year averages				
	Adj. R^2	F	p	t		Adj. R^2	F	p	t
All sites combined	0.14	16.37	<0.001		**All sites combined**	0.18	4.76	0.005	
Ericaceae			0.0001	3.88	WTD			< 0.001	−3.61
Viau temperature			0.0004	−3.51	Ericaceae			0.05	1.99
Bryophytes			0.007	2.68	%N			0.06	−1.91
%N			0.08	9.88	**Burnt Village Bog**	0.74	7.9	0.009	
Burnt Village Bog	0.24	6.922	<0.001		Bryophytes			0.002	−4.85
Bryophytes			0.003	−3.01	WTD			0.006	−3.83
Monocots			0.034	−2.15	%N			0.04	−2.59
%N			0.11	−1.59	Ericaceae			0.04	−2.46
WTD			0.12	1.56	Monocots			0.05	2.39
Petite Bog	0.05	2.686	0.016		**Petite Bog**	0.48	7.48	0.002	
Viau temperature			0.01	−2.42	WTD			0.001	−3.77
Monocots			0.02	−2.27	Bryophytes			0.005	3.24
%N			0.16	1.381	Ericaceae			0.116	1.65
WTD			0.33	−0.97	**Sidney Bog**	0.45	5.44	0.01	
Sidney Bog	0.12	4.283	<0.001		Bryophytes			0.001	3.92
Bryophytes			0.002	3.23	Monocots			0.008	3.13
%N			0.03	2.19	WTD			0.17	1.44
Ericaceae			0.09	1.71					
Viau temperature			0.12	−1.54					

accumulation associated with precession-driven multi-millennial temperature changes.

4.1. Spatial patterns of accumulated carbon

The total carbon accumulated over the last 8000 years for the sites is only partly consistent with the hypothesis that higher temperatures lead to higher carbon accumulation rates (Table 2). Climate data show that summer temperatures are around 6 °C lower at BVB compared to PTB and SYB and that GDD0 and PAR0 are 30–40 % lower (Table 1). This climate gradient is associated with a general increase in carbon accumulation rates from north to south (Table 2). This broad relationship is similar to spatial patterns that have been found for regions such as western Siberia (Beilman et al., 2009) and for northern peatlands in their entirety (Charman et al., 2013) for total carbon accumulated over the last 1000–2000 years. However, comparing 2000 year intervals (Table 2), shows that this spatial relationship holds true for only the last 4000 years, breaking down for the intervals 6000–4000 and 8000–6000 years ago. Over the whole 8000 year period, the northernmost site at Burnt Village Bog in Newfoundland accumulated only 65% of the southernmost site Sidney Bog in Maine, but a similar amount to Petite Bog (BVB = 193.2 kg cm^{-2}, PTB = 188.6 kg cm^{-2}). However, total C accumulation at PTB is limited by extremely slow rates from 8000 to 6000 cal. BP when BVB was experiencing its highest rates. These results suggest either a different spatial pattern in climate or other more dominant drivers of peat accumulation rates for these earlier periods, which we explore below.

Accumulation rates are high for all sites during their earliest stages of development (Figs. 3–6). These periods are also characterised by high %N (Figs. 3–5C) and peat dominated by vascular plants, usually sedges, indicating these are the minerotrophic phases before the formation of the *Sphagnum* dominated raised bog peat (Figs. 3–5). The fen phase as indicated by the vegetation composition and %N finishes at different times, apparently unrelated to climatic setting; *ca.* 6500 cal. BP at BVB, *ca.* 8500 cal. BP at SYB and *ca.* 9500 cal. BP at PTB. These early phases of high C accumulation occur before the main Holocene Thermal Maximum and therefore they appear to be locally controlled, probably driven by topographically and hydrologically determined rates of peat initiation and groundwater influence. The generally high rate of accumulation in vascular plant peats during the colder climate conditions of the early Holocene suggests that NPP was relatively high and decay rates were low, perhaps also related to the stronger seasonality in climate associated with the precessional difference in orbital forcing. Some later periods also show enhanced N levels but these are not associated with clear changes in C accumulation rates or vegetation composition changes. For example, the record of the last 1000 years at BVB (Fig. 3) suggests that changes of up to +2 %N induced no significant change in longer-term vegetation or carbon accumulation rates. This is in contrast to short-term nutrient addition studies (e.g. Bragazza et al., 2012) where higher carbon uptake was associated with N addition, albeit at higher rates of addition. Turunen et al. (2004) also report that anthropogenically enhanced atmospheric N supply is associated with higher recent C accumulation in eastern North America but we see no clear evidence of this recent effect in our cores.

Later periods with relatively high nitrogen content also occur at PTB during a period of very low carbon accumulation *ca.* 8000–6500 cal. BP and over the last 1000 years at BVB and to a lesser extent at SYB. The period of very low C accumulation at PTB is associated with a dry bog surface and fire, as indicated by a major charcoal peak at this time (Fig. 4). The higher %N values are probably a result of fire and mineralisation yielding higher N availability and the dominance of vascular plants. Whilst very large fire events may have had a significant influence on peat accumulation, van Bellen et al. (2012) have suggested that there is rather little correspondence between long-term fire frequency and C accumulation rates in northern peatlands in Québec. However, there is considerable variability between studies; for example Pitkänen et al. (1999) found that charcoal abundance was associated with an overall decrease in carbon accumulation in Finnish mires.

The spatial patterns of total peat accumulation therefore support the hypothesis of a positive relationship between temperature and related variables, and peat growth, but also show that this only holds true for the ombrotrophic phases of peatland development. In earlier peatland development, local influences on peatland geochemistry, hydrology and vegetation modify the spatial relationships with climate, assuming the spatial climate relationships between sites remained similar over time.

4.2. Carbon accumulation trends over the Holocene

Peat accumulation is expected to be higher during the mid-Holocene Thermal Maximum than during the later Holocene as precession-forced cooling occurred, as suggested by overall patterns of northern peatlands over larger spatial scales (Yu et al., 2010; Loisel et al., 2014). However, only BVB shows this long-term trend more typical of northern hemisphere peatlands. SYB shows an increasing trend in C accumulation through the late Holocene and PTB also shows a generally increasing but more gradual trend, albeit with some short-term variability (Fig. 6). We attribute this difference to different initial climate states for the sites.

SYB is at the southern limit of raised peatland development today, which is determined by moisture balance (Davis and Anderson, 2001). During the Holocene Thermal Maximum, it would have been even warmer than it is today and thus probably sub-optimal for peat growth in southern Maine. Cooler temperatures during the later Holocene may therefore have improved the potential for a positive water balance and pushed this region further away from a limiting moisture threshold, especially if there was also increased precipitation. The moisture index (MI) for the site today is 1.68 (Table 1), only just above the threshold for peat growth found for 90 northern hemisphere sites (Charman et al., 2013). PTB is further away from the geographical limit of modern peatland distribution in eastern North America, but the climate data suggest it is still very close to this moisture threshold (MI = 2.04). BVB is well within the moisture limit for peat growth (MI = 2.63) and even with higher evapotranspiration, is unlikely to have been at a growth limit in the mid-Holocene, such that a higher temperature and longer growth season had a positive effect on peat accumulation. The contrasting long-term trends in C accumulation can thus be explained by these differing initial climate states, particularly in relation to moisture status as a limiting variable.

Linear regressions and multivariate modelling of the relationships between carbon accumulation and environmental variables did not reveal any consistent, significant correlations. Early phases of peat accumulation appear to have been influenced by local environmental factors to a much greater extent, especially during fen peat development and early stage succession (Holmquist and Macdonald, 2014). There is also evidence that at particular sites, over particular time periods, such as at PTB from 8000 to 6000 cal. BP, autogenic factors may have been an important driver of carbon accumulation rates. However, the overall conclusion from spatial and temporal comparisons between peat accumulation, climatic and palaeoenvironmental data is that some of the largest differences in C accumulation can be explained by climate, especially during the mid-late Holocene.

4.3. Implications for future peatland carbon accumulation

Future climate change will lead to a shift of bioclimate zones suitable for peat formation (Gallego-Sala et al., 2010; Gallego-Sala and Prentice, 2012). Some areas that are currently suitable for peat growth will be too warm and/or dry for continued peat growth in mid northern latitudes, perhaps including peatlands in the southern part of eastern North America. However, many areas of northern peatlands will remain within a bioclimate zone suitable for continued growth, especially given the likelihood of increased warm season precipitation alongside increased temperature that would extend the growing season (Kirtman et al., 2013). The data presented here largely support the hypothesis that warmer climates with longer growing seasons support faster peat C accumulation (Yu, 2012; Charman et al., 2013). We would therefore expect that under a future warmer climate, the majority of northern peatlands will increase C accumulation rates, unless critically low moisture limits are reached. It is notable that the long-term, broad-scale spatial and temporal differences in C accumulation appear to be largely independent of differences in other environmental variables such as vegetation, hydrology and perhaps fire. This is in contrast to suggestions from modelling (Ise et al. 2008; Dorrepaal et al., 2009) and short-term experiments (e.g. Bragazza et al., 2012) that suggest significant implications for future peatland C balance from changes in decay rates, N deposition and other factors.

For areas that are currently at the southern or northern limit of peat growth, response to future climate change may be more variable. In northern areas, longer growing seasons, higher summer temperatures and increased summer precipitation may result in initiation of new peatlands. Our data suggest that the early successional stages accumulate relatively rapidly, so these peatlands may sequester significant amounts of carbon. This is supported by data from peatlands dominated by sedge communities throughout the Holocene (Yu et al., 2014b), and the shifts between ombrotrophic and minerotrophic systems also have important implications for methane emissions (Packalen and Finkelstein, 2014). For peatlands at the modern southern limit of peatland occurrence, warmer temperatures and the potential for reduced summer precipitation are likely to push peatlands below the moisture threshold where they can benefit from increased growing season length, such that peat accumulation rates will decrease or cease, with the potential for a negative C balance. The lower mid-Holocene accumulation rates of the two southernmost sites (SYB in Maine and PTB in Nova Scotia) suggest that reduced accumulation rates have occurred in the past when temperatures were only slightly higher than present north of 30° N (Marcott et al., 2013).

Past changes are only a guide to the longer term future of northern peatlands and the range of climate and environmental conditions they have been exposed to in the past may be too limited for projection by analogy. However, the growing body of palaeoenvironmental literature suggests that the peatland-climate link warrants further consideration of long-term response to climate and the interaction with successional change.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2015.05.012.

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