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

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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.

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1. Introduction

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

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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 submillennial 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

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