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Autogenic and allogenic controls on carbon dynamics in peatlands from Alaska and Patagonia

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Autogenic and allogenic controls on carbon dynamics in peatlands from Alaska and Patagonia

by

Julie Loisel

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ABSTRACT

In peatlands, both internal dynamics and external forcing drive changes in hydrological conditions and vegetation communities, which affect short- and long-term peat accumulation processes and associated carbon sequestration. Understanding the spatial and temporal dynamics of these autogenic and allogenic controls is of critical importance for documenting peatland development and assessing the peatland carbon-sink function, especially because climatically-induced changes in peatland hydrology and vegetation are likely to have considerable effects on peat-carbon fluxes. In my dissertation, I present a range of evidence from Alaska and Patagonia demonstrating that peatland-carbon dynamics are controlled by hierarchical interactions between regional climate dynamics, landscape morphology, and spatially-explicit local community structures.

PREFACE

Peatlands are wetland ecosystems that are primarily distributed across the high-latitude regions of the world. They cover about 3% of the global land area, and represent at least half of the world's wetlands. In these ecosystems, plant net primary production exceeds peat decomposition, resulting in the accumulation of carbon-rich peat deposits. Since the last deglaciation, peatlands have accumulated over 600 gigatons of organic carbon globally, which constitutes up to about a third of the global soil organic carbon. Peat-core syntheses and modern flux measurements have shown that net peatland carbon balance fluctuates over millennial, centennial, inter-annual, and seasonal timescales. These fluctuations are caused by differences in the balance between plant production and peat decomposition, with time periods dominated by net input from plant production (carbon uptake), and periods dominated by net release from decomposition of dead material and subsequent carbon dioxide (CO_2) and methane (CH_4) emissions to the atmosphere (carbon release). The long-term mean state of climate and short-term weather events are often responsible for shifting the peatland carbon balance, although disturbances (fires, permafrost, land-use change), landscape morphology (slope, topography), and self-regulation mechanisms (peat growth, vegetation succession) can also contribute to these changes.

A key uncertainty for assessing the peatland response to ongoing and projected climatic changes is whether warming-induced increases in carbon release, including CO_2 and CH_4, will be balanced by a corresponding increase in net primary production and subsequent long-term carbon sequestration. This challenging question remains a matter of considerable debate, however, mostly because of our incomplete understanding of fundamental peatland processes. Indeed, peatland dynamics entail a multitude of complex ecohydrological processes that occur at various temporal and spatial scales that are not well documented or understood, hindering our ability to adequately model and predict peatland-carbon-climate interactions in a warmer world.

This doctoral work aims at better understanding the effects of climate (temperature, precipitation and temperature seasonality) and landscape morphology on short- and long-term peat accumulation processes using peat-core data, modeling, and data syntheses. I address the following two outstanding challenges in this dissertation.

(1) Climate-sensitive processes such as species-specific plant production and short-term peat decay largely determine the amount of carbon that will eventually contribute to the long-term peat-carbon store. To assess the impact of global warming on the structure and function of northern peatlands, it is therefore important to document the climate sensitivity of these short-term carbon flux terms. However, decadal- to centennial-scale peat production and decomposition rates have rarely been quantified in the scientific literature. Central to this challenge is the difficulty in integrating processes that operate over very different timescales, including modern primary production, multi-decadal peat decomposition processes, and long-term peat-carbon storage. In Chapter 1, a new modeling approach is proposed to compare short- and long-term peat accumulation rates. In Chapter 2, a global data set of *Sphagnum* (peat moss) growth measurements that encompasses a wide range of climatic conditions is used to determine the role of temperature and moisture on *Sphagnum* net primary production. In Chapter 4, Holocene peat-carbon dynamics in Patagonian peatlands are analyzed on the basis of new peat-core

analysis and a data synthesis of existing records to link peatland dynamics and climatic regimes beyond the northern peatland climate domain.

(2) Over the past decade, multiple large-scale datasets have been used to document spatial patterns of peatland initiation as well as long-term peat accumulation rates. However, the rate, pattern, and timing of lateral expansion across the northern landscape remain largely unknown. As peatland lateral extent is a key boundary condition constraining the dynamics of peatland systems, large-scale estimates of peatland area change over time are in critical need of refinement. Central to this challenge is the current lack of general rules or threshold values describing the relationship between basin slope, topography, and lateral expansion rate. In Chapter 3, a conceptual model where landscape morphology (slope, basin shape) exerts a deterministic control on peatland lateral expansion rate is proposed. On the basis of near-surface geophysical data, peat-core analysis and a data synthesis, this study also shows a power-law relationship between lateral expansion and slope as well as a threshold value above which peatland expansion becomes slope-limited.

CHAPTER 1

Recent acceleration of carbon accumulation in a boreal peatland, south-central Alaska

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Abstract

The ongoing warming in high-latitude regions may be causing rapid changes in the structure and functioning of terrestrial ecosystems. Of particular concern is the fate of belowground soil organic matter stored in peat-accumulating wetlands, as these large carbon pools are sensitive to temperature and moisture conditions. Despite their important role in the global carbon cycle, considerable uncertainty remains over the carbon balance of northern peatlands in a changing climate. We examined the response of vegetation and carbon dynamics in a wet boreal peatland to recent climate warming using empirical peat-core data and a new modeling approach. We observed a widespread shift from herbaceous *Carex* fen peat to *Sphagnum* moss peat around 100 years ago that was accompanied by a sharp increase in peat accumulation rate. The observed apparent carbon accumulation rates over the past 100 years (96.8 g C $m^{-2}yr^{-1}$) were almost ten times greater than those over the past 4000 years (11.5 g C $m^{-2}yr^{-1}$). Once differential decomposition history was considered using three modeling approaches, the expected long-term accumulation rate of recent peat was still three to six times greater than that of the past 4000 years. We propose that recent warming has led to *Sphagnum* establishment, which rapidly altered the peatland surface chemistry and hydrology, further promoting *Sphagnum* growth and enhancing the carbon-sink capacity of this peatland. Longer and warmer growing seasons could also have stimulated plant growth. Accelerated carbon accumulation in some wet peatlands under global warming might offset the carbon losses experienced from other peatland types.

1.1. Introduction

High-latitude regions have warmed much faster than the rest of the world over the past several decades, with surface air temperatures increasing at rates as high as 0.7°C per decade (Polyakov et al., 2002). In addition, instrumental records and climate model projections indicate that precipitation changes are regionally variable across the high latitudes and exhibit complex patterns (ACIA, 2004). Under these rapidly changing conditions, biogeochemical processes such as plant photosynthesis and microbial respiration will likely be altered, with potential for rapid and irreversible changes in terrestrial ecosystem structure and functioning (Solomon et al., 2007; McGuire et al., 2009). The fate of peat-accumulating wetlands (peatlands) is particularly concerning, as these very large pools of soil organic carbon (C) are located within a few meters of the atmosphere and their C balance is sensitive to temperature and moisture conditions (Lund et al., 2010). Climatically-induced alterations of the peatland C-sink capacity could be large enough to affect the global C budget and the climate system, although both the sign and the magnitude of this feedback remain highly uncertain (Wania et al., 2009; Frolking et al., 2011).

Northern peatlands occupy about 3% of the global land area and represent at least half of the world's wetlands. Over the Holocene (past 12,000 years), northern peatlands have accumulated 270-550 gigatons of organic C (up to about 1/3 of the world's soil C) as a result of a positive balance between plant productivity and peat decomposition (Gorham, 1991; Turunen et al., 2002; Yu et al., 2010). Peat-core syntheses and modern flux measurements have shown that net peatland C balance fluctuates over millennial (Yu, 2011), centennial (Malmer and Wallén, 2004), inter-annual (Roulet et al., 2007;

Nilsson et al., 2008), and seasonal timescales (Lafleur et al., 2005; Adkinson et al., 2011). These fluctuations are caused by differences in the balance between plant production and peat decomposition, with time periods dominated by net input from plant production (C uptake), and periods dominated by net release from decomposition of dead material and subsequent carbon dioxide (CO_2) and methane (CH_4) emissions to the atmosphere (C release). Regional climatic conditions, including long-term climatic regimes and short-term weather events, are often responsible for shifting the peatland C balance (e.g., Mauquoy et al., 2002; Malmer and Wallén, 2004; Frolking et al., 2010; Adkinson et al., 2011), although disturbances (fires, permafrost, land-use change), landscape morphology (slope, topography), and self-regulation mechanisms (peat growth, vegetation succession) can also contribute to these changes (e.g., Belyea and Baird, 2006).

A key uncertainty for predicting the northern peatland response to changing climatic conditions is whether warming-induced increases in C release, including CO_2 and CH_4, will be balanced by a corresponding increase in net primary production (NPP) and subsequent long-term C sequestration (e.g., Field et al., 2007; McGuire et al., 2009; Wania et al., 2009). In subarctic peatlands, wetter conditions due to permafrost thaw are expected to substantially increase CH_4 emissions to the atmosphere (Christensen et al., 2003, 2004). On the other hand, many thaw lakes are currently colonized by peatland plants through terrestrialization (lake-infilling) processes, promoting CO_2 sequestration (Myers-Smith et al., 2007; Turetsky et al., 2007; Roach et al., 2011). Further south, warming-induced droughts in low-boreal and temperate peatlands are predicted to accelerate CO_2 efflux to the atmosphere through enhanced oxidation of thick peat deposits (Ise et al., 2008; Dorrepaal et al., 2009), but the increased nutrient availability that co-occurs with greater microbial activity generally promotes NPP in terrestrial ecosystems through carbon-nitrogen interactions (Melillo et al., 2002, 2011). In the boreal and subarctic ecoregions, warming-induced increases in the growing season length (early spring warming) and earlier snowmelt (water availability) are believed to change the phenology of plants, which has been shown to promote C sequestration in these high-latitude regions (e.g., Zhou et al., 2001; Aurela et al., 2004; Menzel et al., 2006; Schwartz et al., 2006; Hudson and Henry, 2009; Stelzer and Post, 2009). Overall, this broad spectrum of peatland responses to global changes makes it challenging to predict whether northern peatlands will significantly contribute to the future atmospheric burden of greenhouse gases (Frolking et al., 2011), and new datasets such as the one presented here are needed to reduce these uncertainties.

In peatlands, climate-sensitive processes such as species-specific plant production and short-term peat decay largely determine the amount of C that will eventually contribute to the long-term peat store (e.g., Yu et al., 2001). To assess the impact of global warming on the structure and function of northern peatlands, it is therefore important to document the climate sensitivity of these short-term C flux terms. However, decadal- to centennial-scale peat production and decomposition rates have rarely been quantified in the scientific literature (but see Belyea and Clymo, 2001 and Wieder, 2001). Central to this challenge is the difficulty in integrating processes that operate over very different timescales, including modern primary production, multi-decadal decomposition processes, and long-term peat-C storage. The objectives of the present study are to fill these data and knowledge gaps by (1) quantifying recent (past 150 years) peat addition and decomposition rates, (2) comparing these recent rates to Holocene peat-C fluxes, and

(3) assessing the potential influence of global warming on recent C flux terms. The modeling approach developed in this paper combines the *exponential decay model* (Clymo, 1984), the *peatland C flux reconstruction model* (Yu, 2011), and the *peat decomposition model* (Frolking et al., 2003). It represents a step forward in linking peatland dynamics over different timescales, from decades to millennia.

In this paper, we reconstructed recent peat addition and decomposition rates of a wet boreal peatland complex in Alaska by combining empirical peat-core data and peatland carbon dynamics modeling. Wet boreal peatlands (fens) are temperature-sensitive ecosystems that partly receive their water from the regional aquifer, so they are not as prone to droughts as precipitation-fed peat bogs (Rydin and Jeglum, 2006). We hypothesize that, under the ongoing climate change with increasing temperature and precipitation, wet boreal peatlands are increasing their peat-C storage because of (1) increased biomass productivity, and (2) changes in the plant community. We speculate that a lengthening of the growing season and subsequent hydrological changes are the main drivers of this enhanced peat-C sequestration. This shift in peatland balance towards a stronger C sink due to increasing ‘greenness’ would induce a negative feedback to the climate system, and could partly offset CO_2 and CH_4 effluxes from other peatland regions.

1.2. Materials and Methods

1.2.1. Study site

Petersville peatland (62°25’N, 150°41’W) is located in the Susitna River basin, in the Cook Inlet region of south-central Alaska (Fig. 1.1). This is one of the few accessible, high-latitude regions in North America where vast peatland complexes are found. The climate in Talkeetna (closest weather station, 40 km to the southeast of Petersville site) is cool continental, with a 30-year (1971–2000) mean annual temperature of 1.0°C, ranging from -11.7°C in January to 14.9°C in July (monthly means). Mean annual precipitation is 715 mm, of which 352 mm falls as snow (Alaska Climate Research Center, 2009). The Talkeetna station has recorded the most dramatic temperature increase of any weather station in Alaska since 1950, with a mean annual temperature increase of almost 3°C over the past 60 years (Alaska Climate Research Center, 2009). Yet, this peatland-rich region remains understudied, and the only published peat-C data from south-central Alaska comes from the Kenai Peninsula, 200 km to the south of Talkeetna (Jones et al., 2009; Jones and Yu, 2010; Fig. 1.1).

Petersville is a sloping peatland (total area of ~1 km^2) located at the top of its watershed (Fig. 1.1). It represents a mosaic of minerogenic and oligotrophic peatland types, with pH ranging from 3.9 to 4.5. The ground layer is dominated by *Sphagnum* (mostly *S. capillifolium*, *S. fuscum* and *S. angustifolium*), although several Amblystegiaceae (brown mosses) including *Drepanocladus* spp. inhabit wet depressions, and sparse *Pleurozium schreberi* (feather moss) colonize the drier peatland margins. The vascular plant assemblage is dominated by ericaceous shrubs such as *Ledum palustre*, *Andromeda glaucophylla* and *Vaccinium vitis-idaea*, and by herbaceous species including *Scheuchzeria palustris* and *Carex pauciflora*. Surrounding upland vegetation is dominated by *Alnus* spp. and *Picea glauca*.

Peat inception age is 13,230 ± 110 cal. BP (UCIAMS-82701), and the peatland reached its modern extent about 8000 years ago (Loisel et al., 2010). We only focus our

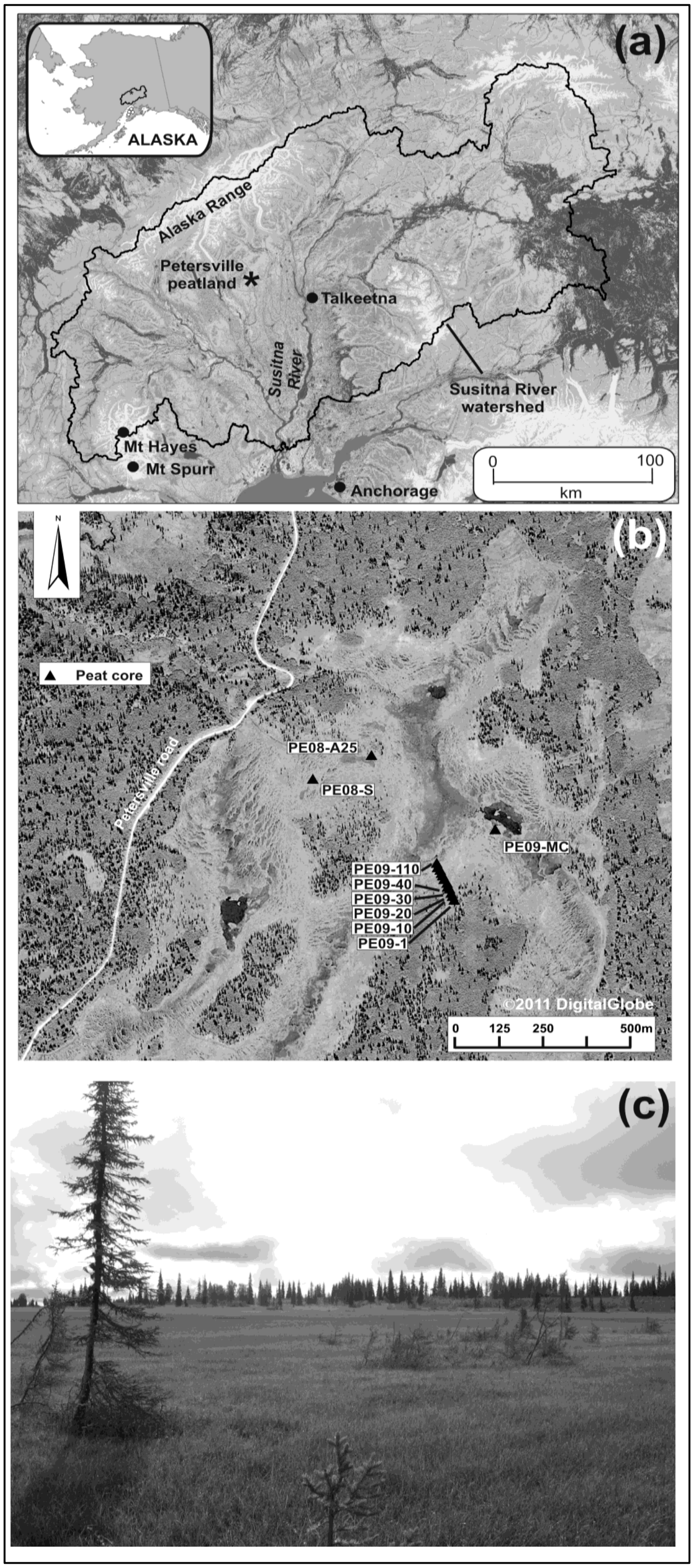

Figure 1.1. Location maps and study site. (a) Digital elevation model (source: 2-arc second dataset, USGS) showing Petersville peatland (62°25’N, 150°41’W, 450 m a.m.s.l.) and local weather station (Talkeetna) within the Susitna River basin. White dots in inset map indicate the location of peat carbon studies by Jones et al. (2009) and Jones and Yu (2010). (b) Quick Bird Image (resolution: 1 m) of Petersville site showing peat core location. Includes material © 2011 DigitalGlobe, Inc. ALL RIGHTS RESERVED. (c) Photo of the study site (looking toward north-east from site PE09-20).

discussion on results for the last 4000 years, as a volcanic ash layer from Mt. Hayes interrupted peat accumulation throughout the study site for about 1000 years during the mid-Holocene (Loisel et al., 2010).

1.2.2. Peat-core sampling and analyses

Fifteen peat cores were collected in 2008 and 2009 from different portions of the peatland complex (Fig. 1.1). Two of them (PE08-A25 and PE08-S) were used to determine millennial- and decadal-scale variability in peat-C accumulation rates and the paleoecology of the peatland. Full peat cores were collected using a Russian-type corer, but the uppermost sections (top 30 to 40 cm) were collected as monoliths to minimize compaction of the fresh layers. *In situ* measurements in 2007 and 2008 show water table depth between 10 and 15 cm below the surface near sites PE08-S and PE08-A25.

Plant macrofossils were identified along both peat profiles. Contiguous peat sub-samples (2 cm^3) were gently boiled in a 5% KOH solution and rinsed with distilled water through a 150-µm sieve. For each sample, Sphagnaceae, Amblystegiaceae, herbaceous, ligneous and unidentifiable organic matter (UOM) material were quantified as a percentage of the total sample by volume. Pollen analysis was also performed along core PE08-S to quantify the abundance of *Sphagnum* spores, which were used to evaluate if *Sphagnum* plants were present in the local vegetation even when macrofossil samples were too decomposed to allow positive identification. For pollen analysis, peat sub-samples (1 cm^3) were gently boiled in a 5% KOH solution for 10 minutes and rinsed with distilled water through 355- and 15-µm sieves. The captured material was stained with safranin, centrifuged, and mounted on glass slides. A sum of at least 200 tree and shrub pollen was counted for each sample, and *Sphagnum* spore percentage was calculated as (*Sphagnum* spore count/ total count)*100.

Peat core chronology was established using AMS radiocarbon (^{14}C) and lead-210 (^{210}Pb) dating methods, as well as three temporally well-constrained tephra layers. Dating material was composed of non-aquatic taxa (e.g., *Sphagnum* stems and leaves, seeds, sedge stem bases), which were hand-picked and cleaned with distilled water. In horizons that lacked good dating material, root-free bulk peat samples were analyzed (Table 1.1). The ^{14}C samples were submitted to Keck AMS Carbon Cycle Lab at University of California, Irvine, and results were calibrated using the program CALIB 6.0 based on the INTCAL09 calibration data set (Reimer et al., 2009; Stuiver and Reimer, 2010). Post-modern ^{14}C dates were calibrated using CALIBomb and a concatenation of the Levin's Vermunt and Schauinsland calibration datasets (Levin and Kromer, 2004). ^{210}Pb measurements were performed on an alpha-spectrometer at GEOTOP (Université du Québec, Montréal) using an acid extraction of Polonium (Flynn, 1968; De Vleeschouwer et al., 2010). The analytical error in ^{210}Pb measurements ranged from 1.6 to 3.8 % and the constant rate of supply model (Appleby and Oldfield, 1978) was used to reconstruct recent peat chronologies since it is believed to constitute the best model for peatlands (Turetsky et al., 2004; Ali et al., 2008). Smoothed age-depth models based on ^{14}C and ^{210}Pb dates as well as the tephra layers were obtained by using a Monte Carlo analysis that simulated 10,000 randomized polynomial curves, or age-depth models, through the probability distribution of each date (2σ for ^{14}C dates, and analytical error for ^{210}Pb dates). The parameters derived from the steepest and the shallowest polynomials were then used to estimate the age-depth model probability interval (or error), while the mean parameters were used to compute the final age-depth model. In total, 23 age determinations were used for core PE08-S, and 18 for PE08-A25.

Contiguous sub-samples (1 cm^3) of peat were dried overnight at 105°C, weighed, and burned at 550°C for two hours to determine bulk density and organic matter content, respectively (Dean, 1974). C content was assumed to be 50% of the organic matter density (Turunen et al., 2002). Long-term rates of peat-C accumulation (in g C m^{-2} yr^{-1}) were calculated by multiplying the C mass of each depth increment (organic matter density x C content) by the interpolated deposition rate of each sample (obtained from the age-depth models minimum, mean, and maximum parameters, as explained above). The peat-C mass of each depth increment was also summed to calculate Petersville's cumulative C pool (CCP, in g C cm^{-2}). Carbon-to-nitrogen (C/N) molar ratios were calculated from C and N concentration measurements on peat sub-samples (1 cm^3) at 2 cm increments along core PE08-S using a PDZ Europa ANCA-GSL elemental analyzer at the Stable Isotope Facility of University of California, Davis.

1.2.3. Peat accumulation and decomposition models

To quantify and compare millennial vs. decadal peat addition and decomposition rates, the acrotelm/catotelm boundary needs to be identified. The acrotelm is the thin, unsaturated portion of the peat profile where aerobic decomposition dominates at decadal timescales, and the catotelm is the waterlogged zone where slow, anaerobic decay takes place over millennial timescales (Blodau, 2002). The long-term maximal depth of the summer water table, reflecting the maximum depth of oxygenated conditions (Ingram, 1978, 1982), is usually used to define the boundary between these two peat layers. For each core, the instantaneous rate of change (1st derivative) of the age-depth model was used to identify the acrotelm/catotelm boundary, which corresponds to the interval showing the greatest change in rates between two adjacent samples. C/N values were used to confirm the position of the acrotelm/catotelm boundary, which occurs when the C/N ratio stabilizes following rapid C loss in the acrotelm (Kuhry and Vitt, 1996).

We used three modeling approaches to estimate decadal and millennial peat-C fluxes: the *exponential decay model* (Clymo, 1984), *peatland C flux reconstruction model* (Yu, 2011), and *peat decomposition model* (Frolking et al., 2003). These models are briefly described in the following paragraphs, and details can be found in the original references.

The *exponential decay model* developed by Clymo (1984) was used to derive peat addition rate (p) and peat decay coefficient (α) from the observed cumulative peat-C pool (CCP). The acrotelm and catotelm were analyzed separately. The exponential decay model assumes that p and α remain constant over time and has the form of

$$\frac{dCCP}{dt} = p - \alpha * CCP \ , \qquad \text{(eq. 1)}$$

which has the analytical solution of

$$CCP = \left(\frac{p}{\alpha}\right) * (1 - e^{-\alpha * t}) \ . \qquad \text{(eq. 2)}$$

The *peatland C flux reconstruction model* described by Yu (2011) uses net peat-C pool (NCP) values obtained from peat cores to back-calculate the amount of peat that was initially deposited (C uptake) by modeling its subsequent decomposition (C release). We adapted this approach to model Petersville's long-term peat-C accumulation rates (catotelm only), which was binned into 100-year intervals. Here, the observed NCP and modeled decay coefficient (α, as calculated using Clymo's decay model) were used to model the net C uptake (NCU) and net C release (NCR) at different time intervals. NCU is considered the initial peat-C input to the catotelm, and NCR represents the summed C release over each time interval of all peat cohorts (k) older than time *t*. Decomposition of all previously buried peat is occurring at every point in time, but at a decreasing rate due to the exponential decay rule. See the paper by Yu (2011) for definition and explanation of these peatland C flux terms, which have the following form

$$NCU_t = \frac{NCP_t}{e^{-\alpha * t}}, \qquad \text{(eq. 3)}$$

$$NCR_t = \sum_{k=t}^{\substack{initiation\\ age}} \left(\frac{NCP_k}{e^{-\alpha * t}} - \frac{NCP_k}{e^{-\alpha *(t-1)}} \right). \qquad \text{(eq. 4)}$$

A simplified version of the *peat decomposition model* (PDM) developed by Frolking et al. (2003) was used to simulate the mass loss of young peat layers to calculate residual peat mass in the acrotelm over time. The formulation consists of a single-exponential linear regression model that decomposes an initial mass of organic matter (M_0) over time (*t*, in annual time steps), where the initial decomposition rate (k_0) decreases as a function of peat mass loss to represent the increasing recalcitrance of the remaining peat (M_t). To model Petersville peatland's recent mass loss, M_0 and k_0 were obtained from Clymo's exponential decay model, so that Clymo's *p* and α replaced Frolking's M_0 and k_0, respectively. The PDM equation thus has the following form

$$M_t = \frac{M_0}{(1 + k_0 * t)} = \frac{p}{(1 + \alpha * t)}. \qquad \text{(eq. 5)}$$

In our approach, the *exponential decay model* was used to derive the rate of peat decay in the catotelm from the cumulative peat-C pool data (obtained directly from peat core analysis). This peat decomposition rate was then used to drive the *peatland C flux reconstruction model,* which decomposes the observed peat-C pool into net C uptake and release terms at 100-year intervals. These values provided an estimate for the amount of peat C that has been entering the top of the catotelm over the past 4000 years. Subsequently, the *exponential decay model* was used to derive the rate of peat addition and decay in the acrotelm. These calculations were directly obtained from peat core analysis. These values were then fed into the *peat decomposition model* as presented in eq. 5 to calculate the progressive peat loss and residual peat mass in the acrotelm over time. At the acrotelm/catotelm boundary, the acrotelm residual peat mass (*peat decomposition model*) is equal to the catotelm net peat-C uptake (*peatland C flux reconstruction model*). Thus, this approach links the acrotelm peat-C fluxes to the long-term rate of peat storage by comparing remaining acrotelm peat mass at the acrotelm/catotelm boundary to the catotelm peat input term.

1.3. Results

1.3.1. Age-depth models and chronology

The ^{14}C dates and calibrated ages of the samples dated from cores PE08-S and PE08-A25 are presented in Table 1.1. Dating uncertainties (2σ range) of calibrated ages varied between 45 and 135 years, and the analytical uncertainty associated with the oldest ^{210}Pb date was about 30 years. While a slightly concave age-depth model characterized the decomposed catotelm, the fresher acrotelm peat yielded noticeably concave age-depth models (Fig. 1.2). Three tephra layers were also identified along the peat cores: (1) the mid-Holocene Hayes eruptions, around 3430-4390 cal. BP (de Fontaine et al., 2007), (2) the late-Holocene Hayes eruption, at 600 cal. BP (Waythomas and Miller, 2002), and (3) the Spurr eruption, in 1992 (McGimsey et al., 2001). The mid-Holocene and 600 cal. BP tephra deposits from Mt. Hayes both left visible layers within the peatland stratigraphy, and their provenance was identified by Kristi Wallace from the Alaska Volcano Observatory on the basis of glass shard mineralogy. The 1992 eruption was detected on the basis of low organic matter content and the presence of glass shards within the peat matrix.

Overall, there is a good agreement between ^{210}Pb-derived chronologies, ^{14}C dates and tephra layers along the peat cores based on visual examination of the age-depth profiles. The only exception is the ^{14}C age of -13 cal. BP, younger than the corresponding ^{210}Pb (10 cal. BP) at 24.5 cm along core PE08-S (Fig. 1.2). Such offsets have been encountered in other peat-core studies (e.g., Belyea and Warner, 1996; Bauer et al., 2009) and have mostly been attributed to the non-uniform and rapidly changing atmospheric distribution of post-bomb ^{14}C (Reimer et al., 2004) and to C relocation within peat profiles (Turestky and Wieder, 1999). Post-depositional mobility of ^{210}Pb could also affect chronologies (Belyea and Warner, 1994), although ^{210}Pb is known to be rapidly immobilized in *Sphagnum* peat (Turetsky et al., 2004). As low and stable ^{210}Pb activity was measured in our older ^{210}Pb-dated peat deposits, we assume that leaching of ^{210}Pb did not occur along the studied profiles.

Table 1.1. AMS radiocarbon (^{14}C) dating results from peat cores at Petersville peatland, south-central Alaska

Core ID	Sample depth (cm)	Dated material	^{14}C age (yr BP)	Calibrated 2σ range (cal yr BP)	Age (cal yr BP)	Lab ID (UCIAMS[*])
PE08-S	24-25	*Sphagnum* stems	-3090 ± 15	-13, -23	-13	58964
	38-39	wood fragment	580 ± 15	540-637	580	54658
	42-43	wood fragment	920 ± 15	790-910	850	58965
	48-49	root-free bulk peat	1410 ± 15	1294-1339	1310	78204
	54-55	root-free bulk peat	1875 ± 15	1737-1873	1850	78205
	62-63	root-free bulk peat	2740 ± 20	2780-2872	2780	58966
PE08-A25	26-27	*Sphagnum* stems	140 ± 20	0-279	10	58967
	33-34	wood fragment	600 ± 15	548-646	450	54657
	37-38	root-free bulk peat	955 ± 15	797-926	980	78206

[*] Keck AMS Carbon Cycle Lab at University of California, Irvine

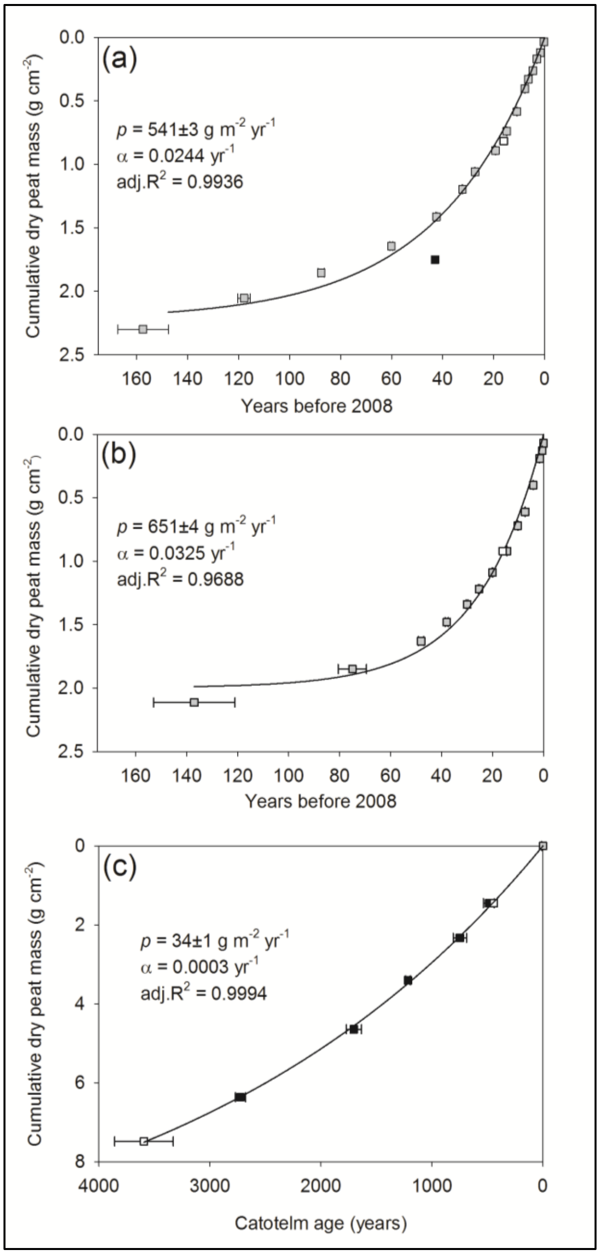

Figure 1.2. Exponential decay modeling results from Petersville peatland in south-central Alaska. Recent (past 150 years) peat growth for cores PE08-S (a) and PE08-A25 (b), and late-Holocene (past 4000 years) peat growth for core PE08-S (c). Black and grey squares indicate ^{14}C- and ^{210}Pb-dated horizons, respectively, and open squares represent tephra layers of known ages. *p*: peat addition rate, and α: decay coefficient. Note that the catotelm peat (bottom panel) was rescaled so that, at the top of the catotelm, time and dry mass are equal to 0.

1.3.2. Paleoecological reconstructions

Macrofossil records for cores PE08-S and PE08-A25 (Fig. 1.3) show that peat sediments have been mostly composed of herbaceous plants (mostly from Cyperaceae) throughout the late Holocene at Petersville site, with a few Amblystegiaceae remains (*Calliergon* cf. *stramineum* and *Drepanocladus* spp.) and high percentages of

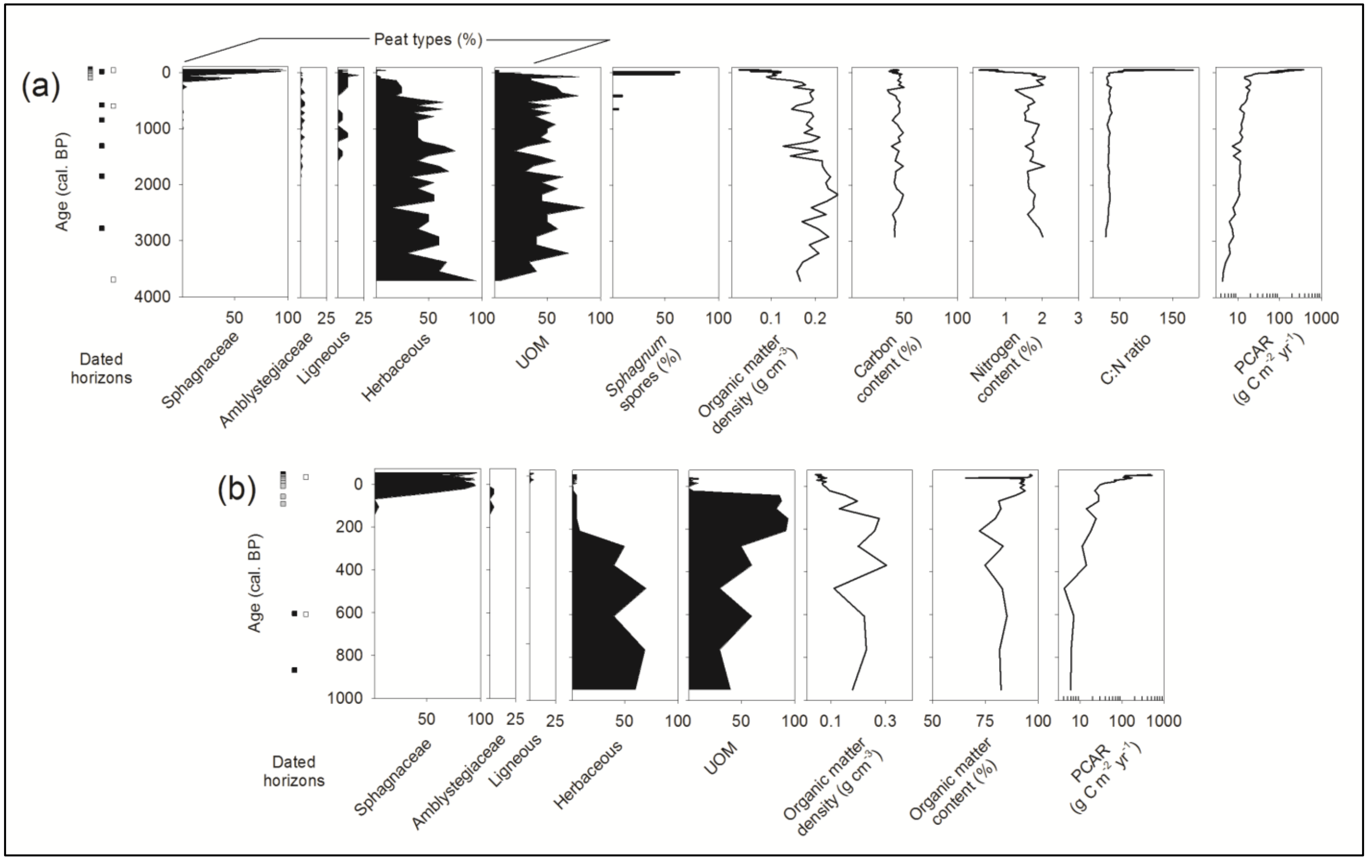

Figure 1.3. Paleoecological reconstructions for cores PE08-S (a), and PE08-A25 (b) at Petersville peatland in south-central Alaska. Black and grey squares indicate ^{14}C- and ^{210}Pb-dated horizons, respectively, and open squares represent tephra layers of known ages. UOM: unidentifiable organic matter; PCAR: peat-carbon accumulation rate.

unidentifiable organic matter (UOM). Along both cores, *Sphagnum* remnants (*S. fuscum* and *S. capillifolium-rubellum* type) only became abundant over the past 100 years (PE08-S: 1906 ± 2.5 A.D.; PE08-A25: 1902 ± 2.5 A.D.). This dramatic change, from herbaceous to *Sphagnum* peat, was also found along 13 other cores that were collected along a hydrological gradient few hundred meters away from coring sites PE08-S and PE08-A25 (Fig. 1.1), although we do not have good dating controls on most of these cores. A few *Bryum* spp. moss leaves and stems were found within the *Sphagnum* matrix near the transition from herbaceous to *Sphagnum* peat. *Sphagnum* spores were found in great abundance within the *Sphagnum*-rich portion of core PE08-S, but were almost absent from the herbaceous peat matrix, confirming the recent *Sphagnum* colonization and associated oligotrophication of the study site.

1.3.3. Peat geochemical properties

The average organic matter density (Fig. 1.3) of catotelm samples (0.19 g cm^{-3}) was much higher than that of acrotelm samples (0.07 g cm^{-3}) for cores PE08-S and PE08-A25, and total peat C content averaged 42.4%. Total N content in the catotelm was about 1.8%, and it rapidly decreased within the acrotelm to reach 0.8% in the surface sample. The opposite pattern was observed for the C/N ratio, with lowest values in the catotelm (mean = 29.5), and highest values close to the peatland surface (>100). These high N percentages (max = 2.1%) and corresponding low C/N ratios (min = 23.9) within the catotelm suggest that peat was mostly composed of herbaceous material, as sedge peat typically has a N content and C/N ratio around 2% and 20, respectively (Aerts et al., 1999; Rydin and Jeglum, 2006). These results are in agreement with our macrofossil and spore analyses.

1.3.4. Apparent peat-C accumulation rates

Over the past 4000 years, the apparent peat-C accumulation rate for core PE08-S averaged 11.5 g C m^{-2} yr^{-1} (Fig. 1.3). This value is lower than a recently compiled northern peatland average of 16.2 g C m^{-2} yr^{-1} for the past 4000 years based on 33 sites with detailed dating information (Yu et al., 2009), but higher than the average of 7.8 g C m^{-2} yr^{-1} (last 4000 years) from four sites on the Kenai Peninsula, Alaska (Jones and Yu, 2010). Recent peat-C accumulation rate for core PE08-S averaged 159.7 g C m^{-2} yr^{-1} for the past 50 years, 96.8 g C m^{-2} yr^{-1} for the past 100 years, and 75.5 g C m^{-2} yr^{-1} for the past 150 years; similar values were calculated for core PE08-A25 (156.9, 95.1 and 75.1 g C m^{-2} yr^{-1} for the last 50, 100 and 150 years, respectively). Incomplete decomposition of plant tissues in the acrotelm is responsible for the fifteen-fold difference between long-term and recent apparent peat-C accumulation rates.

1.3.5. Modeled litter input and peat loss patterns

The exponential decay model (Fig. 1.2) yielded a decay coefficient of 0.0003 yr^{-1} for the catotelm over the last 4000 years for core PE08-S, in line with values from previous studies (Clymo et al., 1998; Yu et al., 2001). The acrotelm peat addition rate (p) and decay coefficient (α) were 541 ± 3 g m^{-2} yr^{-1} and 0.0244 yr^{-1} for core PE08-S, and 651 ± 4 g m^{-2} yr^{-1} and 0.0325 yr^{-1} for core PE08-A25, respectively (Fig. 1.2). These peat addition rates or productivity estimates of 541 and 651 g C m^{-2} yr^{-1} are within the upper range of productivity measurements for northern peatlands (e.g., Szumigalski and Bayley, 1997). It is important to note that neither these field measurements nor our estimated rates of litter input consider belowground root production from vascular plants. This simplifying assumption is adequate for our acrotelm model since shrub and sedge roots were almost absent from the peat cores. The calculated acrotelm α values were comparable to mass loss rates obtained from litterbag experiments (Frolking et al., 2003; Moore et al., 2007), although our α values were two to four times smaller than field-based *Sphagnum* mass loss rates. These discrepancies are expected, as litterbag studies capture the very initial peat mass loss from leaching of soluble organic material, whereas stratigraphic estimates, such as α, mostly integrate the effects of declining litter quality and the deteriorating decomposition conditions over time (Belyea and Warner, 1996; Wieder, 2001). Overall, we argue that the fitted parameters as derived from Clymo's decay model provided reasonable acrotelm values of p and α, and a good basis for the following modeling exercises.

The *peatland C flux reconstruction model* (Fig. 1.4) yielded net peat-C uptake (NCU) values for the catotelm that ranged between 13.5 and 21.2 g C m^{-2} yr^{-1}. These estimates represent the averaged annual peat-C flux that had entered the catotelm over the past 4000 years. The peat decomposition model (Fig. 1.5) simulated peat mass loss in the acrotelm for 300 years. Remaining peat masses of 0.024 ± 0.0001 g cm^{-2} after 50 years (equivalent to 44.4% of initial mass), 0.016 ± 0.00009 g cm^{-2} after 100 years (= 29.6% of initial mass), and 0.0065 ± 0.00004 g cm^{-2} after 300 years (= 12% of initial mass; = 65 ± 1.3 g m^{-2}) were obtained. These values correspond to the amount of peat that would be transferred from the acrotelm into the catotelm at time t; therefore, they can be compared to the modeled NCU values (Fig. 1.5) and allow the linkage between short- and long-term processes of peat-C accumulation. After a 100-year acrotelm decomposition, the remaining peat mass would be about six times higher than the modeled catotelm NCU (based on old peat section). After a conservatively long 300-year acrotelm decomposition, the remaining peat mass would still be three times higher than the modeled catotelm NCU, suggesting a minimal three-fold increase in the peatland C-sink capacity in recent centuries.

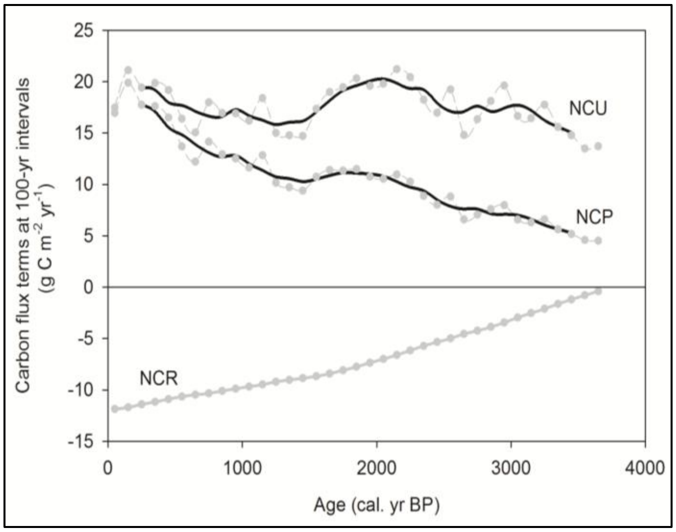

Figure 1.4. Late-Holocene peat-carbon fluxes for core PE08-S, as modeled using the super peatland approach (Yu, 2011). The acrotelm is not included. The net C pool (NCP) represents today's peat stock as reconstructed from peat cores; the net C uptake (NCU) represents the averaged annual peat-C flux that had entered the catotelm over the past 4000 years; the net C release (NCR) represents the summed C release of all peat cohorts over time. Smoothed lines: 5-point moving averages.

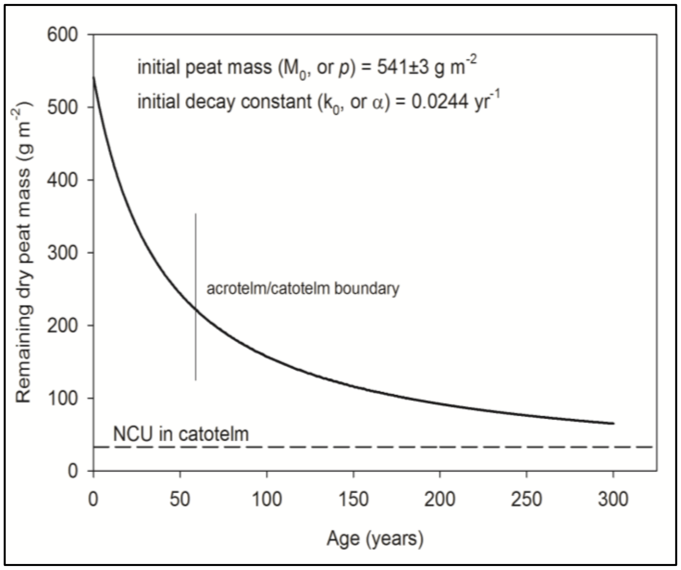

Figure 1.5. Recent peat decomposition modeling results for core PE08-S at Petersville peatland. The initial peat mass (M_0) and initial decomposition rate (k_0) were used to calculate the peat mass loss (solid black curve) as discussed in the text. The dashed line represents the net C uptake (NCU) that was calculated for the catotelm (Fig. 1.4) for the late Holocene. The acrotelm/ catotelm boundary corresponds to the maximal depth of the summer water table.

1.4. Discussion

1.4.1. Recent vegetation shift, oligotrophication and fen-bog transition at Petersville peatland

A rapid transition from *Carex* fen peat to dominant bog vegetation (*Sphagnum* mosses) has occurred over large portions of the study site over the past 100 years. It is well known that reduced minerogenic water inputs to the peat basin are required to trigger oligotrophication processes (Rydin and Jeglum, 2006), but the underlying causes can be diverse and complex. Peatlands have long been viewed as stable ecosystems where the successional change from fen to bog vegetation occurs as a result of slow, internal processes that lead to the gradual accumulation of peat above the groundwater influence (Zobel, 1988). Empirical studies based on peat-core stratigraphic analysis has shown, however, that the fen-bog transition is usually rapid and drastic, rather than slow and gradual (e.g., Kuhry et al., 1993; Almquist-Jacobson and Foster, 1995). In addition, external factors such as hydroclimatic changes could exert a major influence on the fen-bog transition by facilitating *Sphagnum* invasion (Hugues, 2000; Belyea and Malmer, 2004). For example, dry conditions or unstable water levels may trigger oligotrophication processes by enhancing peat decomposition, which leads to the creation of dense peat layers and to a relatively impermeable substrate, which isolates living plants from the influence of groundwater (Hugues, 2000; Hugues and Dumayne-Peaty, 2002). Along the same lines, Granath et al. (2010) recently showed that *Sphagnum fuscum* has the ability to survive and thrive in Amblystegiaceae (brown moss) carpets as long as the risk of submergence remains low, suggesting that drier summer conditions can enable *Sphagnum* growth in fens. In Finland, *Sphagnum* rapidly invaded a rich fen following its drainage in

1968 (Tahvanainen, 2010), lending support to the work by Hugues (2000) and Granath et al. (2010). Once it is introduced, *Sphagnum* increases the acidity of its surroundings by releasing hydrogen ions, which reinforces its own persistence and enables further invasion, leading to rapid oligotrophication of the ecosystem (van Breemen, 1995). Such positive feedback loops are often used to explain how a new ecosystem state can be self-maintained following a catastrophic shift from a previous steady state (Scheffer et al., 2001; Brock and Carpenter, 2010). There is increasing recognition that peatland ecosystems exhibit such non-linear, step-like transitions from one stable state to another (Belyea, 2009); the fen-bog transition constitutes an excellent example of such non-linear behavior.

In the case of Petersville peatland, several causes might have led to the recent *Sphagnum* colonization, including internal (change in local water flow patterns) and external (climate) drivers. Present groundwater inputs seem limited to the central, permanently wet fen area of the peatland (Fig. 1.1), but macrofossil analysis clearly indicates that a much broader portion of the site was under the influence of minerogenic water in the past. This recent change in local hydrology could have been caused by climatically-induced permafrost thaw following the Little Ice Age, which could explain the late-Holocene highly decomposed peat layers and associated slow peat accumulation. However, permafrost indicator species were not found in the macrofossil records (e.g., spruce needles, charcoals, sclerotia). In addition, no topographic features indicating permafrost thaw, such as thermokarst scars, were found near the study site, and the region is permafrost-free at the present (National Park Service, 2009). We therefore assumed that historical permafrost dynamics have not contributed to the observed vegetation change. Hydrological disturbance in the catchment (groundwater source or input rate) could also have initiated the observed vegetation change, but there is no evidence of such altered hydrology in the watershed. Recent anthropogenic changes that could have altered the regional hydrology (river dams, road construction, or mining) have not occurred, and no recently abandoned river channels that could indicate natural flow changes were identified.

Alternatively, the northern high-latitude regions have been experiencing rapid climatic changes over the last century, and more precisely since the early 1900s (Fig. 1.6). This warming trend is widespread and unprecedented since at least 2000 years, as indicated by a synthesis of late-Holocene temperature reconstructions from 23 sites located north of 60°N (Kaufman et al., 2009; Fig. 1.6). Similarly, earlier spring onset and snowmelt as well as drier and longer growing seasons have been recorded in Alaska, especially over the past 50 years (Hartmann and Wendler, 2006; Alaska Climate Research Center, 2009; Fig. 1.6). These warming conditions might have allowed the proliferation of marginal *Sphagnum* mosses towards the central (wet) portion of the peatland, assuming that early spring onset and snowmelt result in earlier snowmelt peak discharge (Aurela et al., 2004) and drier peatland conditions (i.e., not submerged) during part of the growing season. A change in the hydraulic head gradient as a result of altered hydroclimatic conditions is also possible (Glaser et al., 1997). Under this scenario, a climatic trigger led to *Sphagnum* establishment, which rapidly altered the peatland surface chemistry (acidification), further promoting *Sphagnum* colonization and growth (Fig. 1.6, 1.7). Rapid height growth isolated the peat surface from the groundwater influence, further promoting oligotrophication and drier conditions in a positive feedback loop. This autogenic process might have played an important role in the oligotrophication of this peatland (Fig. 1.7).

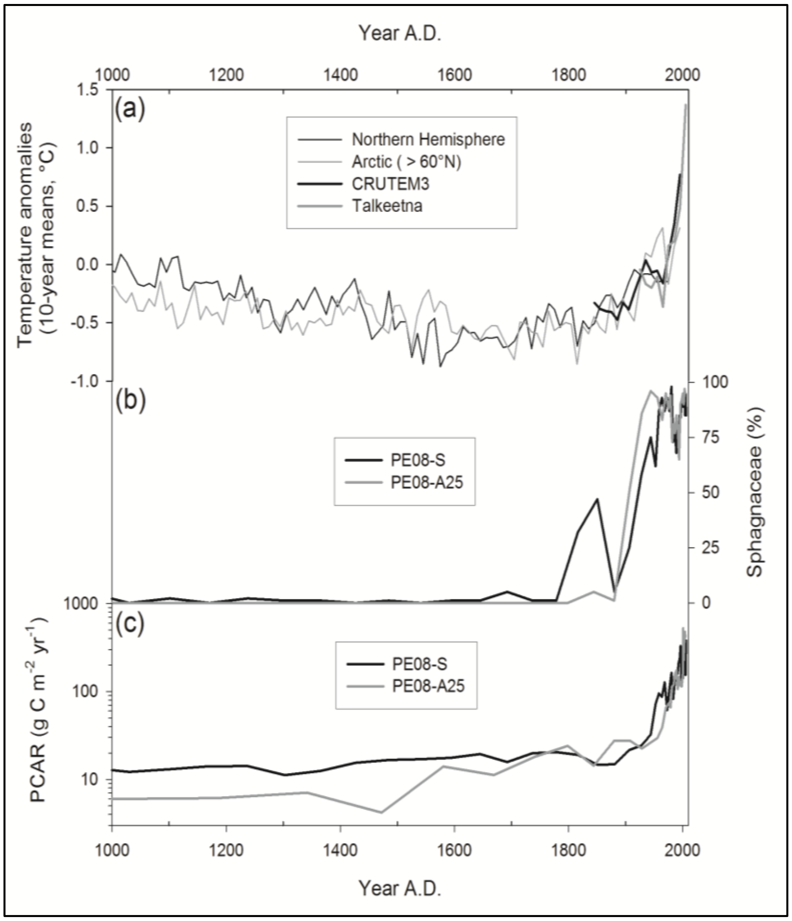

Figure 1.6. Correlations of recent climate warming, vegetation shift, and C accumulation. (a) Temperature anomalies from 1000-year reconstructions for the northern hemisphere (Moberg et al. 2005) and for the Arctic (Kaufman et al. 2009), and instrumental data for global temperature (CRUTEM3 dataset) for the period 1845-2000 (Brohan et al., 2006) and for Talkeetna weather station for the period 1918-2008 (Alaska Climate Research Center, 2009). All four temperature anomaly datasets were calculated based on the 1961-1990 temperature averages. (b) Abundance of *Sphagnum* plant remains from cores PE08-S and PE08-A25 at Petersville peatland during the last 1000 years. (c) Apparent peat carbon accumulation rates (PCAR) from cores PE08-S and PE08-A25 at Petersville peatland during the last 1000 years.

1.4.2. Causes of the rapid increase in peat-C accumulation rates over the last century

Based on the recent peat-core data and modeling analysis, we estimated that 65 ± 1 g m^{-2} yr^{-1} or 160 ± 1 g m^{-2} yr^{-1} would be transferred into the catotelm after 300 or 100 years of aerobic decomposition in the “acrotelm". This is three to six times higher than the rate of peat addition of 13.5 and 21.2 g C m^{-2} yr^{-1} estimated on the basis of peat-core data over the past 4000 years (Fig. 1.6). Using the *peatland C flux reconstruction model* (Yu, 2011), we calculated that a catotelm net C uptake (NCU) of 65 ± 1 g m^{-2} yr^{-1} (our most conservative value) would yield an averaged net C balance (NCB) of 9.8 g C m^{-2} yr^{-1} after 4000 years of catotelm decomposition at a rate of 0.0003 yr^{-1}, a two to three-time increase when compared to the 4.2 g C m^{-2} yr^{-1} observed for 4000 year-old peat at our study site.

The recent increase in C sequestration at the study site is probably partly attributable to *Sphagnum* growth (Fig. 1.6, 1.7). It is well known that *Sphagnum* peat is more efficient at sequestering C than its herbaceous counterpart due to *Sphagnum* recalcitrance to decay as well as its ability to acidify its surroundings, which hamper diagenetic processes (van Breemen, 1995). By retaining nutrients and moisture from atmospheric sources, *Sphagnum* moss carpets also slow down vascular plant growth that relies on mineralized nutrient sources in the root layer, with the effect of delaying peat decomposition (Malmer et al., 2003; Bubier et al., 2007). A recent study has also shown a drop in summer soil temperature following water table drawdown and *Sphagnum* growth in a peatland, which resulted in an overall positive C balance (Straková et al., in press). In a recently drained fen that abruptly switched into a *Sphagnum* bog, a 60% increase in peat growth from the fen to the bog phase was reported (Tahvanainen, 2010). Despite a probable thickening of the acrotelm due to *Sphagnum* invasion, a positive peat-C balance is still possible, as shown by these previous studies and others (e.g., Laiho, 2006).

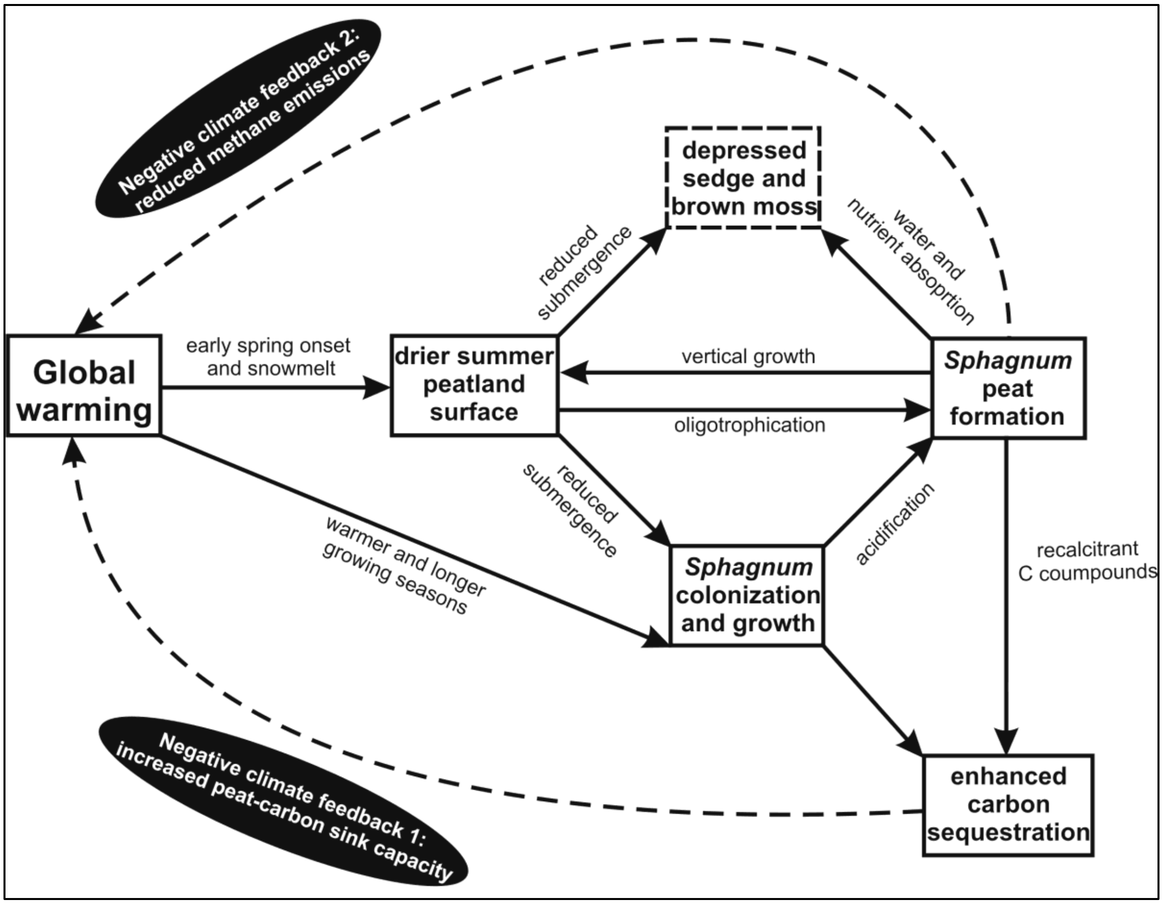

Figure 1.7. Conceptual model linking the ongoing climate warming and peatland C sequestration. The hypothesized sequence of events, including processes (arrows) and consequence (boxes), induces an ecosystem regime shift at Petersville peatland (that is, fen-to bog transition) and subsequent change in ecosystem functioning (C sequestration capacity). Negative feedbacks are indicated by dashed arrowed lines. See section 1.4.

Longer and warmer growing seasons might also be favoring peat-C accumulation by promoting NPP at our study site (Fig. 1.6, 1.7). Supporting this hypothesis is a clear relationship between degree-days, mean annual temperature and long-term peat-C accumulation in Finland and Canada (Clymo et al., 1998). Similarly, photosynthetically active radiation (PAR), growing season length and peat-C accumulation rates over the last millennium were positively correlated throughout the northern hemisphere (D. Charman et al., Climate-driven changes in peatland carbon accumulation during the last millennium, submitted to PNAS, 2011). Modern *Sphagnum* NPP also correlates with PAR and growing season length, as shown on the basis of a meta-analysis that includes 142 *Sphagnum* plants from 52 high-latitude peatlands (J. Loisel et al., Global-scale pattern of peatland *Sphagnum* productivity driven by photosynthetically active radiation and growing season length, submitted to Biogeosciences, 2012). Peatland models have similarly reported an overall positive effect of warmer temperatures on peat-C sequestration: under a scenario where production and decomposition had the same sensitivity to temperature, productivity effects dominated and enhanced peat accumulation (Frolking et al., 2003). To reverse this trend, a Q_{10} value of 3 for decomposition rate and a Q_{10} value of 2 for productivity were needed (Frolking et al., 2003). These results clearly show the important role of NPP in controlling peat-C sequestration, in agreement with our study.

The substantial warming in the northern high latitudes over the past decades accelerates both growth and decomposition processes in terrestrial ecosystems (Bunn et al., 2007). The concept of “greening” refers to the overall net carbon gain of high-latitude ecosystems in a warming world, which has been recorded by atmospheric CO_2 data (Keeling et al., 1996), satellite measurements (Myneni et al., 1997; Nemani et al., 2003), and ecosystem-scale flux measurements (Aurela et al., 2004). Warmer and longer growing seasons are enhancing aboveground vegetation growth in temperature-sensitive ecosystems, and especially in those that are not particularly prone to droughts such as wet tundra (Bunn et al., 2007). Although ecosystem greenness generally refers to an increase in photosynthetic activity as shown by the satellite-derived normalized difference vegetation index (NDVI), which is not ideal for quantifying aboveground productivity in peatlands, our study suggests that peatland ‘greening’ (i.e., climatically-induced increase in NPP) might be occurring in temperature-sensitive wet boreal peatlands.

Other global environmental changes could have modified the carbon accumulation rate at Petersville peatland. For example, atmospheric nitrogen deposition has been shown to promote carbon sequestration in peatlands (Vitt et al., 2003; Turunen et al., 2004) up to an optimal level of about 1 g N m^{-2} yr^{-1} (Jauhiainen et al., 1994). Above this level, N becomes detrimental to *Sphagnum* growth due to nutrient toxicity and accelerated growth of rooted vascular plants (Bubier et al., 2007). In line with these results, Gunnarsson et al. (2008) observed a recent reduction in the peat-C sink of a bog with high N deposition (1.25 g N m^{-2} yr^{-1}) in southwest Sweden. Nitrogen enrichment was probably negligible at Petersville peatland since this region only receives about 0.055 g N m^{-2} yr^{-1} (Dentener, 2006). In addition, the surface peat N content (Fig. 1.3) was relatively low (< 0.25%).

1.4.3. Impact of warmer climates on peatland structure and functioning

Recent studies have indicated that Alaskan peatlands (Jones et al., 2009; Jones and Yu, 2010) and northern peatlands as a whole (Yu et al., 2009) were rapidly accumulating large quantities of organic C during the Holocene Thermal Maximum (HTM), the warmest time period since the last deglaciation (Kaufman et al., 2004). Comprehensive datasets of basal peat ages indicate that new peatland formation and lateral expansion were also occurring rapidly over the northern landscape during this period (e.g., MacDonald et al., 2006; Gorham et al., 2007; Korhola et al., 2010). In light of these results, it was hypothesized that enhanced peat-C sink capacity was stimulated by increased plant production during warmer-than-today summers (e.g., MacDonald et al., 2006), but that peat decomposition might have been limited during colder-than-today winters (Jones and Yu, 2010).

Similarly, peatlands throughout the northern hemisphere showed higher C sequestration rates during the Medieval Climate Anomaly (MCA), about 800 years ago, than during the Little Ice Age (LIA), about 250 years ago (Mauquoy et al., 2002; D. Charman et al., Climate-driven changes in peatland carbon accumulation during the last millennium, submitted to PNAS, 2011). Based on available datasets, however, the unusually rapid peat-C sequestration rates that characterized the HTM were not attained during the MCA, possibly because the MCA warmer interval was occurring in a context of reduced temperature seasonality (i.e., warm summers, but also warmer winters). Nonetheless, increased peat accumulation was recorded during the MCA (and a decrease during the LIA), clearly showing the key control of growing season temperatures on the C sink functioning in northern peatlands.

In our study, the recent increase in peat accumulation was indirectly induced by a change in ecosystem structure (fen-to-bog transition), which led to a change in ecosystem function (enhanced C sequestration). Here, indirect impacts of climate warming (early spring warming and snowmelt, and drier late summer) have facilitated *Sphagnum* colonization due to drier peatland conditions (Fig. 1.6); peat mosses then reinforced their own growth via vigorous autogenic processes that further limited sedge and Amblystegiaceae growth due to nutrient interception and acidification, leading to an ecosystem regime shift (Fig. 1.7). The positive impact of longer and warmer growing seasons also came into play by directly promoting *Sphagnum* NPP. The recalcitrant C compounds (lipids and acids) found in *Sphagnum* plants allowed rapid vertical growth to occur, further reinforcing the stability of this drier alternative state. Finally, the long-term increase in peat formation has led to greater peat-C sequestration (Fig. 1.7). As peat decomposition is also sensitive to temperature and moisture content, peatland models that incorporate both temperature and moisture functions of production and decomposition should be used to complement our study and predict if the observed increase in peat-C sequestration following the fen-to-bog transition will be transient or long-held.

Ecologically speaking, Petersville peatland has reached maturity, as it is more than 13,000 years old and it has accumulated large amounts of peat that must greatly impede groundwater flow. This situation is similar to most northern peatlands, which are, on average, over 8000 years old (MacDonald et al., 2006). As temperature increases, these ecosystems might become more prone to vegetation shifts similar to what was observed at the Petersville site. Based on our findings, we argue that such mature ecosystems might have reached a point of increased sensitivity to droughts. As a result, warmer and longer growing seasons might increase the likelihood of regime shifts in these wet systems, potentially leading to abrupt changes in peatland functioning as observed at our study site.

1.5. Conclusions and Implications

We have shown that wet boreal peatlands such as Petersville site might be sensitive to stimulation of production and carbon sequestration by climate warming. Our results show that a climatic trigger has led to *Sphagnum* establishment, which rapidly altered the peatland surface chemistry (acidification), further promoting *Sphagnum* growth and enhancing the peatland carbon sink capacity. Longer and warmer growing seasons could also be playing a key role in the observed recent increase in peat-carbon accumulation rate by stimulating net primary production.

In addition to increasing the peat carbon sink capacity, peatland ‘greening’ could also reduce peatland methane emission to the atmosphere due to lower water table levels (Bubier et al., 1995) and dominance of *Sphagnum* mosses, providing an additional negative feedback to climate change. These results are contrary to the widespread notion that higher temperature will increase peat decay and associated carbon dioxide release from peatlands to the atmosphere, contributing to the positive carbon cycle feedback to global warming.

There has a been a growing effort to evaluate the role of northern peatlands in the global carbon cycle with regards to their past, present and future carbon dioxide and methane exchanges with the atmosphere. Flux tower measurements have been characterizing the contemporary carbon balance of these ecosystems (Roulet et al., 2007; Nilsson et al., 2008; Lund et al., 2010), and peat-core analysis have been used to quantify long-term peat-carbon accumulation rates and to reconstruct Holocene peat-carbon flux histories (Beilman et al., 2009; Yu et al., 2009, 2010, 2011; Yu, 2011), but very little effort has been put to describe decadal-scale peatland dynamics despite their critical role in the contemporary and future peat-carbon balance (Wieder, 2001). It is well known that plant production and aerobic peat decay are sensitive to hydroclimatic conditions and that they greatly influence the amount of peat-carbon that will reach the catotelm (e.g., Yu et al., 2001), as well as carbon dioxide and methane release to the atmosphere (e.g., Moore et al., 1998). Quantifying recent net rates of organic matter accumulation is therefore crucial, and the approach developed in this paper represents a step in that direction as it links short- and long-term peatland dynamics.

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1.7. References

ACIA (2004), *Impacts of a warming climate*, Cambridge University Press, Cambridge, UK.

Adkinson, A.C., Syed, K.J. and L.B. Flanagan (2011), Contrasting responses of growing season ecosystem CO_2 exchange to variation in temperature and water table depth in two peatlands in northern Alberta, Canada, *Journal of Geophysical Research*, *116*, G01004, doi:10.1029/2010JG001512.

Aerts, R., Verhoeven, J.T.A. and D.F. Whigham (1999), Plant-mediated controls on nutrient cycling in temperate fens and bogs, *Ecology*, *80*, 2170–2180.

Alaska Climate Research Center (2009), *Temperature change in Alaska*, Geophysical Institute, University of Alaska Fairbanks, http://climate.gi.alaska.edu/.

Ali, A.A., Ghaleb, B., Garneau, M., Asnong, H. and J. Loisel (2008), Recent peat accumulation rates in minerotrophic peatlands of the James Bay region, Eastern Canada, inferred by ^{210}Pb and ^{137}Cs radiometric techniques, *Applied Radiation and Isotopes*, *66*, 1350-1358.

Almquist-Jacobson, H. and D.R. Foster (1995), Toward an integrated model for raised-bog development: theory and field evidence, *Ecology*, *76*, 2503-2516.

Appleby, P.G. and F. Oldfield (1978), The calculation of ^{210}Pb dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment, *Catena*, *5*, 1-8.

Aurela, M., Laurila, T. and J.-P. Tuovinen (2004), The timing of snow melt controls the annual CO_2 balance in a subarctic fen, *Geophysical Research Letters*, *31*, L16119, doi: 10.1029/2004/GL020315.

Bauer, I.E., Bhatti, J.S., Swanston, C., Wieder, R.K. and C.M. Preston (2009), Organic matter accumulation and community change at the peatland-upland interface: inferences from ^{14}C and ^{210}Pb dated profiles, *Ecosystems*, *12*, 636-653.

Beilman, D.W., MacDonald, G.M., Smith, L.C. and P.J. Reimer (2009), Carbon accumulation in peatlands of West Siberia over the last 2000 years, *Global Biogeochemical Cycles*, *23*, GB1012, doi: 10.1029/2007GB003112.

Belyea, L.R. (2009), Non-linear dynamics of peatlands and potential feedbacks on the climate system, in *Northern peatlands and carbon cycling, American Geophysical Union Monograph Series*, edited by A. Baird et al., AGU, Washington, DC.

Belyea, L.R. and A.J. Baird (2006), Beyond 'The limits to peat bog growth': cross-scale feedback in peatland development, *Ecological Monographs*, *76*(3), 299-322.

Belyea, L. and R.S. Clymo (2001), Feedback control of the rate of peat formation, *The Royal Society*, *268*, 1315-1321.

Belyea, L.R. and B.G. Warner (1994), Dating of the near-surface layer of a peatland in northwestern Ontario, Canada, *Boreas*, *23*, 259–269.

Belyea, L.R. and B.G. Warner (1996), Temporal scale and the accumulation of peat in a *Sphagnum* bog, *Canadian Journal of Botany*, *74*, 366–377.

Blodau, C. (2002), Carbon cycling in peatlands - A review of processes and controls, *Environmental Reviews*, *10*, 111-134.

Brock, W.A. and S.R. Carpenter (2010), Interacting regime shifts in ecosystems: implication for early warnings, *Ecological Monographs*, *80*(3), 353-367.

Brohan, P., Kennedy, J.J., Harris, I., Tett, S.F.B. and P.D. Jones (2006), Uncertainty estimates in regional and global observed temperature changes: a new dataset from 1850. *Journal of Geophysical Research*, *111*, D12106, doi:10.1029/2005JD006548.

Bubier, J.L., Moore, T.R., Bellisario, L. and N.T. Comer (1995), Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochemical Cycles, 9*(4), 455-470.

Bubier, J., Moore, T.R. and Bledzki, L.A. (2007), Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, *Global change Biology*, *13*, 1-19.

Bunn, A.G., Goetz, S.J., Kimball, J.S. and K. Zhang (2007), Northern high-latitude ecosystems respond to climate change, *Eos Transactions*, *American Geophysical Union, 88*(34), 333-335.

Christensen, T.R., Ekberg, A., Ström, L., Mastepanov, M., Panikov, N., Öquist, M., Svensson, B.H., Nykänen, H. and P.J. Martikainen (2003), Factors controlling large scale variations in methane emissions from wetlands, *Geophysical Research Letters, 30*(7), 1414, doi:10.1029/2002GL016848.

Christensen, T.R., Johansson, T., Åkerman, H.J., Mastepanov, M., Malmer, N., Friborg, T., Crill, P. and B.H. Svensson (2004), Thawing sub-arctic permafrost: effects on vegetation and methane emissions, *Geophysical Research Letters, 31*, L04501, doi:10.1029/2003GL018680.

Clymo, R.S. (1984), The limits to peat growth, *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *303*(1117), 605-654.

Clymo, R.S., Turunen, J. and K. Tolonen (1998), Carbon accumulation in peatlands, *Oikos*, *81*, 368–388.

Dean Jr, W.E. (1974), Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods, *Journal of Sedimentary Petrology*, *44*(1), 242-248.

de Fontaine, C.S., Kaufman, D.S., Anderson, R.S., Werner, A., Waythomas, C.F. and T.A. Brown (2007), Late Quaternary distal tephra-fall deposits in lacustrine sediments, Kenai Peninsula, Alaska, *Quaternary Research*, *68*, 64-78.

Dentener, F.J. (2006), Global maps of atmospheric nitrogen deposition, 1860, 1993, and 2050 data set, http://daac.ornl.gov/, doi:10.3334/ORNLDAAC/830.

De Vleeschouwer, F., Sikorski, J. and N. Fagel (2010), Development of lead-210 measurement in peat using polonium extraction - a procedural comparison, *Geochronometria*, *36*, 1-8.

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V. and R. Aerts (2009), Carbon respiration from subsurface peat accelerated by climate warming in the subarctic, *Nature*, *460*, 616-620.

Field, C.B., Lobell, D.B., Peters, H.A. and N.R. Chiariello (2007), Feedbacks of terrestrial ecosystems to climate change, *Annual Review of Environment and Resources*, *32*, 1-29.

Flynn, W.W. (1968), The determination of low levels of polonium-210 in environmental materials, *Analytica Chimica Acta*, *43*, 221-227.

Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M. and S. Muller (2003), Modeling northern peatland decomposition and peat accumulation, *Ecosystems, 4*, 479-498.

Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J. and P.J.H.

Richard (2010), A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation, *Earth Systems Dynamics Discussions*, *1*, 115-167.

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.-S. and N. Roulet (2011), Peatlands in the Earth's 21st century coupled climate-carbon system, *Environmental Reviews*, *19*, 371-396.

Glaser, P.H., Siegel, D.I., Romanowicz, E.A. and Y.P. Shen (1997), Regional linkages between raised bogs and the climate, groundwater, and landscape of north-western Minnesota, *Journal of Ecology*, *85*(1), 3-16.

Gorham, E., Lehman, C., Dyke, A., Janssens, J. and L. Dyke (2007), Temporal and spatial aspects of peatland initiation following deglaciation in North America, *Quaternary Science Reviews*, 26, 300–311.

Granath, G., Strengbom, J. and H. Rydin (2010), Rapid ecosystem shifts in peatlands: linking plant physiology and succession, *Ecology*, *91*(10), 3047-3056.

Gunnarsson, U., Boresjö Bronge, L., Rydin, H. and M. Olson (2008), Near-zero recent carbon accumulation in a bog with high nitrogen deposition in SW Sweden, *Global Change Biology*, *13*, 2152-2165.

Hartmann, B. and G. Wendler (2006), The significance of the 1976 Pacific climate shift in the climatology of Alaska, *Journal of Climate*, *18*, 4824-4839.

Hudson, J.M.G. and G.H.R. Henry (2009), Increased plant biomass in a High Arctic heath community from 1981 to 2008, *Ecology*, *90*(10), 2657-2663.

Hugues, P.D.M. (2000), A reappraisal of the mechanisms leading to ombrotrophy in British raised mires, *Ecology Letters*, *3*, 7-9.

Hugues, P.D.M. and L. Dumayne-Peaty (2002), Testing theories of mire development using multiple successions at Crymlyn Bog, West Glamorgan, South Wales, UK, *Journal of Ecology*, *90*, 456-471.

Ingram, H.A.P. (1978), Soil layers in mires: functions and terminology, *Journal of Soil Science*, *29*, 224-227.

Ingram, H.A.P. (1982), Size and shape in raised mire ecosystems: a geophysical model, *Nature*, *297*, 300-303.

Ise, T., Dunn, A.L., Wosfy, S.C. and P.R. Moorcroft (2008), High sensitivity of peat decomposition to climate change through water-table feedback, *Nature Geoscience*, *1*, 763-766.

Jauhiainen, J. Vasander, H. and J. Silvola (1994), Response of *Sphagnum fuscum* to N deposition and increased CO_2, *Journal of Bryology*, *18*, 83-95.

Jones, M.C., Peteet, D.M., Kurdyla, D. and T. Guilderson (2009), Climate and vegetation history from a 14,000-year peatland record, Kenai Peninsula, Alaska, *Quaternary Research*, *72*, 207-217.

Jones, M.C. and Z. Yu (2010), Rapid deglacial and early Holocene expansion of peatlands in Alaska, *Proceedings of the National Academy of Sciences of the USA*, *107*(16), 7347-7352.

Kaufman, D.S., Ager, T.A., Anderson, N.J., Anderson, P.M., Andrews, J.T., Bartlein, P.J., Brubaker, L.B., Coats, L.L., Cwynar, L.C., Duvall, M.L., Dyke, A.S., Edwards, M.E., Eisner, W.R., Gajewski, K., Geirsdottir, A., Hu, F.S., Jennings, A.E., Kaplan, M.R., Kerwin, M.W., Lozhkin, A.V., MacDonald, G.M., Miller, G.H., Mock, C.J., Oswald W.W., Otto-Bliesner, B.L., Porinchu, D.F., Ruhland, K.R., Smol, J.P., Steig, E.J. and B.B. Wolfey (2004), Holocene thermal maximum in the western Arctic (0-180°W), *Quaternary Science Reviews*, *23*, 529-560.

Kaufman, D., Schneider, D.P., McKay, N.P., Ammann, C.M., Bradley, R.S., Briffa, K.R., Miller, G.H., Otto-Bliesner, B.L., Overpeck, J.T., Vinther, B.M. and Arctic Lakes 2k Project Members (2009), Recent warming reverses long-term Arctic cooling, *Science*, *325*, 1236-1239.

Keeling, C.D., Chin, J.F.S. and T.P. Whorf (1996), Increased activity of northern vegetation inferred from atmospheric CO_2 measurements, *Nature*, *382*, 146-149.

Korhola, A., Ruppel, M., Seppä, H., Väliranta, M., Virtanen, T. and J. Weckström (2010), The importance of northern peatland expansión to the late-Holocene rise of atmospheric methane, *Quaternary Science Reviews*, *29*(5-6), 611-617.

Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H. and S.E. Bayley (1993), Development of *Sphagnum*-dominated peatlands in boreal continental Canada, *Canadian Journal of Botany*, *71*, 10-22.

Kuhry, P. and D.H. Vitt (1996), Fossil carbon/nitrogen ratios as a measure of peat decomposition, *Ecology*, *77*(1), 271-275.

Lafleur, P.M., Hember, R.A., Admiral, S.W. and N.T. Roulet (2005), Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada, *Hydrological Processes*, *19*, 3533-2550.

Laiho, R. (2006), Decomposition in peatlands: reconciling seemingly contrasting results on the impacts of lowered water levels, *Soil Biology and Biochemistry*, *38*, 2011-2024.

Levin I. and B. Kromer (2004), The tropospheric $^{14}CO_2$ level in mid-latitudes of the

Northern Hemisphere, *Radiocarbon, 46*, 1959-2003.

Loisel, J., Nolan, J., Yu, Z., Parsekian A. and L. Slater (2010), The influence of landscape morphology on peatland dynamics and carbon accumulation inferred from ground penetrating radar (GPR) and peat core analysis, Abstract *EP21B-0747* presented at 2010 Fall Meeting, AGU, San Francisco, Calif., 13-17 Dec.

Lund, M., Lafleur, P.M., Roulet, N.T., Lindroth, A., Christensen, T.R., Aurela, M., Chojnick, B.H., Flanagan, L.B., Humphreys, E.R., Laurila, T., Oechel, W.C., Olejnik, J., Rinne, J., Schubert, P. and M. Nilsson (2010), Variability in exchange of CO_2 across 12 northern peatland and tundra sites, *Global Change Biology*, *16*, 2436-2448.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C. and A.A. \ Valichko (2006), Rapid early development of circumarctic peatlands and atmospheric CH_4 and CO_2 variations, *Science, 314*, 285-288.

Malmer, N., Albinsson, C., Svensson, B.H. and B. Wallén (2003), Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation, *Oikos*, *100*, 469–482.

Malmer, N. and B. Wallén (2004), Input rates, decay losses and accumulation rates of carbon in bogs during the last millenium: internal processes and environmental changes, *The Holocene*, *14*(1), 111-117.

Mauquoy, D., Engelkes, T., Groot, M.H.M., Markesteijn, F., Oudejans, M.G., van der Plicht, J. and B. van Geel (2002), High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs, *Paleogeography, Paleoclimatology, Paleoecology, 186*, 275-310.

McGimsey, R.G., Neal, C.A. and C.M. Riley (2001), Areal distribution, thickness, mass, volume, and grain size of tephra-fall deposits from the 1992 eruptions of Crater Peak vent, Mt. Spurr volcano, Alaska, *United States Geological Survey*, open-file report 01-370.

McGuire, A.D., Anderson, L.G., Christensen, T.R., Dallimore, S., Guo, L., Hayes, D.J., Heimann, M., Lorenson, T.D., MacDonald, R.W. and N. Roulet (2009), Sensitivity of the carbon cycle in the Arctic to climate change, *Ecological Monographs*, *79*(4), 523-555.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T. and Morrisseau, S. (2002), Soil warming and carbon-cycle feedbacks to the climate system, *Science*, *298*, 2173-2176.

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steugler, P., Lux, H., Burrows, E., Bowles, F., Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M. and J. Tang (2011), Soil warming, carbon-nitrogen interactions, and forest carbon budgets, *Proceedings of the National Academy of Sciences USA*, *108*(23), 9508-9512.

Menzel , A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., De Fila, C., Donnelly, A., Filella, Y., Jatcza, K., Måge, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S. and A. Zust (2006), European phenological response to climate change matches the warming pattern, *Global Change Biology*, *12*, 1969-1976.

Moberg, A., Sonechkin, D.M., Holmgren, K., Datsenko, N.M. and W. Karlén (2005), Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data, *Nature*, *433*, 613-617.

Moore, T.R., Bubier, J.L. and L. Bledzki (2007), Litter decomposition in temperate peatland ecosystems: the effect of substrate and site, *Ecosystems*, *10*, 949-963.

Moore, T.R., Roulet, N.T. and J.M. Waddington (1998), Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands, *Climatic Change*, *40*, 229-245.

Myers-Smith, I.H., McGuire, A.D., Harden, J.W. and F.S. Chapin III (2007), Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest, *Journal of Geophysical Research*, *112*, G04017, doi:10.1029/2007JG000423, 2007.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and R.R. Nemani (1997), Increased plant growth in the northern high latitudes from 1981 to 1991, *Science*, *386*, 698-702.

National Park Service (2009), *Permafrost landscapes, Denali National Park and Preserve*, U.S. Department of the Interior, www.nps.gov/dena/naturescience/upload/Permafrost-Landscapes.pdf.

Nemani,, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneli, R.B. and S.W. Running (2003), Climate-driven increases in global terrestrial net primary production from 1982 to 1999, *Science*, *300*, 1560-1563.

Nilsson, M., Sagerford, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., Klemedtsson, L, Weslien P. and A. Lindroth (2008), Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire – a significant sink after accounting for all C-fluxes, *Global Change Biology*, *14*, 2317-2332.

Polyakov, I.D., Alekseev, G.V., Bekryaev, R.V., Bhatt, U., Colony, R., Johnson, M.A., Karklin, V.P., Makshtas, A.P., Walsh, D. and A.V. Yulin (2002), Observationally based assessment of polar amplification of global warming, *Geophysical Research Letters*, *29*, 1878, doi:10.1029/2001GL011111.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C., Blackwell, P.G., Buck, C.E., Burr, G., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.M., Hughen, K.A., Kromer, B., McCormac, F.G., Manning, S., Bronk Ramsey, C., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J. and C.E. Weyhenmeyer (2009), IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP, *Radiocarbon*, *51*(4), 1111-1150.

Reimer, P.J., Brown, T.A. and R.W. Reimer (2004), Discussion: reporting and calibration of post-bomb ^{14}C data, *Radiocarbon*, *46*, 1299–1304.

Roach, J., Griffith, B., Verbyla, D. and J. Jones (2011), Mechanisms influencing changes in lake area in Alaskan boreal forest, *Global Change Biology*, *17*, 2567-2583.

Roulet, N.T., Lafleur, P.M., Richard, P.J.H., Moore, T.R., Humphreys, E.R. and J.L. Bubier (2007), Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, *Global Change Biology*, *13*, 397–411.

Rydin, H. and J. Jeglum (2006), *The Biology of Peatlands*, Oxford University Press, Oxford.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. and B. Walker (2001), Catastrophic shifts in ecosystems, *Nature*, *413*, 591-596.

Schwartz, M.D., Ahas, R. and A. Aasa (2006), Onset of spring starting earlier across the Northern Hemisphere, *Global Change Biology*, *12*, 343-351.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and H.L. Miller (Eds.) (2007), *Climate Change 2007 - The Physical Science Basis*, Contribution of working group I to the Fourth Assessment Report of the IPCC, Cambridge University Press, Cambridge, UK.

Steltzer, H. and E. Post (2009), Seasons and life cycles, *Science*, *324*, 886-887.

Straková, P., Penttilä, T., Laine, J. and R. Laiho (in press), Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands, *Global Change Biology*, doi: 10.1111/j.1365-2486.2011.02503.x.

Stuiver, M. and P.J. Reimer (2010), *CALIB6.0 radiocarbon calibration program*, ^{14}Chrono Centre, Queens University, Belfast, Ireland.

Szumigalski, A.R. and S.E. Bayley (1997), Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors, *Écoscience*, *4*(3), 385-393.

Tahvanainen, T. (2010), Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment, *Journal of Ecology*, doi: 10.1111/j.1365-2745.2010.01778.x

Turetsky, M.R. and R.K. Wieder (1999), Boreal bog *Sphagnum* refixes soil-produced and respired $^{14}CO_2$, *Écoscience*, *6*, 587–91.

Turetsky, M., Manning, S.W. and K.R. Wieder (2004), Dating recent peat deposits, *Wetlands*, *24*(2), 324-356.

Turetsky, M.R., Wieder, R.K., Vitt, D.H., Evans, R.J. and K.D. Scott (2007), The disappearance of relict permafrost in boreal north America: effects on peatland carbon storage and fluxes, *Global Change Biology*, *13*, 1922-1934.

Turunen, J., Roulet, N.T. and T.R. Moore (2004), Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada, *Global Biogeochemical Cycles*, *18*, GB3002, doi: 10.1029/2003GB002154.

Turunen, J., Tomppo, E., Tolonen, K. and A. Reinikainen (2002), Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions, *The Holocene*, *12*(1), 69-80.

van Breemen, N. (1995), How *sphagnum* bogs down other plants, *Trends in Ecology and Evolution*, *10*(7), 270-275.

Vitt, D.H., Wieder, K., Halsey, L.A. and M. Turetsky (2003), Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada, *The Bryologist*, *106*(2), 235-245.

Wania, R., Ross, I. and I.C. Prentice (2009), Integrating peatlands and permafrost into a dynamic global vegetation model: 2. Evaluation and sensitivity of vegetation and carbon cycle processes, *Global Biogeochemical Cycles*, *23*, GB3015, doi:10.1029/2008GB003413.

Waythomas, C.F. and Miller, T.P. (2002), Preliminary volcano-hazard assessment for Hayes volcano, Alaska, *United States Geological Survey*, open-file report 02-072.

Wieder, R.K. (2001), Past, present, and future peatland carbon balance: an empirical model based on ^{210}Pb-dated cores, *Ecological Applications*, *11*(2), 327-342.

Yu, Z. (2011), Holocene carbon flux histories of the world's peatlands: global carbon-cycle implications, *The Holocene*, *21*(5), 761-774.

Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P. and D.J. Charman (2011) Peatlands and their role in the global carbon cycle, *Eos Transactions, American Geophysical Union*, *92*(12), 97-98.

Yu, Z., Beilman, D.W. and M.C. Jones (2009), Sensitivity of northern peatland carbon dynamics to Holocene climate change, in *Northern peatlands and carbon cycling*, *American Geophysical Union Monograph Series*, edited by A. Baird et al., AGU, Washington, DC.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W. and S.J. Hunt (2010) Global peatland dynamics since the Last Glacial Maximum, *Geophysical Research Letters*, *37*, L13402, doi:10.1029/2010GL043584.

Yu, Z., Turetsky, M.R., Campbell, I.D. and D.H. Vitt (2001), Modelling long-term peatland dynamics. II. Processes and rates inferred from litter and peat-core data, *Ecological Modelling*, *145*, 159-173.

Zhou, L., Tucker , C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V. and R.B. Myneni (2001), Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999, *Journal of Geophysical Research*, *106*(D17), 20069-20083.

Zobel, M. (1988), Autogenic succession in boreal mires – a review, *Folia Geobotanica et Phytotaxonomica*, *28*, 417-445.

CHAPTER 2

Global-scale pattern of peatland *Sphagnum* growth driven by photosynthetically active radiation and growing season length

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Abstract

High-latitude peatlands contain about one third of the world's soil organic carbon, most of which is derived from partly decomposed *Sphagnum* (peat moss) plants. We conducted a meta-analysis based on a global dataset of *Sphagnum* growth measurements collected from published literature to investigate the effects of bioclimatic variables on *Sphagnum* growth. Analysis of variance and general linear models were used to relate *Sphagnum magellanicum* and *S. fuscum* growth rates to photosynthetically active radiation integrated over the growing season (PAR0) and a moisture index. We found that PAR0 was the main predictor of *Sphagnum* growth for the global dataset, and effective moisture was only correlated with moss growth at continental sites. The strong correlation between *Sphagnum* growth and PAR0 suggests the existence of a global pattern of growth, with slow rates under cool climate and short growing seasons, highlighting the important role of temperature and growing season length in explaining peatland biomass production. Large-scale patterns of cloudiness during the growing season might also limit moss growth. Although considerable uncertainty remains over the carbon balance of peatlands under a changing climate, our results suggest that increasing PAR0 as a result of global warming and lengthening growing seasons could promote *Sphagnum* growth. Assuming that production and decomposition have the same sensitivity to temperature, this enhanced growth could lead to greater peat-carbon sequestration, inducing a negative feedback to climate change.

2.1. Introduction

Peatlands are wetland ecosystems that are primarily distributed across the boreal and subarctic regions of the world. They cover about 3% of the global land area, and represent at least half of the world's wetlands. In these ecosystems, net primary production (NPP) exceeds decomposition, resulting in the formation and accumulation of carbon-rich peat deposits that can be up to tens of meters thick (Rydin and Jeglum, 2006). Since the last deglaciation, peatlands have accumulated over 600 gigatons of organic carbon (GtC) globally (Yu et al., 2010), which constitutes up to about a third of the global soil organic C. Many paleoecological and modeling studies have shown that inter-annual, centennial, and millennial changes in peat-C accumulation rates are mainly controlled by the regional climate (e.g., Mauquoy et al., 2002; Malmer and Wallén, 2004; Frolking et al., 2010), and that warming might promote peat-C sequestration in temperature-sensitive regions by increasing NPP more than decomposition (Frolking et al., 2003; Beilman et al., 2009; Jones and Yu, 2010; Charman et al., submitted; Loisel and Yu, submitted). These results point to a potential increase in the peat C-sink capacity under the ongoing and projected climate warming, which would result in a negative feedback to climate change. However, this finding remains a matter of considerable debate because warming is also expected to promote peat decomposition via direct enhanced microbial decomposition or indirect drying of the peatland surface (Ise et al., 2008; Dorrepaal et al., 2009).

Sphagnum (peat moss) forms vast, nearly continuous carpets that dominate the groundcover of most high-latitude peatlands. Although these bryophytes usually do not contribute the largest proportion of peatlands NPP (Blodau, 2002), they possess recalcitrant tissues that resist microbial breakdown (van Breemen, 1995) and release phenolic compounds that inhibit microbial decomposition (Freeman et al., 2001), making them more decay-resistant than most other peatland plants. As a result, partly decomposed *Sphagnum* remnants account for about 50% of the peatland organic matter (Rydin and Jeglum, 2006). Over time, the imbalance between production and decomposition leads to the formation of *Sphagnum*-rich peat deposits. For this reason, *Sphagnum* is often referred to as the main ‘peat builder’, and peat mosses might store more organic C than any other plant genus worldwide (Clymo and Hayward, 1982, Wieder, 2006).

Each *Sphagnum* species possesses a well-defined ecological niche that is primarily based on peatland surface-moisture conditions, with dry-adapted species forming hummocks, wet-adapted species growing in hollows, and intermediate species colonizing lawns. In general, *Sphagnum* NPP increases along this dry-to-wet moisture gradient, with highest productivity under wet conditions (van Breemen, 1995). However, the rate of decomposition is also highest in wet microhabitats, as wet-adapted species preferentially allocate their resources into labile metabolic carbohydrates rather than in recalcitrant structural carbohydrates (Turetsky et al., 2008). Mineral nutrient richness and abundance also influence *Sphagnum* distribution in peatlands with, in general, a higher diversity in groundwater-fed systems (fens) and less variety in acidic, precipitation-fed peatlands (bogs). Overall, species that inhabit wet fens (e.g., *Sphagnum cuspidatum*) are generally characterized by the highest growth values, whereas dry bog hummocks (e.g., *Sphagnum fuscum*) have the lowest productivity (Gunnarsson, 2005).

Sphagnum growth form is sensitive to local environmental conditions as mosses are unable to actively regulate carbon uptake and water loss because they lack stomata. For example, mosses growing in wet hollows reside in a less dense carpet than mosses growing on drier hummocks (Titus and Wagner, 1984). These wet-adapted species also possess less-developed capillary water transport systems and have a smaller water-holding capacity than dry-adapted species. As a result, mosses growing in wet hollows are typically responsible for the largest variability in growth rate at the local scale: as soon as the water table gets closer to the peatland surface, they grow quickly because of efficient resource allocation strategies, but they also desiccate quickly following water table drawdown (Titus and Wagner, 1984). Dry-adapted species are more resilient to local moisture changes, mostly because of their ability to retain moisture (Luken, 1985). For example, *Sphagnum fuscum* and *S. magellanicum* are generally considered dry-adapted species, as they typically grow on hummocks and lawns, where they form densely packed communities to avoid desiccation (Rydin and Jeglum, 2006). This growth form is a consequence of the preferential resource allocation to structural carbohydrates (Turetsky et al., 2008), and results in a strongly vertical growth component.

Sphagnum productivity has been the object of a series of observational and modeling studies over the past 30 years (see Wieder (2006) for a review). Many studies have found a positive relationship between *Sphagnum* NPP and annual or summer temperature (Moore 1989, Dorrepaal et al., 2003; Gunnarsson, 2005; Breeuwer et al., 2008), or higher *Sphagnum* productivity at lower latitudes (Wieder and Lang, 1983). However, several studies have found no temperature effect or even a reduction in NPP with increasing temperature, possibly because of moisture stress and dehydration

(Weltzin et al., 2001; Gerdol et al., 2007). It was also suggested that higher evapotranspiration as a result of higher temperature might lead to reduced *Sphagnum* NPP (Skre and Oechel, 1981).

In his review on *Sphagnum* productivity, Gunnarsson (2005) found that moss growth was strongly correlated to taxonomic sections (Acutifolia vs. Cuspidata), site-specific microhabitat characteristics (hummocks vs. hollows), and broad climatic gradients. He shows that mean annual temperature and precipitation together explained about 40% of the variance in moss growth, with temperature having the most important effect. The study by Gunnarsson (2005) constituted the first and only compilation effort that aimed at understanding both local- and large-scale controls on peat moss growth. In terms of identifying the effects of climate on *Sphagnum* growth, however, the work by Gunnarsson (2005) has one major drawback: the database included 31 *Sphagnum* species, from which many were (i) very poorly represented (22 out of the 31 species have less than 10 growth measurements), (ii) limited in their geographic range (some species are solely found in maritime, subarctic, or nutrient-rich peatlands), and (iii) characterized by very different productivity values due to phylogeny and microhabitat preferences (e.g., oligotrophic hummock species vs. eutrophic hollow species). This collection of a large number of species might have hindered the detection of fundamental effects of climatic gradients on *Sphagnum* productivity. In contrast, the present study focuses on a synthesis of the climatic factors that influence peatland *Sphagnum* growth using the two most well-studied and abundant species: *S. fuscum* and *S. magellanicum*. This approach should improve our ability to establish large-scale geographic and bioclimatic effects on moss growth by reducing the amount of noise induced by species-specific features.

2.1.1. Research question and rationale

In general, warming is expected to increase plant productivity in cold regions (Nemani et al., 2003; Hudson and Henry, 2009). In the boreal and subarctic ecoregions, warming-induced increases in the growing season length (early spring warming) and earlier snowmelt (water availability) are also believed to change the phenology of plants and promote C sequestration in many ecosystems (e.g., Aurela et al., 2004; Menzel et al., 2006; Schwartz et al., 2006; Stelzer and Post, 2009). These effects should be especially beneficial for *Sphagnum* species because spring photosynthesis starts as soon as (i) the snow cover disappears (or even before complete disappearance), and (ii) daily temperatures reach 0°C, since these non-vascular plants do not root into the colder soil (Moore et al., 2006).

The objective of the present study is to investigate whether the estimated annual growth of two *Sphagnum* species (*S. magellanicum* and *S. fuscum*) can be related to broad environmental controls, namely light, temperature, growing season length, and available moisture. Here we examine large-scale patterns of *Sphagnum* growth using published moss growth values as well as new thermal and moisture indexes. Given that a large amount of peatlands are characterized by extended *Sphagnum* carpets, this study intends to assess the impacts of past, present, and future change in growing season length, PAR, and available moisture on peat biomass production, one of the two most important C flux terms of peatland ecosystems (the other one being peat decomposition).

2.2. Methods

2.2.1. *Sphagnum* growth

We compiled a data set of 142 measurements of *Sphagnum* growth at 52 sites located in North America, Europe, and southern South America. Site latitudes range from 39° to 68° (Fig. 2.1 and Table 2.1). A detailed description of study sites and references can be found in Appendix 2.1. We examined each publication and only recorded data from studies that reported *in situ*, species-specific values of *Sphagnum* stem length growth (LG; cm yr^{-1}). All these measurements were performed following the cranked wire method (Clymo, 1970), a simple but consistent approach that is widely used in peatland ecology. The accuracy of the cranked wire method is mostly limited by the starting and ending dates of the measurements: if the investigator misses out a portion of the early spring and/or late summer growth, the recorded growth increment will not be representative of the entire growing season, and will result in an underestimation of length growth. We assume that all moss growth values used in this study represent all or most of the growing season growth, but we acknowledge that these values most likely represent minimum growth estimates.

Although these LG terms do not take growth form into account, they were preferred over published data of *Sphagnum* biomass and density because the latter two types of data were derived using a wide array of techniques that could not be directly compared. For example, Bauer et al. (2007) used shoot density and shoot mass to determine moss bulk density, Berendse et al. (2001) used the dry weight of the upper 3 cm (including the capitula) of samples that were 7 or 8 cm in diameter, and Gerdol (1995) averaged the dry weight of 10 capitula. As directly comparing these biomass values would have introduced unquantifiable unknowns in our data set (Clymo, 1970), all the measurements were presented as LG values. This approach is justified since

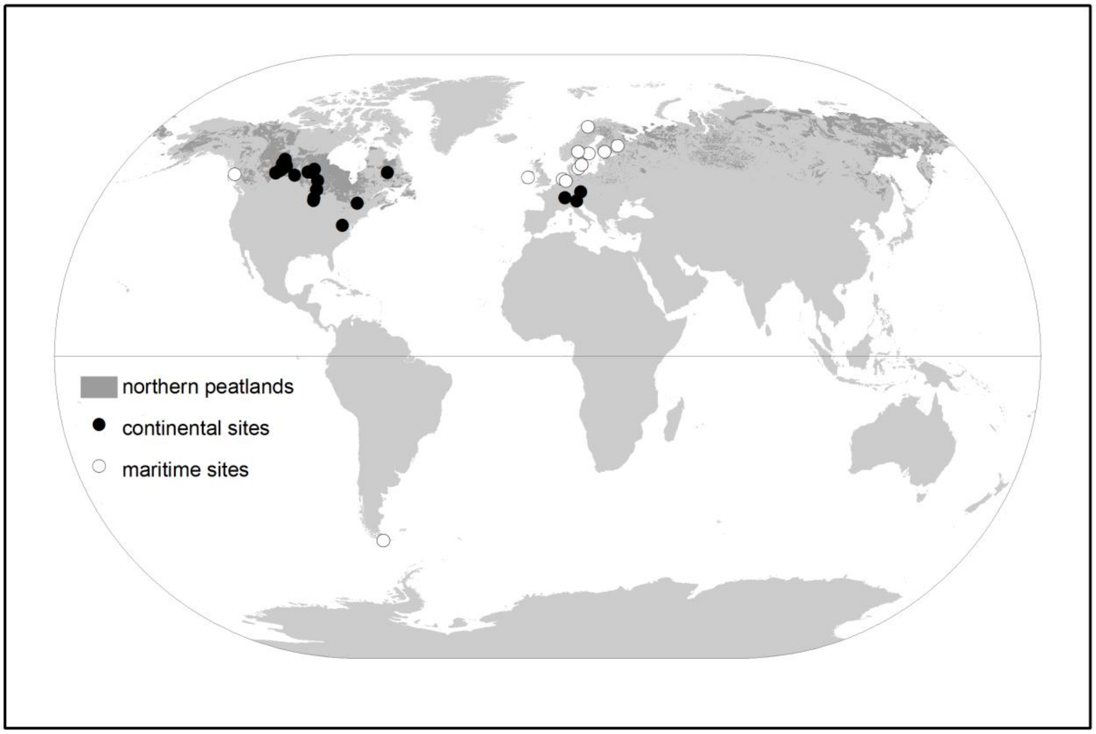

Figure 2.1. Global distribution of study sites (n = 52) with *Sphagnum* growth measurements (n = 142). Black circles indicate continental sites and open circles show maritime sites. The dark shaded area represents the northern peatland extent from Yu et al. (2010).

Table 2.1. Distribution of *Sphagnum* growth measurements in terms of species, peatland type, microform, and continentality.

		number of samples
Species	*Sphagnum fuscum*	100
	Sphagnum magellanicum	42
Peatland type	Bog	111
	Poor fen	20
	Rich fen	11
Microform	Hummock	114
	Lawn	26
	Hollow	2
Continentality	Continental	96
	Maritime	46

Sphagnum growth is predominantly apical, meaning that moss shoots elongate upwards from their apical meristem (Clymo, 1970). From a morphological standpoint, vertical shoot growth is inversely related to branch density so that slower stem growth typically leads to greater branch density. For example, *Sphagnum* length growth will be reduced under dry conditions, but the stem volumetric density will increase, allowing the moss to acquire and retain more moisture (Luken, 1985). This acclimation is partly attributable to the production and 'delivery' mechanisms of branches, which are formed in the capitulum (plant apex) and transferred to the apical meristem as the stem elongates (Rydin and Jeglum, 2006). For these reasons, we assumed that environmental conditions exert a primary control on stem growth, which then influences branch density.

To minimize species-specific differences in length growth, only growth data for *Sphagnum fuscum* (n=100) and *S. magellanicum* (n=42) were compiled. These dry-adapted species were selected due to their ubiquity (Gunnarsson, 2005). We did not use data from fertilized and other experimental treatments, but *Sphagnum* measurements from control plots in experimental manipulation studies were included in the database. For each observation, the peatland type (bog, poor fen, or rich fen), the microform on which the *Sphagnum* was growing (hummock, lawn, or hollow), and site continentality (maritime or continental) were compiled (Table 2.1). Continental and maritime sites were classified using the temperature difference between June and January mean monthly temperatures. If this temperature difference was greater than 25°C, they were classified as continental sites (96 sites); otherwise, they were classified as maritime (46 sites). Only one growth measurement per site, peatland type, microhabitat, year and species was used. If there were many measurements for one of these categories, the mean productivity value was compiled. Species were well distributed among the continentality classes, with each group composed of 60% *Sphagnum fuscum* and 40% *S. magellanicum*. Peatland types were also relatively well distributed among the continentality classes with, for example, 8.3% of continental peatlands being rich fens vs. 6.5% in the maritime group.

2.2.2. Bioclimatic variables

Effects of climate on *Sphagnum* length growth were examined using two compound bioclimatic variables. First, a measure of photosynthetically active radiation integrated over the growing season, i.e. over days with mean temperature above 0°C, (PAR0, in mols photons m^{-2} $season^{-1}$) was computed for each site based on a gridded long-term mean climatology (temperature, precipitation, and sunshine hours) with a spatial resolution of 0.5° for the period 1931-1960 (CLIMATE 2.2; data available at http://www.bridge.bris.ac.uk/ projects/PAIN). PAR0 was calculated from latitude, modern orbital parameters, daily mean temperature values and sunshine hours (Prentice et al., 1993). The instantaneous PAR flux density is first calculated from the incoming shortwave radiation. An integration of this value between sunrise and sunset yields the average daily PAR. This is averaged over the season taking into account latitude and cloudiness. As PAR0 controls plant CO_2 uptake and exerts a direct control on NPP (Chapin et al., 2002), we argue that this variable can be used as a measure of *Sphagnum* carbon fixation potential. Second, the ratio between annual precipitation (P) and the annually integrated equilibrium evapotranspiration (E_q) was used as an index of moisture balance (P/E_q). Both P and E_q were derived from the CLIMATE 2.2 dataset. E_q is a measure of annual potential evapotranspiration that is a function of daily net radiation and temperature (Prentice et al., 1993; Harrison et al., 2010). This moisture index provides a measure of annual plant water availability, and it was preferred to other moisture indexes based on empirical evidence that P/E_q is a superior predictor of the occurrence of peatlands and peatland types (Gallego-Sala et al., 2010; Gallego-Sala and Prentice, submitted). These bioclimatic variables were analyzed to avoid the multicollinearity that often emerges from studies in which predictor variables are closely related to one another (Zar, 2010). Indeed, preliminary analysis showed strong correlations (multicollinearity > 60%) between latitude, growing season temperature (GST) and growing degree days above 0°C (GDD0) for our study sites (data not shown). We avoided such strong intercorrelations in our analysis.

2.2.3. Statistical analysis

Sphagnum length growth values (cm yr^{-1}) were log-transformed to meet the assumption of homoscedasticity before statistical analysis. Growth differences between *Sphagnum* species, peatland types, microforms and continentality classes were tested using one-way analysis of variance (ANOVA). To examine the effect of PAR0 and P/E_q on *Sphagnum* growth, we first determined their respective correlation coefficient (Pearson correlation). Simple linear regressions were also performed to obtain the coefficient of determination between each independent variable and *Sphagnum* growth. These results were then used to build a multiple regression model where the variable with the highest coefficient of correlation was incorporated first, followed by the second variable as well as by their combined effect. Values were centered prior to the multiple regression analyses. Simple and multiple regression analyses of *Sphagnum* growth values were performed on (i) all data altogether, and (ii) each continentality class separately. All analyses were performed using PASW Statistics version 18.0 (SPSS Inc., Chicago, IL, USA).

2.3. Results

2.3.1. Effect of species, peatland type, microform, and continentality on *Sphagnum* productivity

Sphagnum growth rates ranged from 0.1 to 6.0 cm yr^{-1}, with a mean value of 1.4 ± 0.8 (1 SD) cm yr^{-1}. The ANOVA revealed a significant effect of species on productivity (F (1,140) = 5.931, p = 0.016, Table 2.2), with *Sphagnum magellanicum* growing significantly more rapidly than *S. fuscum* (Fig. 2.2). Similarly, continentality had a strong effect on moss growth (F (1,140) = 13.704, $p < 0.0001$, Table 2.2), with continental sites characterized by faster growing samples than maritime sites (Fig. 2.2). Peatland type also had a significant effect on *Sphagnum* growth (F (2,139) = 3.798, p = 0.025, Table 2.2), with rich fens being significantly more productive than bogs (Tukey's LSD: p = 0.01, Fig. 2.2). Finally, the ANOVA performed on microform did not reveal significant moss growth differences between hummocks and lawns-hollows combined (p = 0.181, Table 2.2, Fig. 2.2). For all four ANOVAs, the assumption of equality of variance was met (Levene's test: $p > 0.05$).

2.3.2. Relationships between *Sphagnum* productivity and bioclimatic parameters

The Pearson correlation coefficient between PAR0 and *Sphagnum* growth revealed a positive correlation between these variables (r = 0.48, $p < 0.0001$). However, P/E_q and *Sphagnum* growth were not correlated (r = 0.01, p = 0.456). Similarly, simple

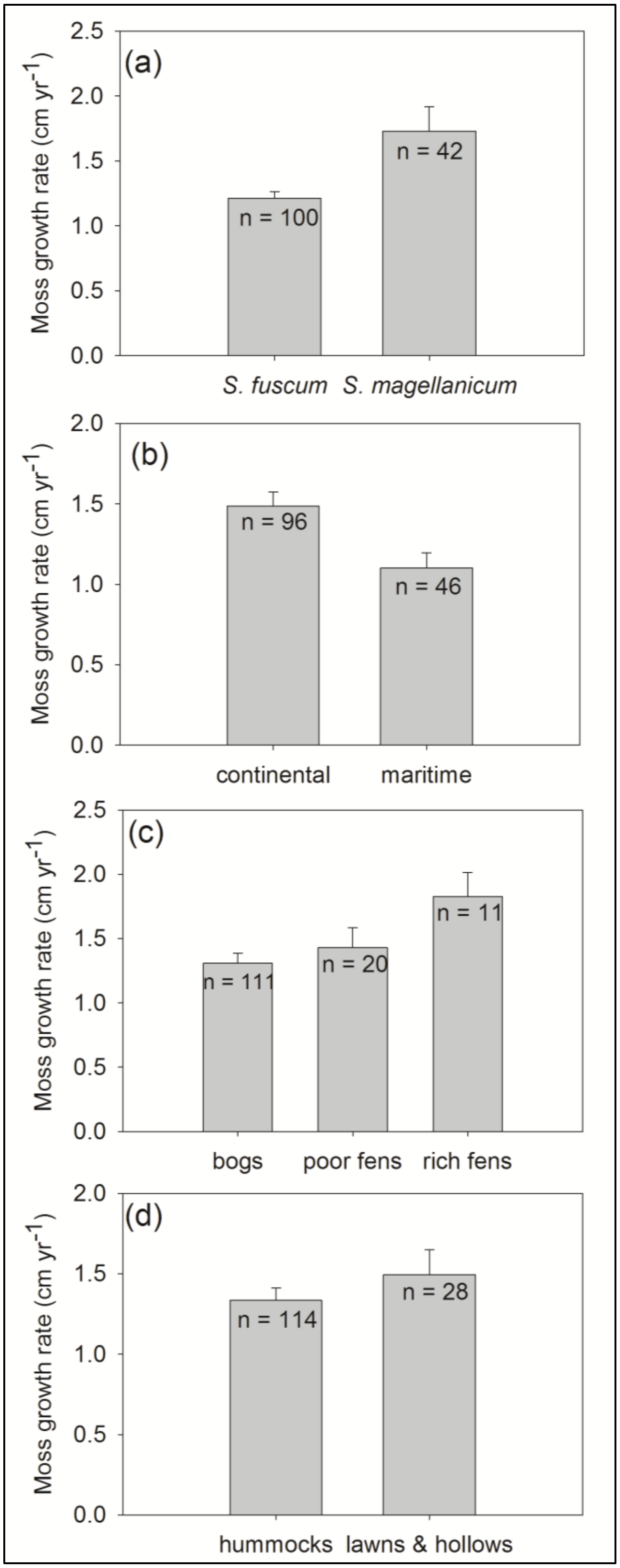

Figure 2.2. *Sphagnum* growth values (mean and standard error) for each species **(a)**, continentality class **(b)**, peatland type **(c)**, and microform **(d)**.

Table 2.2. Results of one-way ANOVA models of *Sphagnum* growth predicted by species, peatland type, microform, and continentality. df: degree of freedom (the comma separates the number of df for the numerator and denominator); p: probability.

	df	F	p
Species	1,140	5.9	0.016
Peatland type	2,139	3.8	0.025
Microform	2,139	1.8	0.181
Continentality	1,140	13.7	<0.0001

Table 2.3. Results of univariate **(a)** and multiple **(b)** regression models of *Sphagnum* growth using all values, continental sites, and maritime sites. df: degree of freedom (the comma separates the number of df for the numerator and denominator); p: probability; PAR0 and P/E_q are defined in the text.

sites	**predictor**	**df**	**adjusted R^2**	**p**
(a) all	PAR0	1, 140	0.23	<0.0001
	P/E_q	1, 140	0.00	0.912
continental	PAR0	1, 94	0.31	<0.0001
	P/E_q	1, 94	0.06	0.009
maritime	PAR0	1, 44	0.02	0.172
	P/E_q	1, 44	0.00	0.690
(b) continental	PAR0	2, 93	0.31	<0.0001
	P/E_q	2, 93	0.01	0.832
	PAR0 x P/E_q	3, 92	0.04	0.444

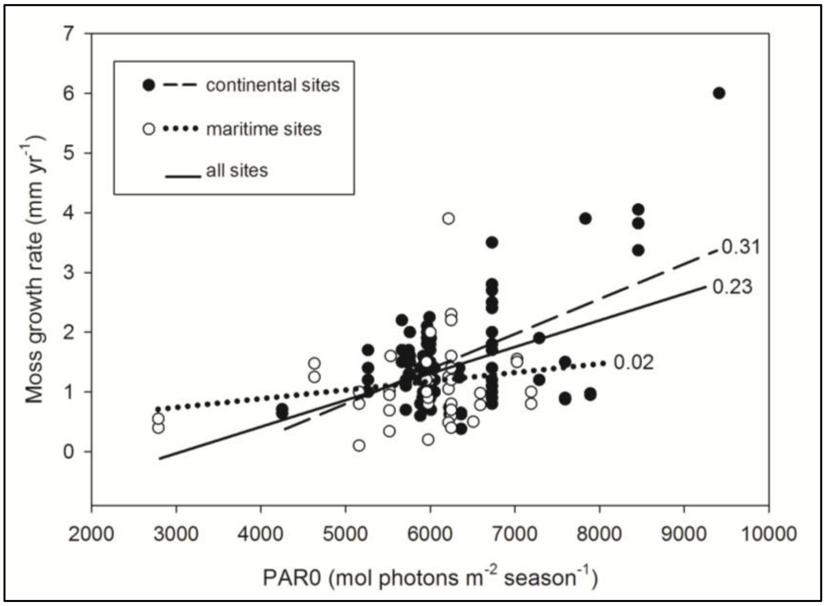

Figure 2.3. Photosynthetically active radiation integrated over the growing season (PAR0) in relation to *Sphagnum* growth. R^2 values are presented next to the regression lines.

linear regressions using all data indicated that PAR0 explained most of the variance in *Sphagnum* growth ($R^2 = 0.23$, $p < 0.0001$, Table 2.3, Fig. 2.3), but that P/E_q did not have a significant effect ($R^2 = 0.00$, $p = 0.912$, Table 2.3). These patterns were somewhat different when continental and maritime sites were examined separately. While PAR0 explained more of the growth variance among continental sites than when all sites were considered ($R^2 = 0.31$, $p < 0.0001$, Table 2.3, Fig. 2.3), it was not significant among maritime sites ($R^2 = 0.02$, $p = 0.172$, Table 3, Fig. 2.3). Interestingly, P/E_q came out as a significant (though poor) predictor of moss growth in continental settings ($R^2 = 0.06$, $p = 0.009$, Table 2.3), but was not significant across the maritime sites ($R^2 = 0.00$, $p = 0.690$, Table 2.3). A multiple regression analysis performed on PAR0 and P/E_q for continental sites indicated that the interaction effect was not significant ($p = 0.444$, Table 2.3), and that these two variables did not explain significantly more variability in *Sphagnum* growth ($R^2 = 0.31$, Table 2.3) than PAR0 alone ($R^2 = 0.31$).

2.4. Discussion

2.4.1. Species, peatland type, and microform effects

At the peatland scale, a large range of *Sphagnum* growth values is generally found (e.g., Moore, 1989; Campbell et al., 2000). This variability has often been attributed to species-specific biochemical mechanisms (Turetsky et al., 2008), and to microhabitat characteristics such as depth to water table (Rydin and Jeglum, 2006) or nutrient input (Bubier et al., 2007). In line with these previous studies, our results indicate that *Sphagnum* growth was different among species (*S. fuscum* vs. *S. magellanicum*) and peatland types (bogs vs. poor fens vs. rich fens). However, growth was not correlated to microform (hummock vs. lawn-hollow), contrary to the idea that wetter microhabitats such as lawns and hollows favor *Sphagnum* growth. Since microform classification is arbitrary, it is possible that microforms with similar hydrological and nutrient conditions were classified as low hummocks at a study site but as lawns in another peatland, limiting our ability to distinguish a microform effect on *Sphagnum* growth. Direct measurements of water table depths would be more useful in analyzing microform influence on moss productivity. A smaller size sample for the lawn-hollow group (n = 28) than for the hummock group (n = 114) might also have limited the potential for a microform effect to be detected (statistical Type II error). Alternatively, it is possible that a microform effect on growth can only be apparent at the peatland scale (i.e., relative differences within a single ecosystem), but cannot be detected at the global scale.

2.4.2. Climatic controls

PAR integrated over the growing season should exert a positive control on peat moss growth in high-latitude regions because plant growth increases with the length and temperature of the growing season. Supporting this hypothesis, PAR0 was the most important variable explaining *Sphagnum* growth in our analysis, with higher PAR0 values associated with greater growth rates. These results suggest that peat moss growth is primarily driven by PAR and the growing season length, and imply that broad-scale controls on *Sphagnum* growth are significant despite the effect of local or site-specific factors such as nutrient influx or depth to water table.

Adequate effective moisture is necessary for peatland development and peat moss growth. In our data synthesis, however, no relationship between moss growth and the moisture index (P/E_q) was found when all sites were considered. These results suggest that, over broad spatial scales, moisture availability does not play a significant role on *Sphagnum* growth. An adequate moisture supply at the local scale is necessary for peat moss growth, but our results suggest it might only play a secondary role when compared to growing season length, temperature, and PAR.

Sphagnum growth from continental sites was mostly sensitive to PAR0 ($p < 0.0001$) and showed an influence of P/E_q ($p = 0.009$). These results suggest that peat moss growth becomes limited with decreasing PAR0 and decreasing moisture availability. In contrast, growth values from maritime sites were neither associated with PAR0 nor P/E_q. These differences between the continentality classes were not due to a species effect since each group was composed of 60% *Sphagnum fuscum* and 40% *S. magellanicum*. Similarly, peatland types were also relatively well distributed among the continentality classes with, for example, 8.3% of continental peatlands being rich fens vs. 6.5% in the maritime group.

The climate space of PAR0 and P/E_q for the northern peatland domain (Yu et al., 2010) is presented to provide context for our results and future work on peatland-climate relationships (Fig. 2.4). Northern peatlands typically occur where PAR0 is between 2000 and 7000 mol photons m^{-2} season^{-1} (mean = 4205), and P/E_q is between 0.3 and 3 (mean = 1.3). Maritime sites from our study were characterized by significantly lower PAR0 and higher P/E_q values than their continental counterpart (Fig. 2.4). The study sites cover the PAR0 and P/E_q climate space relatively well, except for a near-complete absence of data points at PAR0 values lower than 4000 mol photons m^{-2} season^{-1}. Peatland sites where flux tower measurements provide contemporary net ecosystem carbon balance

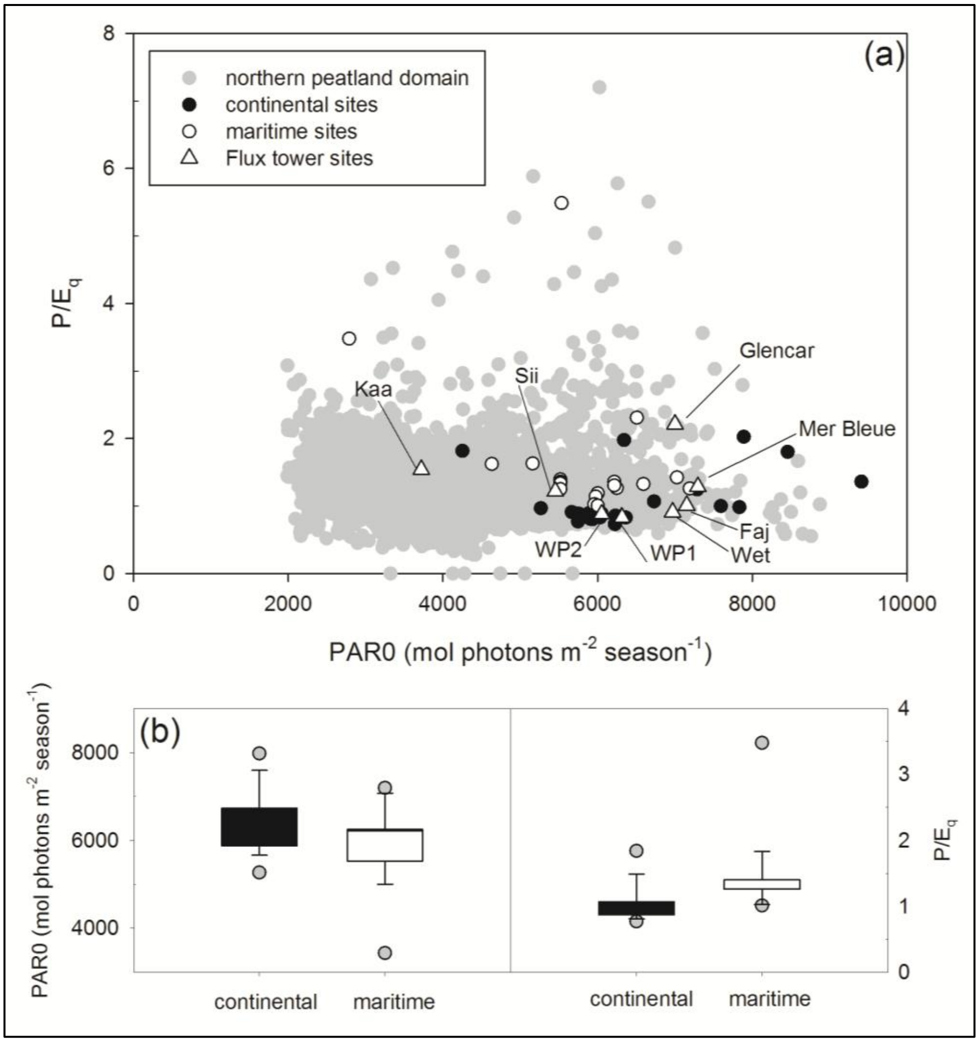

Figure 2.4. *Sphagnum* growth sites in climate space. **(a)** Climate space of photosynthetically active radiation integrated over the growing season (PAR0) and the ratio between annual precipitation and the annually integrated equilibrium evapotranspiration (P/E$_q$) of the northern peatland domain (grey dots) based on 0.5° x 0.5° gridded instrumental climate data (CLIMATE 2.2 dataset) for the period 1960-1990. The northern peatland area is from Yu et al. (2010). Open triangles represent the location (in climate space) of 8 peatland sites where flux tower measurements are available (Lund et al., 2010; Koehler et al., 2011). WP1: western peatland 1 (Canada); WP2: western peatland 2 (Canada); Kaa: Kaamanen (Finland); Wet: Polwet (Poland); Faj: Fajemyr (Sweden); Mer Bleue (Canada); Sii: Siikaneva (Finland); Glencar (Ireland). **(b)** Box plot of PAR and P/E$_q$ values of *Sphagnum* growth sites for continental and maritime sites. The boxes indicate the 25th and 75th percentiles, the whiskers above and below the boxes represent the 10th and 90th percentile, and the circles represent the 5th and 95th percentiles.

budgets are similarly found in the highest PAR0 and lowest P/E_q portion of the climate space (Fig. 2.4). These results imply that much research is needed in colder, higher-latitude regions (with low PAR0), as well as in areas with higher effective moisture (high P/E_q).

Bioclimatic differences between continental and maritime sites could explain the patterns in *Sphagnum* growth. For example, continental sites were characterized by significantly higher PAR0 values than the maritime sites (Fig. 2.4b). In addition, growing season temperature (GST) and July temperature were significantly different between maritime and continental sites (data not shown), with maritime regions characterized by cooler GST and July T than their continental counterparts. Cloudiness may be an important limiting factor for moss growth in maritime settings (Blodau, 2002; Mauquoy et al., 2002). In addition, the short duration or thin snow cover that characterizes peatlands in maritime regions could negatively impact peat moss growth, as snow cover may play a beneficial role in peatlands by preventing freezing-induced damage to *Sphagnum* capitula (Dorrepaal et al., 2003). An extended snow cover during spring time in continental regions might also create a ‘warm’ thermal environment that would allow rapid moss growth during early spring (Tim Moore, pers. comm.). Finally, the effect of diurnal temperature on moisture availability could partly explain why continental sites exhibit significantly higher moss growth than their maritime counterparts, as a greater diurnal temperature difference in continental settings more likely leads to dew formation that provides additional moisture to mosses.

A sampling bias among the maritime sites could also explain the weak correlation between PAR0, P/E_q and moss growth, as well as the overall lower moss growth rates under maritime conditions. As growing season length is relatively long under maritime settings due to mild spring, fall and winter conditions, it is possible that part of the early spring or late fall growth were not measured in the field, resulting in 'minimal' *Sphagnum* growth estimates that are not representative of the entire growing season length. In a study on oxygen isotope analysis ($\delta^{18}O$) of modern *Sphagnum* cellulose in northern England, Daley et al. (2010) showed significant differences between the oxygen isotopic signature of *Sphagnum* cellulose during 'winter' (February, March, November) and 'summer' (May to August), which they attributed to direct water uptake from precipitation year-round. In their study, *Sphagnum* tissues were collected every month of the year and the $\delta^{18}O$ value of alpha-cellulose was measured for each of these monthly samples, as well as in corresponding rain water samples. The isotopic signature of moss samples tracked values obtained from the rain samples, suggesting that water uptake is occurring during 'winter' months in some maritime regions, and that CO_2 uptake and associated plant growth could also be taking place over winter time.

2.4.3. Role of *Sphagnum* growth in regulating peat-C accumulation in northern peatlands

The response of peatlands to warming conditions is tightly coupled to plant growth and peat decomposition. A recent synthesis of 33 northern peatland sites found highly variable peat-carbon accumulation rates over the past 12,000 years, with warming periods coinciding with increases in C accumulation rates (Yu et al., 2009). Similarly, using 77 sites along a north-south transect across the West Siberian Lowlands, Beilman et al. (2009) found a significant correlation between C accumulation and modern mean annual temperature, with warmer sites accumulating more C than colder sites over the past 2000 years. A clear relationship between degree-days and mean annual temperature was also found for long-term peat-C accumulation in Finland and Canada (Clymo et al., 1998), similar to a positive relation between photosynthetically active radiation and growing season length for peat-C accumulation rates over the last millennium throughout the northern hemisphere (Charman et al., submitted). Peatland models have also reported an overall positive effect of warmer temperatures on peat-C sequestration: under a scenario where production and decomposition had the same sensitivity to temperature, productivity effects dominated and enhanced peat accumulation (Frolking et al., 2003). To reverse this trend, a Q_{10} value of 3 for decomposition rate and a Q_{10} value of 2 for productivity were needed. These results clearly show the important role of NPP in controlling peat-C sequestration, and results from our meta-analysis lend support to these paleoecological evidences and modeling results by showing that moss growth primarily responds to photosynthetically active radiation above 0°C over large spatial scales.

2.5. Conclusions and Implication

We showed that *Sphagnum* growth is most strongly controlled by photosynthetically active radiation integrated over the growing season (PAR0), which reflects latitudinal, temperature, and cloudiness gradients. These results indicate the existence of a global pattern in *Sphagnum* growth in relation with broad-scale bioclimatic and geographic gradients. Since *Sphagnum* is the main peat builder in most high-latitude peatlands, these patterns have important implications for our understanding of the biogeographic scaling of *Sphagnum*'s carbon sink function. Our results suggest higher peat production under warming climates if there is no moisture stress, in agreement with the idea that warming could lead to a negative feedback from terrestrial ecosystems as a result of increased net primary production and subsequent increased carbon storage (see Field et al. (2007) for a review). This also supports the recent findings in paleoecological studies by Yu et al. (2009), Beilman et al. (2009), Charman et al. (submitted), and Loisel and Yu (submitted), which suggest that increasing net primary production under warmer conditions during the Holocene may enhance long-term peat-carbon sequestration, contrary to a hypothesized overriding effect of increased peat decomposition under warming conditions (Ise et al., 2008; Dorrepaal et al., 2009). Specifically, increasing *Sphagnum* growth under a warming climate may shift the balance of productivity and decomposition, favoring peat-carbon sequestration. However, the relative importance of change in production and decomposition under warm climates in the future will depend on the direction and magnitude of moisture changes, which can best be evaluated with peatland models that incorporate both temperature and moisture functions of production and decomposition processes. To this effect, the present meta-analysis is particularly useful for testing and validating the peatland ecosystem models that are used for future projections, as it clearly shows the important role of PAR0 on peatland biomass production, a component that is neglected in peatland ecosystem models (e.g., Frolking et al., 2010). Furthermore, important data gaps have been identified from the climate space of PAR0 and available moisture (P/E_q) of the northern peatland domain. Future studies on modern *Sphagnum* growth and contemporary peatland flux measurements should focus on site in these regions to generate maximum knowledge in climate controls over plant production and carbon sequestration in peatlands.

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2.7. References

Aurela, M., Laurila, T. & Tuovinen, J.-P. (2004) The timing of snow melt controls the annual CO_2 balance in a subarctic fen. Geophysical Research Letters, 31, L16119. doi: 10.1029/2004/ GL020315.

Bauer, I.E., Tirlea, D., Bhatti, J.S. & Errington, R.C. (2007) Environmental and biotic controls on bryophyte productivity along forest to peatland ecotones, Canadian Journal of Botany, 85, 463-475.

Beilman, D.W., MacDonald, G.M., Smith, L.C. & Reimer, P.J. (2009) Carbon accumulation in peatlands of West Siberia over the last 2000 years. Global Biogeochemical cycles, 23, GB1012. doi: 10.1029/2007GB003112.

Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H. & Wallén, B. (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs, Global Change Biology, 7, 591-598.

Blodau, C. (2002) Carbon cycling in peatlands - A review of processes and controls, Environmental Reviews, 10, 111-134.

Breeuwer, A. Heijmans, M.P.D., Robroek, B.J.M. & Berendse, F. (2008) The effect of temperature on growth and competition between *Sphagnum* species. Oecologia, 156, 155-167.

Bubier, J.L., Moore, T.R. & Bledzki, L.A. (2007) Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog, Global Change Biology, 13, 1-19.

Campbell, C., Vitt, D.H., Halsey, L.A., Campbell, I.D., Thormann, M.N. & Bayley, S.E. (2000) Net primary production and standing biomass in northern continental wetlands. Natural Resources Canada, Report NOR-X-369, Canadian Forest Service, Edmonton.

Chapin, F.S. III, Matson, P.A. & Mooney, H.A. (2002) Principles of terrestrial ecosystem ecology, Springer.

Charman, D., Beilman, D., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F., Christen, J.A., Gallego-Sala, A.V., Harrison, S.P., Hughes, P.D.M., Jackson, S., Korhola, A., Mauquoy, D., Mitchell, F., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z., Alm, J., Bauer, I.E.,McCorish, Y., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D. & Zhao, Y. (submitted in 2011) Climate-driven changes in peatland carbon accumulation during the last millennium, Proceedings of the National Academy of Sciences of the USA, manuscript 2011-19956.

Clymo, R.S. (1970) The growth of *Sphagnum*: methods of measurement, Journal of Ecology, 58 (1), 13-49.

Clymo, R.S. & Hayward, P.M. (1982) The ecology of *Sphagnum*. Bryophyte ecology (ed. by A.J.E. Smith), pp. 229-289, Chapman & Hall, London.

Clymo, R.S., Turunen, J. & Tolonen, K. (1998) Carbon accumulation in peatlands, Oikos, 81 (2), 368-388.

Daley, T.J., Barber, K.E., Street-Perrott, F.A., Loader, N.J., Marshall, J.D., Crowley, S.F.

& Fisher, E.H. (2010) Holocene climate variability revealed by oxygen isotope analysis of *Sphagnum* cellulose from Walton Moss, northern England, Quaternary Science Reviews, 29, 1590-1601.

Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V. & van Logtestijn, R.S.P. (2003) Summer warming and increased winter snow cover affect *Sphagnum* fuscum growth, structure and production in a sub-arctic bog. Global Change Biology, 10, 93–104.

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V. & Aerts, R. (2009) Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature, 460, 616-620.

Field, C.B., Lobell, D.B., Peters, H.A. & Chiariello, N.R. (2007) Feedbacks of terrestrial ecosystems to climate change, Annual Review of Environment and Resources, 32, 1-29.

Freeman, C., Ostle, N. & Kang, H. (2001) An enzymic ‘latch’ on a global carbon store, Nature, 409, 149.

Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M. & Muller, S.D. (2003) Modeling northern peatland decomposition and peat accumulation, Ecosystems, 4, 479-498.

Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J. & Richard, P.J.H. (2010) A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation, Earth Systems Dynamics Discussions, 1, 115-167.

Gallego-Sala, A.V. & Prentice, I.C. (submitted in 2012) Blanket bog, an endangered biome, Nature Climate Change.

Gallego-Sala, A.V., Clark, J.M., house, J.I., Orr, H.G., Prentice, I.C., Smith, P., Farewell, T. & Chapman, S.J. (2010) Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain, Climate Research, 34, C911, doi: 10.3354/cr00911.

Gerdol, R. (1995) The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures, Journal of Ecology, 83 (3), 431-437.

Gerdol, R., Petraglia, A., Bragazza, L., Iacumin, P. & Brancaleoni, L. (2007) Nitrogen deposition interacts with climate in affecting production and decomposition rates in *Sphagnum* mosses, Global Change Biology, 13, 1810-1821.

Gunnarsson, U. (2005) Global patterns of *Sphagnum* productivity, The Bryologist, 27, 269-279.

Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K.E., Ni, J. & Sutra, J.-P. (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification, 21 (2), 300-317.

Hudson, J.M.G. & Henry, G.H.R. (2009) Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology, 90 (10), 2657-2663.

Ise, T., Dunn, A.L., Wosfy, S.C. & Moorcroft, P.R. (2008) High sensitivity of peat decomposition to climate change through water-table feedback. Nature Geoscience, 1, 763-766.

Jones, M.C. & Yu, Z. (2010) Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proceedings of the National Academy of Sciences of the USA, 107 (16), 7347-7352.

Koehler, A.-K., Sottocornola, M. & Kiely, G. (2011) How strong is the current carbon sequestration of an Atlantic blanket bog? Global change Biology, 17, 309-319.

Loisel, J. and Yu, Z. (submitted in 2011), Recent acceleration of carbon accumulation in a boreal peatland, south-central Alaska, Journal of Geophysical Research - Biogeosciences.

Lund, M., Lafleur, P.M., Roulet, N.T., Lindroth, A., Christensen, T.R., Aurela, M., Chojnicki, B.H., Flanagan, L.B., Humphreys, E.R., Laurila, T., Oechel, W.C., Olejnik, J., Rinne, J., Schubert, P. & Nilsson, M.B. (2010) Variability in exchange of CO_2 across 12 northern peatland and tundra sites, Global Change Biology, 16, 2436-2448.

Luken, J.O. (1985) Zonation of *Sphagnum* mosses: interactions among shoot growth, growth form, and water balance, The Bryologist, 88 (4), 374-379.

Malmer, N. & Wallén, B. (2004) Input rates, decay losses and accumulation rates of carbon in bogs during the last millenium: internal processes and environmental changes. The Holocene, 14 (1), 111-117.

Mauquoy, D., Engelkes, T., Groot, M.H.M., Markesteijn, F., Oudejans, M.G., van der Plicht, J. & van Geel, B. (2002) High-resolution records of late-Holocene climate change and carbon accumulation in two north-west European ombrotrophic peat bogs. Paleogeography, Paleoclimatology, Paleoecology, 186, 275-310.

Menzel , A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., De Fila, C., Donnelly, A., Filella, Y., Jatcza, K., Måge, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S. & Zust, A. (2006) European phenological response to climate change matches the warming pattern, Global Change Biology, 12, 1969-1976.

Moore, T.R. (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada, Canadian Journal of Botany, 67, 1203-1207.

Moore, T.R., Lafleur, P.M., Poon, D.M.I., Heumann, B.W., Seaquist, J.W. & Roulet, N.T. (2006) Spring photosynthesis in a cool temperate bog, Global Change Biology, 12, 2323-2335.

Nemani,, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneli, R.B. & Running, S.W. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999, Science, 300, 1560-1563.

Prentice, I.C., sykes, M.T. & Cramer, W. (1993) A simulation model for the transient effects of climate change on forest landscapes, Ecological Modelling, 65, 51-70.

Rydin, H. & Jeglum, J. (2006) The Biology of Peatlands, Oxford University Press, Oxford.

Schwartz, M.D., Ahas, R. & Aasa, A. (2006) Onset of spring starting earlier across the Northern Hemisphere, Global Change Biology, 12, 343-351.

Skre, O. & Oechel, W.C. (1981) Moss functioning in different taiga ecosystems in interior Alaska, Oecologia, 48 (1), 50-59.

Steltzer, H. & Post, E. (2009) Seasons and life cycles. Science, 324, 886-887.

Titus, J.E. & Wagner, D.J. (1984) Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox, Ecology, 65 (6), 1765-1774.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H. & Wieder, R.K. (2008) Trade-offs in resource allocation among *Sphagnum* species control decomposition in boreal peatlands, Journal of Ecology, 96, 1297-1305.

van Breemen, N. (1995) How *Sphagnum* bogs down other plants, Trends in Ecology and Evolution, 10 (7), 270-275.

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J. & Vonderharr, M. (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations, Oecologia, 128 (4), 557-565.

Wieder, R.K. & Lang, G.E. (1983) Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia, The Bryologist, 86 (3), 280-286.

Wieder, R.K. (2006) Primary production in boreal peatlands. Boreal peatland ecosystems (ed. by R.K. Wieder & D.H. Vitt), pp. 145-163, Ecological Studies 188, Springer-Verlag Berlin Heidelberg.

Yu, Z., Beilman, D.W. & Jones, M.C. (2009) Sensitivity of northern peatland carbon dynamics to Holocene climate change. Carbon cycling in northern peatlands (ed. by A.J. Baird, L.R. Belyea, X. Comas, A. Reeve & L. Slater), pp. 55-69, Geophysical Monograph 184, American Geophysical Union, Washington.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W. & Hunt, S.J. (2010) Global peatland dynamics since the Last Glacial Maximum. Geophysical Research Letters, 37, L13402. doi:10.1029/ 2010GL043584

Zar, J.H. (2010) Biostatistical analysis, 5th edition, Pearson Prentice Hall.

2.8. Appendix: Summary of study site information.

ID	1st author	Year publ.	Journal	site	coordinates Y	X	peatland type	microform	*Sphagnum* species	Year meas.	meas. method
1	Asada	2003	*The Bryologist*	Diana Lake	54.22	-130.17	poor fen	hummock	*fuscum*	1999	CW
2	Bauer	2007	*Can J of Bot*	Old Black spruce	53.98	-105.11	poor fen	hummock	*fuscum*	2004	CW
3	Camill	2001	*Ecosystems*	collapse scar	52.35	-94.7	poor fen	hummock	*fuscum*	1996	CW
4	Camill	2001	*Ecosystems*	collapse scar	55.73	-97.85	poor fen	hummock	*fuscum*	1996	CW
5	Camill	2001	*Ecosystems*	collapse scar	54.9	-98.63	poor fen	hummock	*fuscum*	1996	CW
6	Camill	2001	*Ecosystems*	collapse scar	54.88	-100.02	poor fen	hummock	*fuscum*	1996	CW
7	Camill	2001	*Ecosystems*	permafrost plateau	52.35	-94.7	bog	hummock	*fuscum*	1996	CW
8	Camill	2001	*Ecosystems*	permafrost plateau	55.73	-97.85	bog	hummock	*fuscum*	1996	CW
9	Camill	2001	*Ecosystems*	permafrost plateau	54.9	-98.63	bog	hummock	*fuscum*	1996	CW
10	Camill	2001	*Ecosystems*	permafrost plateau	54.88	-100.02	bog	hummock	*fuscum*	1996	CW
11	Camill	2001	*Ecosystems*	permafrost plateau	52.35	-94.7	bog	hummock	*fuscum*	1998	CW
12	Camill	2001	*Ecosystems*	permafrost plateau	55.73	-97.85	bog	hummock	*fuscum*	1998	CW
13	Camill	2001	*Ecosystems*	permafrost plateau	54.9	-98.63	bog	hummock	*fuscum*	1998	CW
14	Camill	2001	*Ecosystems*	permafrost plateau	54.88	-100.02	bog	hummock	*fuscum*	1998	CW
15	Camill	2001	*Ecosystems*	collapse scar	52.35	-94.7	poor fen	hummock	*fuscum*	1998	CW
16	Camill	2001	*Ecosystems*	collapse scar	55.73	-97.85	poor fen	hummock	*fuscum*	1998	CW
17	Camill	2001	*Ecosystems*	collapse scar	54.9	-98.63	poor fen	hummock	*fuscum*	1998	CW
18	Camill	2001	*Ecosystems*	collapse scar	54.88	-100.02	poor fen	hummock	*fuscum*	1998	CW
19	Chapin	2004	*Wetlands*	Toivola	47.18	-93.73	bog	hummock	*fuscum*	1995	CW
20	Chapin	2004	*Wetlands*	Toivola	47.18	-93.73	bog	hummock	*fuscum*	1996	CW
21	Chapin	2004	*Wetlands*	Toivola	47.18	-93.73	bog	hummock	*fuscum*	1997	CW
22	Damman	1978	*Oikos*	Tranerods Mosse	56.08	13.17	bog	hummock	*fuscum*	1974	CW
23	Dorrepall	2003	*Glob Ch Biol*	Lake Tornetrask	68.35	18.82	bog	hummock	*fuscum*	2001	CW
24	Dorrepall	2003	*Glob Ch Biol*	Lake Tornetrask	68.35	18.82	bog	hummock	*fuscum*	2002	CW
25	Granath	2010	*Ecology*	Ha¨ llefja¨ rd	60.5	17.95	rich fen	hollow	*fuscum*	2006	CW
26	Granath	2010	*Ecology*	Hallefjard	60.5	17.95	rich fen	lawn	*fuscum*	2006	CW
27	Granath	2010	*Ecology*	Hallefjard	60.5	17.95	rich fen	hummock	*fuscum*	2006	CW
28	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*fuscum*	1996	CW
29	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*fuscum*	1997	CW
30	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*fuscum*	1998	CW
31	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*fuscum*	1996	CW

32	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*fuscum*	1997	CW
33	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*fuscum*	1998	CW
34	Hajek	2009	*Boreal Env Res*	Rokytecka slat	49.02	13.42	bog	hummock	*fuscum*	2001	CW
35	Lindholm	1990	*Ann Bot Fennici*	Laaviosuo	61.03	25	bog	hummock	*fuscum*	1975	CW
36	Lindholm	1990	*Ann Bot Fennici*	Laaviosuo	61.03	25	bog	hummock	*fuscum*	1976	CW
37	Lindholm	1990	*Ann Bot Fennici*	Laaviosuo	61.03	25	bog	hummock	*fuscum*	1977	CW
38	Lindholm	1990	*Ann Bot Fennici*	Laaviosuo	61.03	25	bog	hummock	*fuscum*	1978	CW
39	Moore	1989	*Can J of Bot*	Site D	54.8	-66.82	poor fen	hummock	*fuscum*	1984	CW
40	Moore	1989	*Can J of Bot*	Site D	54.8	-66.82	poor fen	hummock	*fuscum*	1985	CW
41	Moore	2002	*J of Ecol*	Mer Bleue	45.68	-75.8	bog	hummock	*fuscum*	1999	CW
42	Robroek	2007	*Plant Ecol*	Mongan Bog	53.32	-7.97	bog	hummock	*fuscum*	2003	see paper
43	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	hummock	*fuscum*	1984	CW
44	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	hummock	*fuscum*	1985	CW
45	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	hummock	*fuscum*	1986	CW
46	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	hummock	*fuscum*	1987	CW
47	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	hummock	*fuscum*	1984	CW
48	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	hummock	*fuscum*	1985	CW
49	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	hummock	*fuscum*	1986	CW
50	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	hummock	*fuscum*	1987	CW
51	Thormann	1997	*Ecoscience*	Bog site	54.68	-113.35	bog	hummock	*fuscum*	1993	CW
52	Thormann	1997	*Ecoscience*	Bog site	54.68	-113.35	bog	hummock	*fuscum*	1994	CW
53	Vitt	2003	*The Bryologist*	Steppbank	56.88	-111.27	bog	hummock	*fuscum*	2000	CW
54	Vitt	2003	*The Bryologist*	Anzac West	56.45	-111.05	bog	hummock	*fuscum*	2000	CW
55	Vitt	2003	*The Bryologist*	Anzac East	56.45	-111.03	bog	hummock	*fuscum*	2000	CW
56	Vitt	2003	*The Bryologist*	Thickwood Hills	56.78	-112.02	bog	hummock	*fuscum*	2000	CW
57	Vitt	2003	*The Bryologist*	Wandering River	55.28	-112.47	bog	hummock	*fuscum*	2000	CW
58	Vitt	2003	*The Bryologist*	Bleak Lake	54.68	-113.47	bog	hummock	*fuscum*	2000	CW
59	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*fuscum*	1980	CW
60	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*fuscum*	1981	CW
61	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*fuscum*	1982	CW
62	Wieder	2010	*J of Paleolimn*	Birch Mountains 7	58.67	-112.27	bog	hummock	*fuscum*	2005	CW
63	Wieder	2010	*J of Paleolimn*	Birch Mountains 10	57.32	-112.4	bog	hummock	*fuscum*	2005	CW
64	Wieder	2010	*J of Paleolimn*	Birch Mountains 11	57.7	-111.9	bog	hummock	*fuscum*	2005	CW
65	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 7	57.15	-110.87	bog	hummock	*fuscum*	2005	CW

66	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 10	56.63	-110.2	bog	hummock	*fuscum*	2005	CW
67	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 11	57.28	-111.23	bog	hummock	*fuscum*	2005	CW
68	Wieder	2010	*J of Paleolimn*	Stony Mountains 7	55.68	-111.83	bog	hummock	*fuscum*	2005	CW
69	Wieder	2010	*J of Paleolimn*	Stony Mountains 8	56.22	-111.2	bog	hummock	*fuscum*	2005	CW
70	Wieder	2010	*J of Paleolimn*	Stony Mountains 9	56.22	-111.25	bog	hummock	*fuscum*	2005	CW
71	Wieder	2010	*J of Paleolimn*	W Fort McMurray 4	57.15	-111.98	bog	hummock	*fuscum*	2005	CW
72	Wieder	2010	*J of Paleolimn*	Birch Mountains 7	58.67	-112.27	bog	hummock	*fuscum*	2006	CW
73	Wieder	2010	*J of Paleolimn*	Birch Mountains 10	57.32	-112.4	bog	hummock	*fuscum*	2006	CW
74	Wieder	2010	*J of Paleolimn*	Birch Mountains 11	57.7	-111.9	bog	hummock	*fuscum*	2006	CW
75	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 7	57.15	-110.87	bog	hummock	*fuscum*	2006	CW
76	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 10	56.63	-110.2	bog	hummock	*fuscum*	2006	CW
77	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 11	57.28	-111.23	bog	hummock	*fuscum*	2006	CW
78	Wieder	2010	*J of Paleolimn*	Stony Mountains 7	55.68	-111.83	bog	hummock	*fuscum*	2006	CW
79	Wieder	2010	*J of Paleolimn*	Stony Mountains 8	56.22	-111.2	bog	hummock	*fuscum*	2006	CW
80	Wieder	2010	*J of Paleolimn*	Stony Mountains 9	56.22	-111.25	bog	hummock	*fuscum*	2006	CW
81	Wieder	2010	*J of Paleolimn*	W Fort McMurray 4	57.15	-111.98	bog	hummock	*fuscum*	2006	CW
82	Wieder	2010	*J of Paleolimn*	Birch Mountains 7	58.67	-112.27	bog	hummock	*fuscum*	2007	CW
83	Wieder	2010	*J of Paleolimn*	Birch Mountains 10	57.32	-112.4	bog	hummock	*fuscum*	2007	CW
84	Wieder	2010	*J of Paleolimn*	Birch Mountains 11	57.7	-111.9	bog	hummock	*fuscum*	2007	CW
85	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 7	57.15	-110.87	bog	hummock	*fuscum*	2007	CW
86	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 10	56.63	-110.2	bog	hummock	*fuscum*	2007	CW
87	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 11	57.28	-111.23	bog	hummock	*fuscum*	2007	CW
88	Wieder	2010	*J of Paleolimn*	Stony Mountains 7	55.68	-111.83	bog	hummock	*fuscum*	2007	CW
89	Wieder	2010	*J of Paleolimn*	Stony Mountains 8	56.22	-111.2	bog	hummock	*fuscum*	2007	CW
90	Wieder	2010	*J of Paleolimn*	Stony Mountains 9	56.22	-111.25	bog	hummock	*fuscum*	2007	CW
91	Wieder	2010	*J of Paleolimn*	W Fort McMurray 4	57.15	-111.98	bog	hummock	*fuscum*	2007	CW
92	Wieder	2010	*J of Paleolimn*	Birch Mountains 7	58.67	-112.27	bog	hummock	*fuscum*	2008	CW
93	Wieder	2010	*J of Paleolimn*	Birch Mountains 10	57.32	-112.4	bog	hummock	*fuscum*	2008	CW
94	Wieder	2010	*J of Paleolimn*	Birch Mountains 11	57.7	-111.9	bog	hummock	*fuscum*	2008	CW
95	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 7	57.15	-110.87	bog	hummock	*fuscum*	2008	CW
96	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 10	56.63	-110.2	bog	hummock	*fuscum*	2008	CW
97	Wieder	2010	*J of Paleolimn*	NE Fort McMurray 11	57.28	-111.23	bog	hummock	*fuscum*	2008	CW
98	Wieder	2010	*J of Paleolimn*	Stony Mountains 7	55.68	-111.83	bog	hummock	*fuscum*	2008	CW
99	Wieder	2010	*J of Paleolimn*	Stony Mountains 9	56.22	-111.25	bog	hummock	*fuscum*	2008	CW

100	Wieder	2010	*J of Paleolimn*	W Fort McMurray 4	57.15	-111.98	bog	hummock	*fuscum*	2008	CW
101	Aerts	1992	*J of Ecol*	Akhul	57.08	14.5	bog	lawn	*magellanicum*	1990	CW
102	Aerts	2001	*J of Ecol*	Akhul	57.08	14.5	bog	lawn	*magellanicum*	-	CW
103	Berendse	2001	*Glob Ch Biol*	Salmisuo	62.78	30.93	bog	lawn	*magellanicum*	1998	CW
104	Berendse	2001	*Glob Ch Biol*	Kopparasmyren	57.13	14.5	bog	lawn	*magellanicum*	1998	CW
105	Berendse	2001	*Glob Ch Biol*	Chaux-des-Breuleux	47.22	7.05	bog	lawn	*magellanicum*	1998	CW
106	Berendse	2001	*Glob Ch Biol*	Dwingeloo	52.82	6.42	bog	lawn	*magellanicum*	1998	CW
107	Berendse	2001	*Glob Ch Biol*	Salmisuo	62.78	30.93	bog	lawn	*magellanicum*	1998	CW
108	Berendse	2001	*Glob Ch Biol*	Kopparasmyren	57.13	14.5	bog	lawn	*magellanicum*	1998	CW
109	Berendse	2001	*Glob Ch Biol*	Chaux-des-Breuleux	47.22	7.05	bog	lawn	*magellanicum*	1998	CW
110	Berendse	2001	*Glob Ch Biol*	Dwingeloo	52.82	6.42	bog	lawn	*magellanicum*	1998	CW
111	Damman	1978	*Oikos*	Tranerods Mosse	56.08	13.17	bog	hummock	*magellanicum*	1974	CW
112*	Gerold	1995	*J of Ecol*	I Dossi	46.32	11.67	bog	hummock	*magellanicum*	1989	CW
113*	Gerold	1995	*J of Ecol*	I Dossi	46.32	11.67	bog	hummock	*magellanicum*	1990	CW
114*	Gerold	1995	*J of Ecol*	I Dossi	46.32	11.67	bog	hummock	*magellanicum*	1991	CW
115	Grigal	1985	Can J of Bot	Marcel Exp Forest	46.5	-93.5	bog	hummock	*magellanicum*	1983	CW
116	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*magellanicum*	1996	CW
117	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*magellanicum*	1997	CW
118	Gunnarsson	2000	*New Phytol*	Akhultmyr	57.1	14.55	bog	hummock	*magellanicum*	1998	CW
119	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*magellanicum*	1996	CW
120	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*magellanicum*	1997	CW
121	Gunnarsson	2000	*New Phytol*	Luttumyr	61.03	13.37	bog	hummock	*magellanicum*	1998	CW
122*	Hajek	2009	*Boreal Env Res*	Rokytecka slat	49.02	13.42	bog	hummock	*magellanicum*	2001	CW
123	Limpens	2004	*Ecosystems*	Clara Bog	52.32	7.6	bog	lawn	*magellanicum*	1998	CW
124	Limpens	2004	*Ecosystems*	Clara Bog	52.32	7.6	bog	lawn	*magellanicum*	1999	CW
125	Limpens	2004	*Ecosystems*	Clara Bog	52.32	7.6	bog	lawn	*magellanicum*	2000	CW
126	Limpens	2004	*Ecosystems*	Clara Bog	52.32	7.6	bog	lawn	*magellanicum*	2001	CW
127	Moore	2002	*J of Ecol*	Mer Bleue	45.68	-75.8	bog	hollow	*magellanicum*	1999	CW
128	Robson	2003	*New Phytol*	Tierra del Fuego NP	-54.85	-68.6	bog	lawn	*magellanicum*	1999	CW
129	Robson	2003	*New Phytol*	Tierra del Fuego NP	-54.85	-68.6	bog	lawn	*magellanicum*	2000	CW
130	Robson	2003	*New Phytol*	Tierra del Fuego NP	-54.85	-68.6	bog	lawn	*magellanicum*	2001	CW
131	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	lawn	*magellanicum*	1984	CW
132	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	lawn	*magellanicum*	1985	CW
133	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	lawn	*magellanicum*	1986	CW

134	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	poor fen	lawn	*magellanicum*	1987	CW
135	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	lawn	*magellanicum*	1984	CW
136	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	lawn	*magellanicum*	1985	CW
137	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	lawn	*magellanicum*	1986	CW
138	Rochefort	1990	*Ecology*	Exp Lakes Area	49.67	-93.72	rich fen	lawn	*magellanicum*	1987	CW
139	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*magellanicum*	1980	CW
140	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*magellanicum*	1981	CW
141	Wallen	1988	*Holarctic Ecol*	Akhultmyren	57.1	14.53	bog	hummock	*magellanicum*	1982	CW
142	Wieder	1983	*The Bryologist*	Big Run Bog	39.12	-79.58	bog	hummock	*magellanicum*	1981	CW

References

Aerts, R., Wallén, B. & Malmer, N. (1992) Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply, Journal of Ecology, 80 (1), 131-140.

Asada, T., Warner, B.G. & Banner, A. (2003) Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada, The Bryologist, 106 (4), 516-527.

Bauer, I.E., Tirlea, D., Bhatti, J.S. & Errington, R.C. (2007) Environmental and biotic controls on bryophyte productivity along forest to peatland ecotones, Canadian Journal of Botany, 85, 463-475.

Berendse, F., van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H. & Wallén, B. (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs, Global Change Biology, 7, 591-598.

Camill, P., Lynch, J.A., Clark, J.S., Adams, J.B. & Jordan, B. (2001) Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada, Ecosystems, 4 (5), 461-478.

Chapin, C.T., Bridgham, S.D. & Pastor, J. (2004) pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen, Wetlands, 24 (1), 186-201.

Damman, A.W.H. (1978) Distribution and movement of elements in ombrotrophic peat bogs, Oikos, 30 (3), 480-495.

Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V. & van Logtestijn, R.S.P. (2003) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. Global Change Biology, 10, 93–104.

Gerold, R. (1995) The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures, Journal of Ecology, 83 (3), 431-437.

Granath, G., Strengbom, J. & Rydin, H. (2010) Rapid ecosystem shifts in peatlands: linking plant physiology and succession, Ecology, 91 (10), 3047-3056.

Grigal, D.F. (1985) *Sphagnum* production in forested bogs of northern Minnesota, Canadian Journal of Botany, 63, 1204-1207.

Gunnarsson, U. & Rydin, H. (2000) Nitrogen fertilization reduces *Sphagnum* production in bog communities, New Phytologist, 147 (3), 527-537.

Hajek, T. (2009) Habitat and species controls on *Sphagnum* production and decomposition in a mountain raised bog, Boreal Environmental Research, 14, 947-958.

Limpens, J., Berendse, F. & Klees, H. (2004) How phosphorus availability affects the impact of nitrogen deposition on *Sphagnum* and vascular plants in bogs, Ecosystems, 7 (8), 793-804.

Lindholm, T. (1990) Growth dynamics of the peat moss *Sphagnum fuscum* on hummocks on a raised bog in southern Finland, Ann Bot Fennici, 27, 67-78.

Moore, T.R. (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada, Canadian Journal of Botany, 67, 1203-1207.

Moore, T.R., bubier, J.L., Frolking, S.E., Lafleur, P.M. & Roulet, N.T. (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog, Journal of Ecology, 90 (1), 25-36.

Robroek, B.J.M., Limpens, J., Breeuwer, A. & Schouten, M.G.C. (2007) Effects of water level and temperature on performance of four *Sphagnum* mosses, Plant Ecology, 190, 97-107.

Robson, T.M., Pancotto, V.A., Flint, S.D., Ballare, C.L., Sala, O.E., Scopel, A.L. & Caldwell, M.M. (2003) Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatlands, New Phytologist, 160 (2), 379-389.

Rochefort, L., Vitt, D.H. & Bayley, S.E. (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions, Ecology, 71 (5), 1986-2000.

Thormann, M.N. & Bayley, S.E. (1997) Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada, Ecoscience, 4 (3), 374-384.

Vitt, D.H., Wieder, K., Halsey, L.A. & Turetsky, M. (2003) Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada, The Bryologist, 106 (2), 235-245.

Wallén, B., Falkengren-Grerup, U. & Malmer, N. (1988) Biomass, productivity and relative rate of photosynthesis of *Sphagnum* at different water levels on a south Swedish peat bog, Holarctic Ecology, 11 (1), 70-76.

Wieder, R.K. & Lang, G.E. (1983) Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia, The Bryologist, 86 (3), 280-286.

Wieder, R.K., Vitt, D.H., Burke-Scoll, M., Scott, K.D., House, M. & Vile, M.A. (2010) Nitrogen and sulphur deposition and the growth of *Sphagnum fuscum* in bogs of the Athabasca Oil Sands Region, Alberta, Journal of Paleolimnology, 69 (1), 161-170.

CHAPTER 3

Quantifying landscape morphology influence on peatland lateral expansion using ground penetrating radar (GPR) and peat core analysis

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Abstract

Northern peatlands contain vast amounts of organic carbon. Large-scale datasets have documented spatial patterns of peatland initiation as well as vertical peat accumulation rates. However, the rate, pattern, and timing of lateral expansion across the northern landscape remain largely unknown. As peatland lateral extent is a key boundary condition constraining the dynamics of peatland systems, understanding this process is essential. Here we use ground penetrating radar (GPR) and peat core analysis to study the effect of local slope and topography on peatland development at a site in south-central Alaska. The study site is unique in that a thick tephra (volcanic ash) layer, visible in the GPR data, interrupted the peatland development for about one thousand years during the mid Holocene. In our analysis, this tephra layer serves as a re-initiation point for peatland development. By comparing the initial mineral basin vs. the post-tephra surfaces, the influence of topography and slope on peatland expansion rate and peat-carbon sequestration was analyzed. Our results show that: (1) peatland surface slope becomes progressively shallower over the Holocene; (2) slope affects peatland lateral expansion non-linearly; (3) the relationship between lateral expansion rate and slope follows a power-law behavior, and (4) peatland expansion becomes slope-limited above a threshold (0.5°). Furthermore, we propose a conceptual model linking slope to peatland lateral expansion where slope gradient and basin topography exert deterministic controls on peatland lateral expansion directly or through hydrology and vertical accumulation rates.

3.1. Introduction

The timing of peatland initiation across the circum-arctic region of the globe is relatively well established and is based on large-scale compilations of radiocarbon-dated basal peat samples (MacDonald et al., 2006; Gorham et al., 2007; Korhola et al., 2010; Yu et al., in review). However, the spatial and temporal patterns of peatland lateral development and expansion across the northern landscape since the last deglaciation are still poorly constrained. Northern peatlands have been affecting the global carbon (C) cycle as well as the climate system by acting as carbon dioxide (CO_2) sinks and methane (CH_4) sources to the atmosphere since the last deglaciation, about 15,000 years ago (e.g., MacDonald et al., 2006; Yu, 2011). As peatland spatial extent is a key dimensional parameter that is included in peatland carbon flux calculations (Korhola et al., 2010; Yu et al., 2010), large-scale estimates of peatland area change over time are in critical need of refinement. A process-based understanding of lateral expansion dynamics paired with regional-scale reconstructions of peatland spreading rates would provide new means to evaluate this important control on peat C-flux terms.

Comprehensive datasets of basal peat ages indicate that new peatland formation peaked between 10,000 and 8000 years ago in the northern hemisphere as a result of (1) land availability following deglaciation, and (2) orbitally-induced warm summer temperatures (MacDonald et al., 2006; Gorham et al., 2007; Yu et al., 2010). In large-scale estimates of Holocene peat-C fluxes, this period of ‘explosive’ peatland initiation is assumed to have led to rapid and expansive peatland spreading over the landscape, although lateral expansion rates have neither been explicitly estimated nor calculated at large scale. Therefore, in large-scale peat-C pool reconstructions, frequencies of basal initiation dates are oftentimes used as a proxy for peatland area change over time, and peatland area is thus assumed to increase linearly over time after the peatland initiation (MacDonald et al., 2006; Frolking and Roulet, 2007; Gorham et al., 2007; Yu et al., 2010). Given the documented control exerted by landscape morphology on peatland development (e.g., Korhola, 1994; 1996; Borren et al., 2004), this assumption significantly limits our ability to reconstruct realistic past large-scale peat-C pools and associated C flux histories (Yu, 2011).

Most northern peatlands formed by paludification, that is, by peat inception over mineral soils (Heinselman, 1970; Sjörs, 1983). Peat formation typically begins in waterlogged topographic depressions (Anderson et al., 2003; Ireland and Booth, 2010), and subsequent lateral expansion is mostly driven by local- and regional-scale hydrological processes, which are closely linked to landscape morphology (Fig. 3.1). For example, topography, slope, and parent material (substrate) exert fundamental constraints on peatland development by controlling water storage as well as flow direction and stability (Graniero and Price, 1999). In return, peatland bodies probably contribute to their own expansion pattern by locally impeding drainage, which saturates the surrounding mineral soils and allows further expansion (Korhola et al., 2010). Although very few studies have examined peatland lateral expansion processes, internal peatland mechanisms such as water retention due to low hydraulic conductivity, decreasing soil permeability because of acidic compound leaching, and vertical accumulation of organic matter that raises the local water table have also been proposed as important autogenic drivers for lateral expansion patterns (Belyea, 2009). Finally, climatic conditions likely play an important, though likely secondary, role in lateral expansion by influencing peatland hydrology and moisture, which in turn controls vegetation dynamics and biological processes such as plant growth and peat decay (Belyea and Malmer, 2004). Vertical peat accumulation rates are also sensitive to temperature (Yu et al., 2011). Overall, it is generally assumed that local factors such as basin slope and topography constrain the rate of lateral peatland expansion across the high latitudes (Fig. 3.1; Bauer et al., 2003; Mäkilä and Moisanen, 2007), though general rules or threshold values describing these relationships remain elusive.

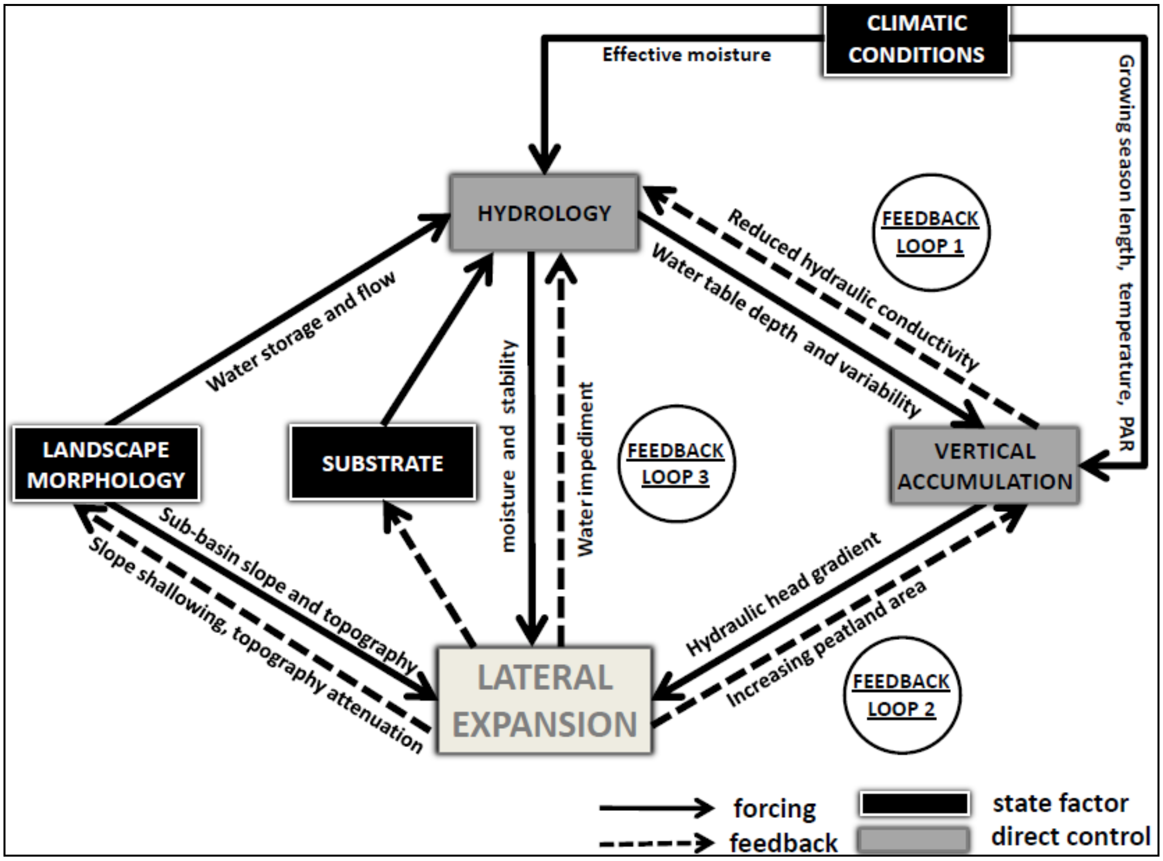

Figure 3.1. Conceptual model of peatland lateral expansion. The influence of state factors (black boxes) and other controlling factors (gray boxes) as well as the processes (solid arrows) and feedbacks (dashed arrows) involved in lateral expansion are presented. Feedback loops 1, 2, and 3 are discussed in section 3.4.1.

Peatland lateral expansion rates have been the object of empirical studies based on radiocarbon (^{14}C) dates of several basal peat samples collected along transects at individual sites (e.g., Ugolini and Mann, 1979; Damman, 1979; Foster and King, 1984; Foster et al., 1988; Foster and Wright, 1990; Korhola, 1994, 1995; 1996; Mäkilä, 1997; Crawford, 2000; Anderson et al., 2003; Bauer et al., 2003; Asselin and Payette, 2006; Mäkilä and Moisanen, 2007; Tipping, 2008; Peregon et al., 2009; van Bellen et al., 2011). These studies have shown that lateral expansion does not take place in an even manner; while steadily decreasing rates of lateral expansion have been reconstructed at several peatland sites (e.g., van Bellen et al., 2011), distinctly faster and slower phases seem to characterize other peatland systems (e.g., Korhola, 1996). These different temporal patterns suggest the existence of several modes of peatland development that relate to topographic constraints (Fig. 3.1), or to relationships between rates of vertical growth and lateral expansion (Belyea and Baird, 2006; Fig. 3.1). In an idealized concentric raised bog, for example, the ecosystem size and shape is internally controlled by geophysical constraints such that height growth leads to concentric lateral expansion, as long as there are no topographic barriers (Ingram, 1982; Foster and Wright, 1990). In reality, however, this developmental model would reach a growth limit if effective moisture remained stable: as the bog spreads concentrically across a flat plain, it increases in height which increases the hydraulic head and leads to drying conditions. Therefore, effective moisture must play an important role in the development of raised bogs, as they lack a surface water catchment area. Conversely, non-raised peatland development across the high-latitude regions is probably more closely linked to the initial mineral basin topography and slope than to climatic conditions, as the surrounding catchment areas may mediate the amount of water run-on to peatlands (Fig. 3.1).

Northern peatlands today occupy about 3% of the global land area, but the rate and temporal pattern of lateral expansion during their development history remain largely unknown. As peatland lateral extent is a key boundary condition constraining the dynamics of peatland systems, understanding this process is essential to generate more robust estimates of peatland carbon sequestration histories. Here we combine geophysical (ground penetrating radar; GPR) and paleoecological approaches to study the effect of slope and topography on peatland development at a site in south-central Alaska. We argue that GPR provides high-density spatial data that is essential for these analyses because it allows for the calculation of stratigraphic slopes in the immediate vicinity of each peat core. Relying on slopes calculated from solely interpolating depth differences between cores would introduce an unacceptable amount of uncertainty given the relatively large spacing between bore holes and the relatively low slope. In addition, it was suggested that GPR produces highly accurate estimates of peat thickness, typically with much less than 10% discrepancy from core data (Rosa et al., 2008). Another study has similarly found that GPR provides a more accurate measure of peat thickness than manual probing when the peat-to-mineral interface consists of lake sediments or clay (Jol and Smith, 1995). Overall, our study demonstrates that slope gradient and basin topography exert deterministic controls on peatland lateral expansion.

3.2. Materials and methods

3.2.1. Study site

Petersville peatland (62°25’N, 150°41’W, 450 m above mean sea level) is located in the Susitna River basin, in the Cook Inlet region of south-central Alaska (Fig. 3.2a). The regional climate is cool continental, with 30-year (1971–2000) monthly mean temperatures of -11.7°C in January and 14.9°C in July (as recorded in Talkeetna, 40 km to the south-east of Petersville site). Mean annual temperature is 1.0°C, and mean annual precipitation is 715 mm, of which 352 mm falls as snow (*Alaska Climate Research Center*, 2009).

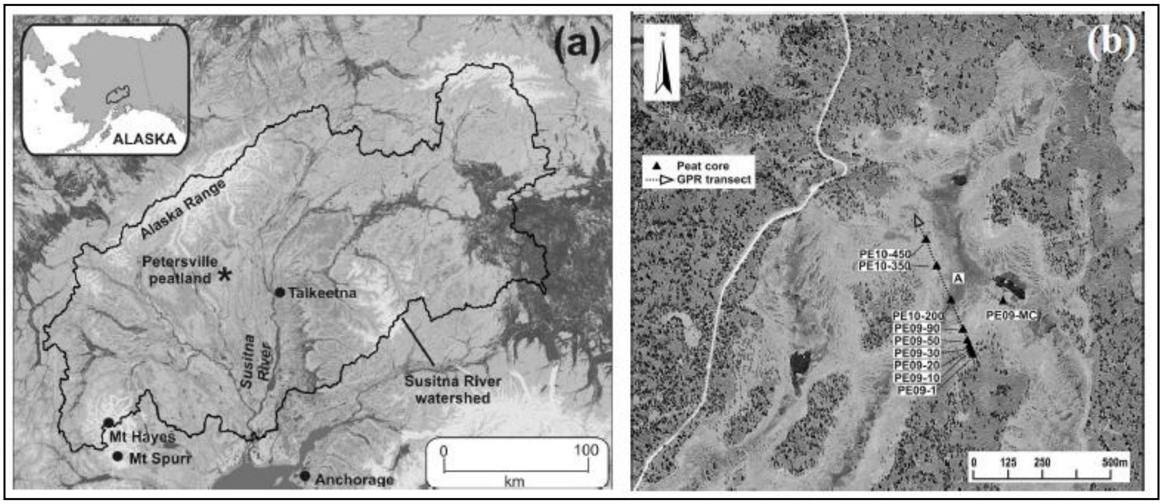

Figure 3.2. Location maps and study site. (a) Digital elevation model (source: 2-arc second dataset, USGS) showing Petersville peatland (62°25’ N, 150°41’ W, 450 m a.s.l.) and local weather station (Talkeetna) within the Susitna River basin (black line). Inset shows the location of the basin in Alaska. (b) Quick Bird Image (resolution: 1 m) of Petersville site showing location of the GPR transect, peat cores, and water table wells. Image: © 2011 DigitalGlobe, Inc. ALL RIGHTS RESERVED.

Petersville site is a sloping patterned peatland (~ 1 km^2) that has developed over glacial clay and has a general northeast-southwest slope, with an elevation difference of about 10 m between the highest (NE) and lowest (SW) portions. This peatland represents a mosaic of minerotrophic and oligotrophic peatland types, with pH values ranging from

3.9 to 4.5. The ground layer is dominated by *Sphagnum* (peat moss), although several Amblystegiaceae (brown mosses) including *Drepanocladus* spp. inhabit wet depressions, and sparse *Pleurozium schreberi* (feather moss) colonize the drier peatland margins. The vascular plant assemblage is dominated by ericaceous shrubs and by herbaceous species including *Scheuchzeria palustris* and *Carex pauciflora*. Surrounding upland vegetation is dominated by *Alnus* spp. and *Picea glauca*.

A 15- to 25-cm-thick tephra layer was identified along the peat cores and corresponds to the mid-Holocene Mount Hayes eruptions (3490-4330 cal. BP; de Fontaine et al., 2007). Mount Hayes is located about 100 km to the south-west of the study site (Fig. 3.2a). The ash layer provenance within our peat samples was confirmed on the basis of glass shard mineralogy (Kristi Wallace, 2008, pers. comm.). The absence of plant remains and the low organic matter content (< 25%) of the tephra layer suggest that most of the peatland plants were buried and killed by this catastrophic perturbation.

3.2.2. General approach and study design

To determine the effect of topography and slope on peatland development, we reconstructed peatland lateral expansion rates along a 500-m-long transect by combining peat-core analysis with GPR and total station surveys (Fig. 3.2b). The transect runs across two different sub-surface slope settings (shallow vs. steep). In addition, the thick ash layer, visible in the GPR data due to its very low water content (Fig. 3.3; Topp et al., 1980; Huisman et al., 2003), was used as a stratigraphic marker to compare the initial lateral expansion rate over the mineral basin (14 ka, 1 ka = 1000 calibrated years before present) to the post-tephra (3.4 ka) expansion rate across the transect. This combined approach allows us to survey a large area of the peatland using GPR and to obtain detailed stratigraphic information using peat core analysis.

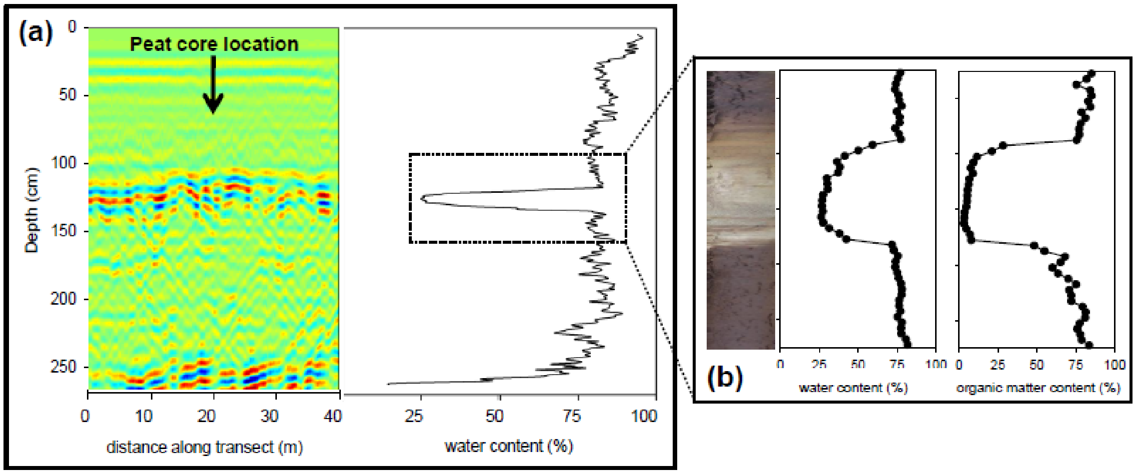

Figure 3.3. Mid-Holocene Hayes tephra layer at Petersville peatland, core PE09-MC. (a) GPR survey from above the peat core location and water content. (b) Core photograph showing the tephra layer, as well as water and organic matter content across the peat-to-tephra interface.

3.2.3. Field survey and sampling

The mineral basin topography and the relative position of the tephra layer within the peat matrix were determined using GPR in March 2010 along a 500-m-long transect established across the deepest portion of the basin as well as two upland edges (Fig. 3.2b). The survey was performed along the transect using a Malå RAMAC/GPR CUII system (Malå, Sweden) equipped with 200 MHz antennas. The antenna separation was 60 cm and step size was 10 cm. This frequency provided a high vertical measurement resolution while maintaining adequate penetration depth along the profile (Kettridge et al., 2008). GPR data were processed using the MATGPR (Tzanis, 2006) and ReflexW (Sandmeier, 2008) software. Processing steps include correction of time zero, dewow (low frequency noise reduction) and a linear/exponential gain function to compensate for attenuation and signal spreading. Depth conversion was done by calibrating the GPR data to the known depth to the tephra and mineral basin reflector based on measurements from the peat cores (calculated velocity = 0.0367 ± 0.0016 m ns^{-1}). Migration was performed on the transect using the calculated velocity, however due to the shallow slopes observed throughout the peatland, no variation was observed between the non-migrated profile outside the uncertainty range. Unmigrated GPR data is presented to retain clarity. Reflection events associated with the tephra and basin outline were digitized from the radargram and output for slope analysis. Variable surface topography was accounted for after depth data was extracted from the radargrams.

In the summer of 2010, peatland surface elevation along the transect was obtained using a total station (DeWalt automatic level, Baltimore, USA). The step size was 100 cm and the vertical accuracy was 0.32 cm. Nine peat cores were also collected along the transect in summers of 2009 and 2010 using a Russian-type peat corer (Fig. 3.2b).

3.2.4. Peat core analysis

Plant macrofossils were identified within the basal peat samples as well as above the Hayes tephra layer to determine the type of peatland formation processes (terrestrialization vs. paludification). Peat sub-samples (2 cm^3) were gently boiled in a 5% KOH solution and rinsed with distilled water through a 150-µm sieve. For each sample, Sphagnaceae (peat mosses), Amblystegiaceae (brown mosses), herbaceous, ligneous and unidentifiable organic matter (UOM) material were quantified as a percentage of the total sample by volume. To determine water content, bulk density, and organic matter content, peat sub-samples (1 cm^3) were dried overnight at 105°C, weighed, and burned at 550°C for two hours (Dean, 1974).

Peat inception age was established using AMS radiocarbon (^{14}C) dating. For each core, the basal peat sample was identified as the deepest layer with a minimum organic matter content of 50% based on loss-on-ignition at 550°C. Dating material was composed of non-aquatic plants taxa (e.g., *Scorpidium* stems and leaves), which were hand-picked and cleaned with distilled water. In horizons that lacked good dating material, root-free bulk peat samples (size fraction: 63 to 125 μm) were analyzed (Table 3.1). The ^{14}C samples were submitted to Keck AMS Carbon Cycle Lab at University of California, Irvine, and results were calibrated using the program CALIB 6.0 based on the INTCAL09 calibration data set (Reimer et al., 2009; Stuiver and Reimer, 2010).

3.2.5. Tephra analysis

A 10-cm-long tephra sample from a peat core was analyzed for particle texture. The analysis was completed using a LS 13 320 laser diffraction particle size analyzer (Zobeck, 2004). A sub-sample from each 2 cm interval of the core was taken, air-dried and passed through a 0.2 cm sieve. Samples were homogenized and an average sample weight of about 0.3 g was used for analysis. Two sub-samples were run for each interval (Table 3.2).

3.2.6. Water table depth monitoring

Three water level probes (Odyssey Dataflow loggers, Christchurch, New Zealand) were installed in 1 m-long PVC monitoring wells in August 2009. While one of the wells was set up at the peatland-upland interface, the other two were installed at 40 m and 90 m

Table 3.1. AMS radiocarbon (^{14}C) dating results from peat cores at Petersville peatland, south-central Alaska

	Core ID	Sample depth (cm)	Material dated	^{14}C date ± error (yr BP)	Calibrated 2σ range (cal yr BP)	Age (cal yr BP)	Lab ID (UCIAMS[*])
post-tephra	PE09-1	29.5	root-free bulk peat	2855 ± 30	2876-3069	2970 ± 100	69781
	PE09-90	91.5	root-free bulk peat	3020 ± 15	3163-3325	3240 ± 80	77137
	PE09-200	183.5	root-free bulk peat	3685 ± 20	3931-4088	4010 ± 80	81453
	PE09-450	77.5	root-free bulk peat	3405 ± 35	3564-3820	3690 ± 130	81451
mineral basin	PE09-30	95.5	root-free bulk peat	6370 ± 200	6794-7610	7200 ± 410	69778
	PE09-50	120.5	root-free bulk peat	5910 ± 60	6566-6893	6730 ± 160	69780
	PE09-90	163.5	root-free bulk peat	7830 ± 30	8544-8697	8620 ± 80	69777
	PE09-200	310.5	*Scorpidium* spp.	11,360 ± 50	13,120-13,346	13,230 ± 110	82701
	PE09-450	137.5	root-free bulk peat	10,200 ± 150	11,310-12,415	11,860 ± 550	81452

[*] Keck AMS Carbon Cycle Lab at University of California, Irvine

towards the peatland center, along the transect (Fig. 3.2b). Water table depth variability between and within each of these sites was recorded every 60 minutes from August 15th 2009 to August 31st 2011.

Table 3.2. Grain-size analysis result of the mid-Holocene Hayes tephra samples at Petersville peatland (core PE08-A35).

Sample depth (cm)	Clay (%)	Silt (%)	Sand (%)	USDA classification
80-82	6.0	47.5	46.5	sandy loam
80-82, duplicate	6.3	47.8	45.9	sandy loam
82-84	5.4	39.3	55.3	sandy loam
82-84, duplicate	6.0	42.0	52.0	sandy loam
84-86	6.6	51.2	42.2	silt loam
84-86, duplicate	6.5	51.9	41.6	silt loam
88-90	5.3	55.3	39.4	silt loam
88-90, duplicate	4.9	53.2	41.9	silt loam

3.3. Results

3.3.1. Identifying the tephra layer using ground penetrating radar

The mid-Holocene tephra layer was clearly visible along the entire length of the GPR survey and represented by a clear reflection (Fig. 3.3, 3.4a). The relative thinness of the tephra layer combined with its low clay content (Table 3.2) probably explains the good signal penetration below this layer. The identification of this ‘tephra reflection’ was confirmed through measurements of low water and organic matter content along peat profiles (Fig. 3.3).

3.3.2. Changes in topography, slope, and lateral expansion rates

The mineral-to-peat interface was sharp and easily identifiable along the GPR profile, enabling accurate determination of the peatland basin morphology along the transect (Fig. 3.4a). Peat thickness was highly variable, from 3.29 ± 0.25 m in the center of the peatland to 0.30 ± 0.04 m along the peatland margins. In addition to the mineral basin and tephra layers, other reflections were recorded along the profile, likely corresponding to changes in peat stratigraphy and moisture content within the peat (Slater and Reeve, 2002; Comas et al., 2005; Fig. 3.3; 3.4a).

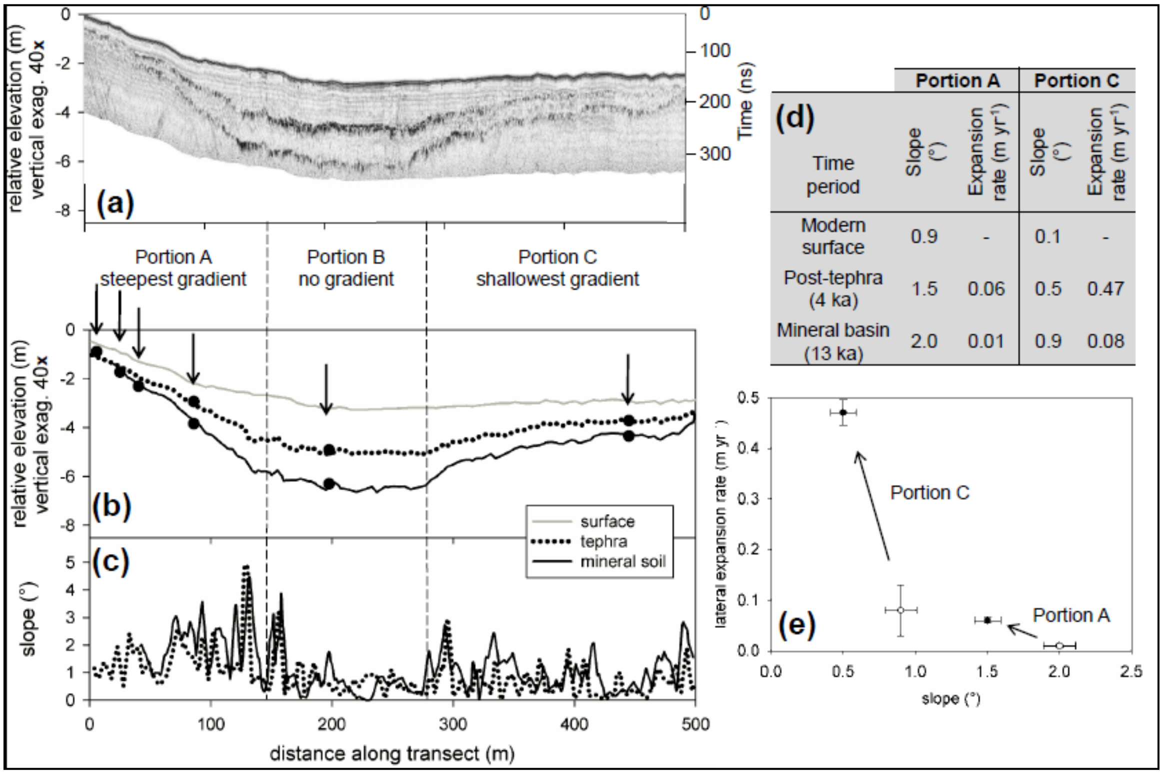

Figure 3.4. Peat basin morphology along the studied transect. (a) GPR profile (corrected for elevation) highlighting the mineral basin morphology and the mid-Holocene Hayes tephra layer (dark subsurface reflectors). (b) Relative elevations of peatland surface, tephra, and mineral basin as inferred from the total station survey combined with the GPR data. Peat core location (black arrows) and radiocarbon-dated peat samples (solid circles) are also shown. The transect was divided into three portions on the basis of slope steepness (steep, flat, and shallow; see the text for details). (c) Instantaneous slope (first derivative of distance over elevation change) of the mineral basin and tephra (shown as 5-point moving averages). (d) Mean mineral basin, post-tephra, and modern surface slopes and expansion rates for the two portions of the transect. (e) Mean slope in relation to lateral expansion rates. Open and solid circles represent mineral basin and post-tephra values, respectively.

Slope steepness of the mineral basin (mineral-to-peat interface), the post-tephra (tephra-to-peat interface), and the modern surfaces were calculated using peat thickness values (GPR data) combined with peatland surface elevation (data from total station). Slope values ranged between 0 and 4.9 ± 0.11° (Fig. 3.4c). Uncertainties for the slope of the tephra (± 0.09°) and for the mineral basin (± 0.11°) were determined using the velocity range (0.034 to 0.039 m ns^{-1}) that was calculated for the study site. The initial mineral basin topography was characterized by a moderate gradient (mean slope = 2°) along the first portion of the transect (0-150 m), followed by a flat (mean slope < 0.4°) central portion (150-290 m), and finally by a shallow gradient (mean slope = 0.9°) along the third part of the transect (290-500 m; Fig. 3.4c). Post-tephra topography had a similar pattern but was characterized by more gentle slope gradients, with mean values of 1.5° and 0.5° for the first and third portions of the transect, respectively (Fig. 3.4e). Likewise, the modern surface topography was shallower than the post-tephra surface, with mean slope values of 0.9° and 0.1° for the first and third portions of the transect, respectively (Fig. 3.4e). Here it is assumed that the mineral basin and the modern surface slope calculations are unbiased, that is, these two surfaces have not been subject to peat compaction. On the other hand, it is possible that post-tephra slope values have progressively steepened over the past 4000 years due to peat accumulation atop the ash layer. As a result, the post-tephra slopes represent maximum values.

Initial mineral basin and post-tephra lateral expansion rates were calculated on the basis of peat sample ages (Table 3.1) and distance from the center. Expansion rates varied from 0.01 m yr^{-1} for the steepest slope (2°), to 0.47 m yr^{-1} for the shallowest slope (0.5°). Intermediate rates (0.06 and 0.08 m yr^{-1}) were found for intermediate slope gradients

(1.5° and 0.9°, respectively). Overall, faster rates are associated with shallower slopes (Fig. 3.4d).

3.3.3 Changes in peat stratigraphy, thickness and bulk density

Basal peat deposits accumulated on glacial clay and were composed of herbaceous peat (Cyperaceae (sedge) fragments) with large fractions of unidentifiable organic matter (UOM; Fig. 3.5c). Post-tephra peat deposits were similarly composed of Cyperaceae fragments, herbaceous rootlets, and high proportions of unidentifiable organic matter.

Both initial and post-tephra peat deposits were dense at the peatland margins and becoming less dense towards the central portion of the transect (Fig. 3.5a, b). Similarly, peat thickness and distance from the central portion of the transect were strongly correlated (minimum $R^2 = 0.92$, $p = 0.003$) under both initial and post-tephra geomorphic conditions, with the thickest peat deposits found within the central portion of the transect (Fig. 3.5d). These results emphasize that age alone does not explain peat thickness and bulk density differences between the central vs. marginal portions of the peat basin, so that the oldest deposits are not necessarily the deepest ones.

3.3.4. Water table depth and variability along the transect

Continuous water table depth fluctuations are presented in Fig. 3.6. Throughout the non-frozen time periods, the well closest to the peatland margin has experienced the driest and most variable conditions (mean = 17.8 cm below the land surface, 1standard deviation (σ) = 14.6 cm), as well as the driest recorded value (34.3 cm). Conversely, the well closest to the peatland center (at 90 m) was characterized by the wettest and least variable mean conditions (mean = 11.5 cm, 1 σ = 3.6 cm). Water table depth values for the well at 40 m along the transect were wetter and less variable than at the peatland

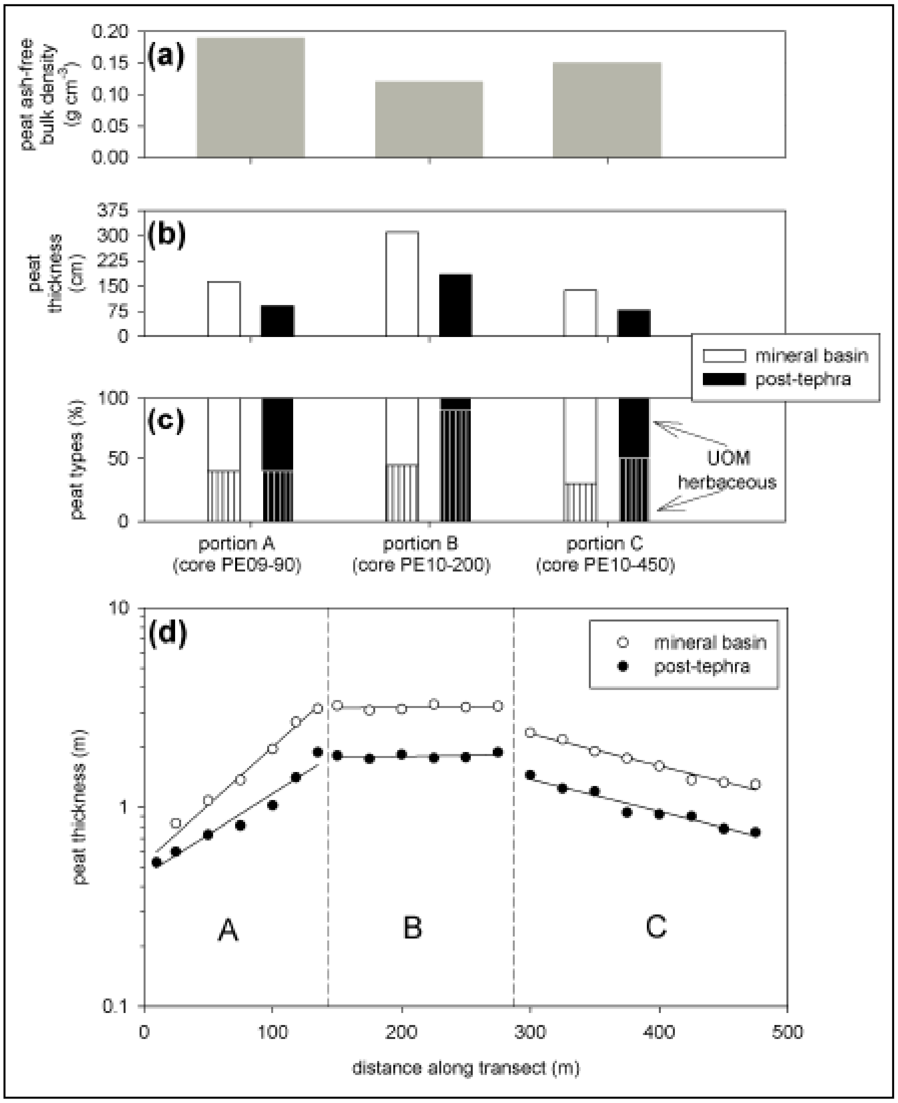

Figure 3.5. Lithological and plant macrofossil data for peat sediments along the transect. (a) bulk density values, (b) peat thickness at coring sites (from peat cores), and (c) peat composition from peat-core analysis. (d) Relationships between distance from the peatland center and peat thickness (from GPR data; minimum $R^2 = 0.92$, $p = 0.003$). UOM: unidentifiable organic matter (fine debris).

margin, but also drier and slightly more variable than at the center (mean = 15.9 cm, 1 σ = 3.9 cm). An analysis of variance (ANOVA) confirmed the statistical significance of these observations between all three wells (*F* (2, 860) = 17.26, p < 0.0001), and a Tukey's pairwise comparison further indicated statistical differences between the 40m and 90m time series (p < 0.0001), as well as between the upland and 90m data sets (p = 0.0001). The upland and 40m time series were not statistically different (p = 0.253).

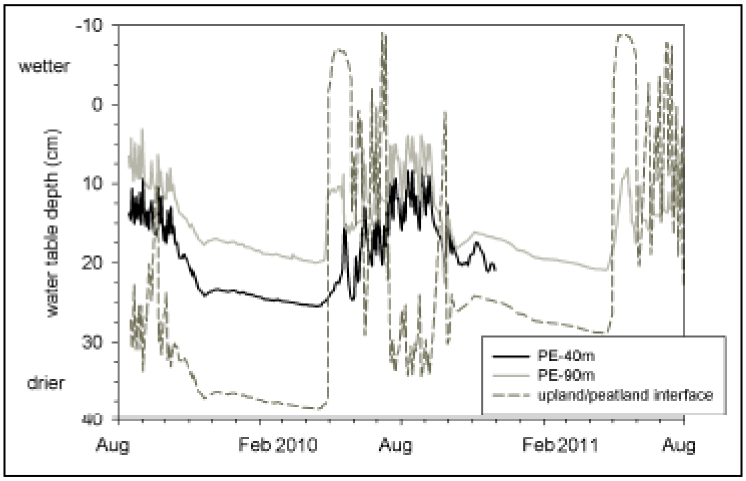

Figure 3.6. Water table depth fluctuations between August 2009 and August 2011 at Petersville peatland. Monitoring wells were installed at the upland/peatland interface (dashed gray line), at 40 m (solid black line), and 90 m (solid gray line) along the transect. Water table depth values from these three wells are statistically different (*F* (2, 860) = 17.26, p < 0.0001).

3.4. Discussion

3.4.1. Peatland basin development and lateral expansion process

Cross-sectional views of the transect at Petersville confirm a simple concave basin structure with the greatest peat thickness in the central portion of the basin and becoming shallower towards the margins (Fig. 3.4b, 3.5d). In addition, lithological data showed that peat density increased as peat thickness decreased, such that peat deposits became thinner and denser towards the peatland margins (Fig. 3.5a). Bauer et al. (2009) have similarly reported high bulk density values for peat samples taken at the peatland-upland interface at sites in northern Canada. Although peat inception at Petersville occurred several thousand years earlier in the center of the peatland than at the margins (Fig. 3.4c), differences in peat thickness and density between the central and marginal portions of the transect cannot only be attributable to age, as this pattern repeats itself following the ashfall event (Fig. 3.4c, 3.5d). Therefore, we propose that slope and topography have exerted fundamental controls on the peatland development and associated lateral expansion rate through the following direct and indirect mechanisms.

(1) Prior to peat inception, the mineral basin across the central portion of the transect was characterized by a flat surface (slope < 0.5°) that was surrounded by higher grounds. These conditions likely enabled water impediment and reduced flow in the peatland center, which resulted in a shallow water table depth and wet conditions with a reduced variability (see Foster et al., 1983; Fig. 3.1).

(2) Under these wet and resultant anoxic conditions, peat started accumulating throughout the flat and depressed portion of the basin around 13,000 years ago due to limited plant and peat decomposition, further increasing water retention locally through a positive feedback mechanism: vertical peat accumulation → reduced hydraulic conductivity → increased water retention → vertical peat accumulation (see Ingram, 1982; Fig. 3.1).

(3) Over time, peat accumulation in the center of the basin raised the water table, allowing peat to spread laterally over surrounding sloping mineral soils, which increased the total peatland area and further isolated the peatland center from the regional water regime through a second positive feedback mechanism: lateral expansion → increased

peatland area → peatland center is farther away from the margins → reduced water level variability at the center → peat buildup at the center → lateral expansion (Fig. 3.1).

(4) At any point during peatland development, peatland margins probably experienced larger water table fluctuations than the peatland center (Hendon et al., 2001; Loisel and Garneau, 2010), owing to (a) a greater influence from the highly variable regional water balance, or (b) a self-regulation mechanism where peatland height rises during wetter time periods and sinks under drier conditions as a result of changes in plant productivity and aerobic peat decay (e.g., Belyea, 2007). In addition, the margins most likely receive mineral-rich runoff from the upland. All these conditions have potential for accelerating peat decay, resulting in highly decomposed, thin and dense peat deposits that further impede water flow through a third positive feedback mechanism: peat decay at the margins → increased bulk density at the margins → reduced water level variability at the peatland center → peat buildup at the center → lateral expansion → peat decay at the 'new' margins (Fig. 3.1). Our observations from monitoring wells along the transect at Petersville provide support to this hypothesis, as we have recorded drier and more variable water table depths at the peatland margin vs. wetter and less variable values toward the peatland center (Fig. 3.6).

3.4.2. Self-regulated surface slope shallowing and slope threshold for lateral expansion

By comparing the mineral basin, post-tephra, and modern surface slope steepness across the three portions of the transect, we observed a progressive 'slope shallowing' over time (Fig. 3.4b, 3.5d). Indeed, the calculated mineral basin slopes were steeper than the corresponding post-tephra slopes, which were steeper than the modern surface values (Fig. 3.4c, d). We speculate that slope shallowing has occurred as a direct consequence of peat 'basin infilling', where the formation and accumulation of thick deposits in the central portion of the peatland vs. thin and dense deposits towards the margins has progressively leveled out the peatland surface (Fig. 3.1). From an ecosystem dynamics standpoint, slope shallowing can thus be viewed as a stabilizing mechanism that reduces water flow and increases water storage over large area, further promoting peat formation (Foster et al., 1983; Fig. 3.1). In other words, by smoothing out basin irregularities and generating a gentler slope for itself, the net effect is that the peatland is self-regulating with respect to its hydrology (water table depth), which should limit peat decay and facilitate peat accumulation (Foster et al., 1983). Our results on lateral expansion lend support to this idea (Fig. 3.4d), as shallow slopes were associated with rapid expansion.

To quantify the relationship between slope and lateral expansion, we used our own data combined with a data synthesis from published studies (Fig. 3.7; Foster and King, 1984; Korhola, 1994; Mäkilä, 1997; Asselin and Payette, 2006; Tipping, 2008; Peregon et al., 2009). For the data synthesis, slope was directly obtained from the published figures (peatland cross-sectional views where elevation and distance along a transect are available) using Data Thief III (Tummers, 2006). Lateral expansion rates were calculated by dividing the horizontal distance between two peat cores of known ages (^{14}C-dated basal peat). If not already calibrated, the published ^{14}C age estimates were calibrated using the program CALIB 6.0 based on the INTCAL09 calibration data set (Reimer et al., 2009; Stuiver and Reimer, 2010). Age uncertainties associated with ^{14}C dating were included in our lateral expansion rate calculations (error bars in Fig. 3.7). A summary of peatland site information is presented in Table 3.3. Lateral expansion rates were anti-correlated with slope and followed a power-law relationship ($R^2 = 0.59$, $p < 0.0001$; Fig. 3.7b), implying a scale-invariance pattern. The existence of a 'slope threshold' (approximate 0.5°) below which peat can rapidly spread laterally was also found (Fig. 3.7a). We speculate that basins with slopes greater than ~ 0.5° fall into the 'slope-limited regime' where the expansion is controlled by the slope, whereas basins having slopes less than ~ 0.5° fall into the 'growth-limited regime' where expansion is limited by factors determining how fast bryophytes can colonize, survive, and grow (i.e. substratum, species and climate dependent). The wide spread of lateral expansion rates that characterizes the 'growth-limited regime' peatland domain (Fig. 3.7a) lends support to our hypothesis. This finding implies that vast and flat peatland-rich areas such as the Hudson Bay Lowlands in northern Canada, which have an averaged regional slope of 0.5-0.7 m km^{-1} (0.03-0.04°), probably experienced very rapid expansion following deglaciation and peat inception, due to their shallow slope but also a favorable climate (Glaser et al., 2004; Gorham et al., 2007; Yu et al., 2009; Jones and Yu, 2010). Therefore, current estimates of peatlands CO_2 sequestration and CH_4 emission for the early Holocene, which are based on the implicit or explicit assumption that individual peatlands expanded linearly in their area since inception (MacDonald et al., 2006; Yu et al., 2010; 2011; Yu, 2011), might be minimum values as they probably underestimate rates of lateral expansion in flat, peatland-rich regions including the Yukon Flats (Canada and Alaska), the Hudson Bay Lowlands, and West Siberia. We suggest that future research should further explore the subsurface slopes of peat-filled basins using GPR, and use this conceptual model to predict future peat growth potential.

At Petersville site, early peatland development was characterized by high lateral expansion rates as peat was rapidly spreading across the central and flat portion of the transect and presumably the basin. By 8000 cal. BP, 86% of the transect was colonized by peat. Following this early stage, rates of lateral expansion slowed down as basin steepness increased towards the modern margins. Early rapid development patterns were similarly found by Mäkilä (1997) and Mäkilä and Moisanen (2007) in Finnish mires, as well as by van Bellen et al. (2011) in northern Québec. On the other hand, on the basis of a large dataset (n = 954) of multiple basal peat ages from individual peatlands that presumably accounts for horizontal growth of northern peatlands, Korhola et al. (2010) proposed that extensive lateral expansion of high-latitude peatlands occurred between 5000 and 3000 cal. BP (i.e., many thousands of years after peat inception) due to the Neoglacial climate cooling and wet conditions (Korhola et al., 2010). Though climatic conditions might play a role in peat lateral expansion by modifying moisture inputs to peat basins and affecting net peat accumulation (Fig. 3.1), we argue that landscape morphology provides fundamental constraints on lateral expansion rates that can be aided or hindered by climatic conditions, especially under the 'growth-limited' regime (slope less than 0.5°).

The importance of mineral basin slope and water flow in controlling lateral expansion processes has important implications for the interaction between vertical accumulation and lateral expansion. Based on the premise that peat growth occurs under more variable conditions at the margins than at the peatland center, long-term rates of vertical peat accumulation are expected to be higher towards the peatland center than at its margins. In other words, peat accumulation rates as reconstructed from peat cores are probably sensitive to the coring location: if early-stage peat accumulation occurred close to the ‘paleo’ margin but that the peatland kept spreading laterally over time, increasing vertical peat accumulation rates should be expected for that particular coring site simply because of changing distance from the expanding peatland margin.

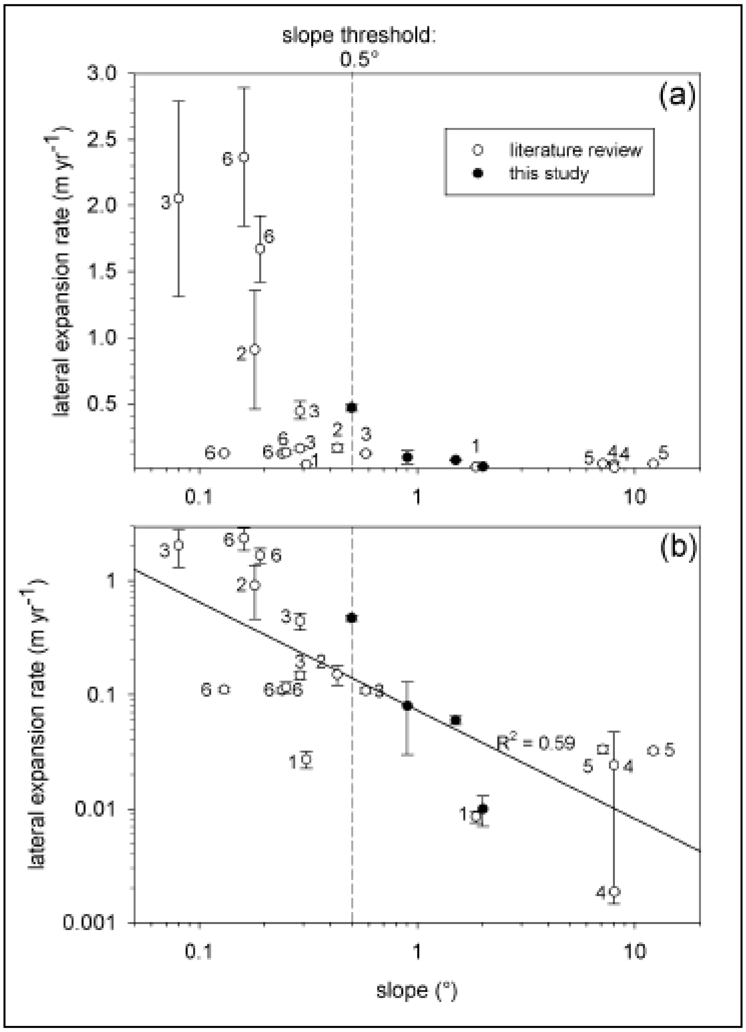

Figure 3.7. Peatland lateral expansion rate (m yr^{-1}) in relation to slope (°). (a) Values from published datasets (solid circles) are compared to those obtained for Petersville site (open circles). Error bars were calculated based on dating uncertainties (2σ range) of the calibrated ^{14}C ages. (b) Once plotted on a log-log scale, these same values exhibited a power-law relationship (solid black line; $y = 0.0699x^{-0.875}$, $R^2 = 0.59$; $p < 0.0001$). Literature data (see also Table 3): (1) *Foster and King* (1984), (2) *Korhola* (1994), (3) *Mäkilä* (1997), (4) *Asselin and Payette* (2006), (5) *Tipping* (2008) and (6) *Peregon et al.* (2009).

Table 3.3. Summary of peatland sites used in the data synthesis (see Fig. 3.7).

ID	Study site	Country	Coordinates Y	Coordinates X	Peatland type	Slope (°)	Expansion rate (m yr^{-1})	Reference
1	Leech Fen	Canada (Labrador)	53.1	-57.5	patterned fen	0.3	0.03 ± 0.0046	Foster and King, 1984
						1.9	0.01 ± 0.0010	
2	Munasuo	Finland (south)	60.6	26.5	concentric bog	0.2	0.91 ± 0.4482	Korhola, 1994
						0.4	0.15 ± 0.0294	
3	Haukkasuo	Finland (southeast)	60.8	26.9	raised bog	0.6	0.11 ± 0.0056	Mäkilä, 1997
						0.3	0.15 ± 0.0120	
						0.3	0.44 ± 0.0741	
						0.1	2.05 ± 0.7399	
4	Rivière Boniface	Canada (Québec)	57.8	-76.3	fen	8.1	0.01 ± 0.0001	Asselin and Payette, 2006
						8.0	0.02 ± 0.0228	
5	Rotten Bottom	Scotland (highlands)	55.4	-3.4	blanket mire	7.1	0.02 ± 0.0006	Tipping, 2008
						12.1	0.03 ± 0.0013	
6	Great Vasyugan Mire	Siberia (west)	56.9	78.5	bog	0.2	2.36 ± 0.5240	Peregon et al., 2009
						0.2	0.11 ± 0.0052	
						0.1	0.11 ± 0.0055	
						0.2	0.12 ± 0.0127	
						0.2	1.67 ± 0.2500	

This study	Petersville	Alaska	62.4	-150.7	patterned sloping mire	2.0	0.01 ± 0.0030
						1.5	0.06 ± 0.0050
						0.5	0.47 ± 0.0250
						0.9	0.08 ±0.0500

3.5. Conclusions and implication

Peatland lateral extent is a key boundary condition constraining the carbon dynamics of peatland systems. By combining peat-core analysis with surface and subsurface landscape morphological surveys along a 500-m-long transect at Petersville peatland, we have demonstrated that slope gradient and basin topography exert deterministic controls on peatland development (Fig. 3.1). We have found that, over their developmental history, peatlands have the tendency and ability to smooth out basin irregularities and generate a gentler slope for themselves. This self-generated slope shallowing and stabilizing mechanism reduces water flow and increases water storage, further promoting peat formation (Foster et al., 1983). On the basis of our new data and data synthesis, we also demonstrated that (i) shallow slopes are associated with rapid expansion, (ii) lateral expansion rate and slope follow a power-law relationship, and (iii) there exists a slope threshold (approximate 0.5°). Overall, the power-law distribution and implied scale-invariance allow for prediction of lateral expansion rates over a wide range of scales, and the slope threshold implies that lateral expansion in basins with slopes greater than ~ 0.5° is slope-limited, whereas lateral expansion in basins with less than ~ 0.5° are peat growth-limited. Therefore, flat peatland-rich areas probably experienced rapid expansion rates following deglaciation and peat inception, and current estimates of peatlands carbon sequestration and methane emissions for the early Holocene are probably erroneous as they have probably underestimated the rate of lateral expansion across these regions.

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3.7. References

Alaska Climate Research Center (2009), *Temperature change in Alaska*, Geophysical Institute, University of Alaska Fairbanks, http://climate.gi.alaska.edu/.

Anderson, R.L., Foster, D.R. and G. Motzkin (2003), Integrating lateral expansion into models of peatland development in temperate New England, *Journal of Ecology*, *91*, 68-76.

Asselin, H. and S. Payette (2006), Origin and long-term dynamics of a subarctic tree line, *Ecoscience*, *13* (2), 135-142.

Bauer, I.E., Gignac, D.L. and D.H. Vitt (2003), Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation, *Canadian Journal of Botany, 81*, 833-847.

Bauer, I.E., Bhatti, J.S., Swanston, C., Wieder, R.K. and C.M. Preston (2009), Organic matter accumulation and community change at the peatland-upland interface: inferences from ^{14}C and ^{210}Pb dated profiles, *Ecosystems*, *12*, 636-653.

Belyea, L.R. (2007), Climatic and topographic limits to the abundance of bog pools, *Hydrological Processes*, *21*, 675-687.

Belyea, L.R. (2009), Non-linear dynamics of peatlands and potential feedbacks on the climate system, in *Northern peatlands and carbon cycling*, *American Geophysical Union Monograph Series*, edited by A. Baird, L. Belyea, X. Comas, A. Reeve and L. Slater, AGU, Washington, DC.

Belyea, L.R. and A.J. Baird (2006), Beyond ‘The limits to peat bog growth’: cross-scale feedback in peatland development, *Ecological Monographs*, *76*(3), 299-322.

Belyea, L.R. and N. Malmer (2004), Carbon sequestration in peatland: patterns and mechanisms of response to climate change, *Global Change Biology*, *10*, 1043–1052.

Borren, W., Bleuten, W. and E.D. Lapshina (2004), Holocene peat and carbon accumulation rates in the southern taiga of western Siberia, *Quaternary Research*, *61,* 42-51.

Clymo, R.S. (1984), The limits to peat growth, *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 303*(1117), 605-654.

Comas, X., Slater, L. and A. Reeve (2005), Stratigraphic controls on pool formation in a domed bog inferred from ground penetrating radar (GPR), *Journal of Hydrology*, *315* (1-4), 40-51.

Crawford, R.M.M. (2000), Ecological hazards of oceanic environments, *New Phytologist*, *147*(2), 257-281

Damman, A.H.W. (1979), Geographic patterns in peatland development in eastern North America. *Proceedings of the International Symposium on Classification of Peat and Peatlands (International Peat Society)*, 42-57.

de Fontaine, C.S., Kaufman, D.S., Anderson, R.S., Werner, A., Waythomas, C.F. and T.A. Brown (2007), Late Quaternary distal tephra-fall deposits in lacustrine sediments, Kenai Peninsula, Alaska, *Quaternary Research*, *68,* 64-78.

Dean Jr., W.E. (1974), Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods, *Journal of Sedimentary Petrology, 44*(1), 242-248.

Foster, D.R. and G.A. King (1984), Landscape features, vegetation and developmental history of a patterned fen in south-eastern Labrador, Canada, *Journal of Ecology*, *72* (1), 115-143.

Foster, D.R. and H.E. Wright Jr. (1990), Role of ecosystem development and climate change in bog formation in central Sweden, *Ecology*, *71* (2), 450-463.

Foster, D.R., King, G.A., Glaser, P.H. and H.E. Wright Jr. (1983), Origin of string patterns in boreal peatlands, *Nature*, *306*, 256-258.

Foster, D.R., Wright, Jr., H.E., Thelaus, M. and G.A. King (1988), Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada, *Journal of Ecology*, *76* (4), 1164-1185.

Frolking, S. and N.T. Roulet (2007), Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, *13*, 1–10.

Glaser, P.H., Chanton, J.P., Morin, P., Rosenberry, D.O., Siegel, D.I., Ruud, O., Chasar, L.I. and A.S. Reeve (2004), Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. *Global Biogeochemical Cycles, 18*, GB1003, doi:10.1029/2003GB002069.

Gorham, E., Lehman, C., Dyke, A., Janssens, J. and L. Dyke (2007), Temporal and spatial aspects of peatland initiation following deglaciation in North America, *Quaternary Science Reviews*, 26, 300–311.

Graniero, P.A. and J. Price (1999), The importance of topographic factors on the distribution of bog and heath in a Newfoundland blanket bog complex, *Catena*, *36*, 233-254.

Heinselman, M.L. (1970), Landscape evolution, peatland types, and the environment in the Lake Agassiz peatlands natural area, Minnesota, *Ecological Monographs*, *40*(2), 235-261.

Hendon, D., Charman, D.J. and M. Kent (2001), Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications, *The Holocene*, *11* (2), 127-148.

Huisman, J.A., S.S. Hubbard, J.D. Redman and A.P. Annan, (2003), Measuring soil water content with ground penetrating radar: a review, *Vadoze Zone Journal*, *2*, 476-491.

Ingram, H.A.P. (1982), Size and shape in raised mire ecosystems: a geophysical model, *Nature*, *297*, 300-303.

Ireland, A.W. and R.K. Booth (2010), Hydroclimatic variability drives episodic expansion of a floating peat mat in a North American kettlehole basin, *Ecology*, *92* (1), 11-18.

Jol, H.M. and D.G. Smith (1995), Ground penetrating radar surveys of peatlands for oilfield pipelines in Canada, *Journal of Applied Geophysics*, *34*, 109–123.

Jones, M.C. and Z. Yu (2010), Rapid deglacial and early Holocene expansion of peatlands in Alaska, *Proceedings of the National Academy of Sciences of the USA*, *107*(16), 7347-7352.

Kettridge, N., Comas, X., Baird, A., Slater, L., Strack, M., Thompson, D., Jol, H. and A. Binley (2008), Ecohydrologically important subsurface structures in peatlands revealed by ground-penetrating radar and complex conductivity surveys, *Journal* *of Geophysical Research-Biogeosciences*, *113*, G04030, doi:10.1029/2008JG000787.

Korhola, A. (1994), Radiocarbon evidence for rates of lateral expansion in raised mires in southern Finland. *Quaternary Research*, *42*, 299-307.

Korhola, A. (1995), Holocene climatic variations in southern Finland reconstructed from peat-initiation data, *The Holocene*, *5*, 43-58.

Korhola, A. (1996), Initiation of a sloping mire cimplex in southwestern Finland: Autogenic *versus* allogenic controls, *Ecoscience*, *3* (2), 216-222.

Korhola, A., Ruppel, M., Seppä, H., Väliranta, M., Virtanen, T. and J. Weckström (2010), The importance of northern peatland expansión to the late-Holocene rise of atmospheric methane, *Quaternary Science Reviews*, *29*(5-6), 611-617.

Loisel, J. and M. Garneau (2010), Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives, *Palaeogeography, Palaeoclimatology, Palaeoecology*, *291*, 493-533.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C. and A.A. Valichko (2006), Rapid early development of circumarctic peatlands and atmospheric CH_4 and CO_2 variations, *Science, 314*, 285-288.

Mäkilä, M. (1997), Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland, *Boreas*, *26* (1), 1-14, doi:10.1111/j.1502-3885.1997.tb00647.x.

Mäkilä, M. and M. Moisanen (2007), Holocene lateral expansion and carbon accumulation of Luovuoma, a northern fen in finnish Lapland, *Boreas*, *36* (2), 198-210, doi:10.1111/j.1502-3885.2007.tb01192.x.

Peregon, A., Uchida, M. and Y. Yamagata (2009), Lateral extensión in *Sphagnum* mires along the southern margin of the boreal region, Western Siberia, *Environmental Research Letters*, *4*, doi:10.1088/1748-9326/4/4/045028.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C., Blackwell, P.G., Buck, C.E., Burr, G., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.M., Hughen, K.A., Kromer, B., McCormac, F.G., Manning, S., Bronk Ramsey, C., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J. and C.E. Weyhenmeyer (2009), IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP, *Radiocarbon*, *51*(4), 1111-1150.

Rosa, É., Larocque, M., Pellerin, S., Gagné, S. and B. Fournier (2009), Determining the number of manual measurements required to improve peat thickness estimations by ground penetrating radar, *Earth Surface Processes and Landforms*, *34*(3), 377–383, doi:10.1002/esp.1741.

Sandmeier, K.J. (2008), *ReflexW* (version 5.0) program for processing and interpretation of reflection and transmission data. Karlsruhe, Germany, Sandmeier software.

Slater, L. and A. Reeve (2002), Investigating peatland stratigraphy and hydrology using integrated electrical geophysics, *Geophysics*, *67*, 365-378.

Sjörs, H. (1983), Mires of Sweden, in *Mires: swamp, bog, fen and moor*, *Ecosystems of the world* vol. 4B, edited by Gore, A.J.P., Elsevier.

Stuiver, M. and P.J. Reimer (2010), *CALIB6.0 radiocarbon calibration program*, ^{14}Chrono Centre, Queens University, Belfast, Ireland.

Tipping, R. (2008), Blanket peat in the Scottish Highlands: timing, cause, spread and the myth of environmental determinism, *Biodiversity and Conservation*, *17*, 2097-2113.

Topp, G.C., J.L. Davis, and A.P. Annan (1980), Electromagnetic determination of soil-water content: Measurements in coaxial transmission lines, *Water Resources Research*, *16*, 574-582, doi:10.1029/WR016i003p00574.

Tummers, B. (2006), *Data Thief III*, http://datathief.org/.

Tzanis, A. (2006), MATGPR: A freeware MATLAB package for the analysis of common-offset GPR data, *Geophysical Research Abstracts*, Vol. 8, 09488.

Ugolini, F.C. and D.H. Mann (1979), Biopedological origin of peatlands in South East Alaska, *Nature*, *281*, 366-368.

van Bellen, S., Dallaire, P.-L., Garneau, M. and Y. Bergeron (2011), Quantifying spatial and temporal Holocene carbon accumulation in ombrotrophic peatlands of the Eastmain region, Quebec, Canada, *Global Biogeochemical Cycles*, *25*, GB2016, doi:10.1029/2010GB003877.

Yu, Z. (2011), Holocene carbon flux histories of the world's peatlands: global carbon-cycle implications, *The Holocene*, *21*(5), 761-774.

Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P. and D.J. Charman (2011) Peatlands and their role in the global carbon cycle, *Eos Transactions, American Geophysical Union*, *92*(12), 97-98.

Yu, Z., Beilman, D.W. and M.C. Jones (2009), Sensitivity of northern peatland carbon dynamics to Holocene climate change, in *Northern peatlands and carbon cycling, American Geophysical Union Monograph Series*, edited by A. Baird, L. Belyea, X. Comas, A. Reeve and L. Slater, AGU, Washington, DC.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W. and S.J. Hunt (2010) Global peatland dynamics since the Last Glacial Maximum, *Geophysical Research Letters*, *37*, L13402, doi:10.1029/2010GL043584.

Yu, Z., Loisel, J., Turetsky, M.R., Cai, S., Zhao, Y., Frolking, S., MacDonald, G.M. and J.L. Bubier (in Review), Evidence for elevated emissions from high-latitude wetlands causing high atmospheric methane concentration in the early Holocene, *Global Biogeochemical Cycles, 2011-GB-4222*.

Zobeck, T.M. (2004), Rapid soil particle size analyses using laser diffraction, *Applied Engineering in Agriculture*, *20*, 633–639.

CHAPTER 4

Holocene peatland carbon dynamics in Patagonia

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Abstract

Patagonian peatland ecosystems have received very little attention in the scientific literature despite their widespread distribution in the regional landscape and the growing anthropogenic pressure they experience from the peat extraction industry. The functioning of these southern peatlands is strikingly similar to that of northern peatlands, but they have developed under very different climate boundary conditions. Therefore, studying these ecosystems provides a unique opportunity to test hypotheses about the sensitivity of carbon-rich peat accumulating ecosystems to past and ongoing changes in climate, in addition to fill significant data and knowledge gaps. Here we present the Patagonian peatland climate space to discuss differences in peatland distribution between the northern and southern high latitudes, as well as to assess the control of climate on long-term rates of peat-carbon sequestration. We also provide detailed peat accumulation records for southern Patagonia using a combination of new peat-core analysis (4 sites) and a data synthesis from published studies (19 sites). Results indicate that Patagonian peatlands occupy a distinct climatological niche that corresponds to an end-member of the northern peatland climate domain, with a mild mean annual temperature (from 3 to 9 °C) and very weak temperature seasonality. We also found that Patagonian peatlands have been efficient land carbon sinks since their initiation, with a mean soil carbon density of 168 kg C m^{-2} ± 10%. The total carbon pool for these ecosystems was estimated at 7.6 Gt C. Similarly, modeled peat addition rates to the catotelm in Patagonian peatlands were significantly higher than what has been reported for northern sites, but decay coefficients were similar between these regions. These results support the idea that long, mild growing seasons promote peat formation. Overall, southern peatlands provide

a unique opportunity for studying peatland-carbon-climate linkages under a new set of climatic conditions.

4.1. Introduction

Peat-accumulating wetlands cover extensive areas of the boreal and subarctic regions of the world. In addition to storing about 10% of the world's freshwater (Martini et al., 2006), northern peatlands are globally important as they constitute one of the largest carbon (C) pools in the biosphere (500 ± 100 gigatons of C (GtC); Gorham, 1991; Yu et al., 2010; Yu, in review). Since the last deglaciation (~15 ka; 1 ka = 1000 calibrated years before present), these ecosystems have also played a dynamic role in the global C cycle by acting as carbon dioxide (CO_2) sinks and methane (CH_4) sources to the atmosphere (Frolking and Roulet, 2007; Yu, 2011). However, as peat-C sequestration and peat-C fluxes are sensitive to the regional climate (e.g., Aaby, 1976; Barber, 1981; Chambers and Charman, 2004; Jones and Yu, 2009), their contribution to the atmospheric CO_2 and CH_4 concentrations has varied significantly over time (Yu, 2011; Charman et al., in review), raising concern about the fate of these large C reservoirs in a warmer world. A recent review indicated that the role of peatlands for the 21st century will probably be that of a relatively small (0.2 GtC yr^{-1}), but persistent contributor to the atmospheric CO_2 and CH_4 burdens, with occasional large pulses due to droughts, fires, and permafrost thaw (Frolking et al., 2011). Alternatively, more catastrophic scenarios involving rapid and large C losses to the atmosphere (up to 10 GtC yr^{-1}) have been proposed (e.g., Ise et al., 2008; Dorrepaal et al., 2009; Fenner and Freeman, 2011). Overall, it can be said that climatically-induced alterations of the peatland C-sink capacity have happened in the past and will also take place in the future, but the sign and magnitude of this climate feedback remains uncertain. To alleviate such uncertainties, it appears evident that peatland ecosystems must be better understood in their full complexity to allow for realistic peat-carbon-climate model predictions (see Belyea and Baird, 2006). In addition, new databases of peat-C accumulation in understudied, peatland-rich regions such as Eastern Siberia, northern Canada, and Alaska would better inform the community on the climate sensitivity of peat-C sequestration by providing datasets for new portions of the northern peatland domain (Yu, in review).

Here we present the first Holocene peat-C sequestration history of Patagonian peatlands as a means to expand our current knowledge on global peatland dynamics and linkages to climatic conditions. Patagonian peatlands are strikingly similar to their northern counterparts in terms of structure and functioning (see section 4.2.1; Rydin and Jeglum, 2006), but these southern ecosystems have developed under very different boundary and climatic conditions from northern peatlands (see section 4.2.2). Therefore, we argue that southern peatlands provide a unique opportunity to test hypotheses about the sensitivity of high-latitude, C-rich peatland ecosystems to past and ongoing changes in climate. In this paper, we first examine the Patagonian peatland climate space (temperature, moisture, and temperature seasonality parameters) and compare it to the northern peatland domain to discuss inter-hemispheric differences in peatland distribution on the basis of climatological parameters, as well as to assess the potential control of climate on long-term peat-C sequestration patterns. To our knowledge, this climate envelope analysis is the first to be completed for Patagonian peatlands. Secondly, we provide detailed peat-C accumulation records for southern Patagonia using a combination of new peat-core analysis (4 sites) and a data synthesis from published studies (19 sites). This analysis fills significant data and knowledge gaps on Holocene C dynamics in this region, as peatland initiation, peat-C measurements, and C accumulation rates remain sparse in southern Patagonia and in the southern hemisphere in general (but see Yu et al., 2010). Thirdly, we use an exponential decay model (Clymo, 1984) to estimate long-term peat addition rate (*PAR*) and peat decay coefficient (α) for all 23 sites, which are then compared to northern peatland values. Overall, these results should be particularly useful for testing and validating peatland ecosystem models, in addition to providing new information to policy stake-holders and conservation groups that are evaluating the importance of Patagonian peatlands at the regional scale.

4.2. Patagonian peatlands

4.2.1. Distribution, ecology, and ecosystem dynamics

In southernmost South America, peatlands today cover about 45,000 km^2, roughly equivalent to 25% of the land area (Fig. 4.1; Pisano, 1983; Arroyo et al., 2005; Grootjans et al., 2010; Yu et al., 2010). Throughout the region, peatland complexes have developed following the last deglaciation, around 17 ka (Clapperton, 1993; McCulloch and Davies, 2001; Heusser, 2003). These peatlands are mostly found in valley bottoms and on low-gradient slopes (Rabassa et al., 1996), as well as over glacial deposits, igneous rocks and metamorphic schist that impede drainage locally (Coronato et al., 2006). Peatland types and associated vegetation communities follow a clear spatial distribution across southern Patagonia that is mainly a function of the precipitation regime (Pisano, 1983; Arroyo et al., 2005; Kleinebecker et al., 2007): (1) cushion bogs colonize the coastline and grow under hyper-oceanic and stormy conditions; (2) *Sphagnum*-dominated peat bogs are found on the lee side of the Andes as well as throughout the deciduous and evergreen cool-temperate ecoregions of Tierra del Fuego, and (3) groundwater-fed herbaceous fens (‘steppe bogs’ *sensu* Auer, 1965, or ‘permanently wet vegas’ *sensu* Collantes and Fagi, 1999) are located in the arid Argentinean steppe ecoregion. These peatland types are briefly described in the following paragraphs.

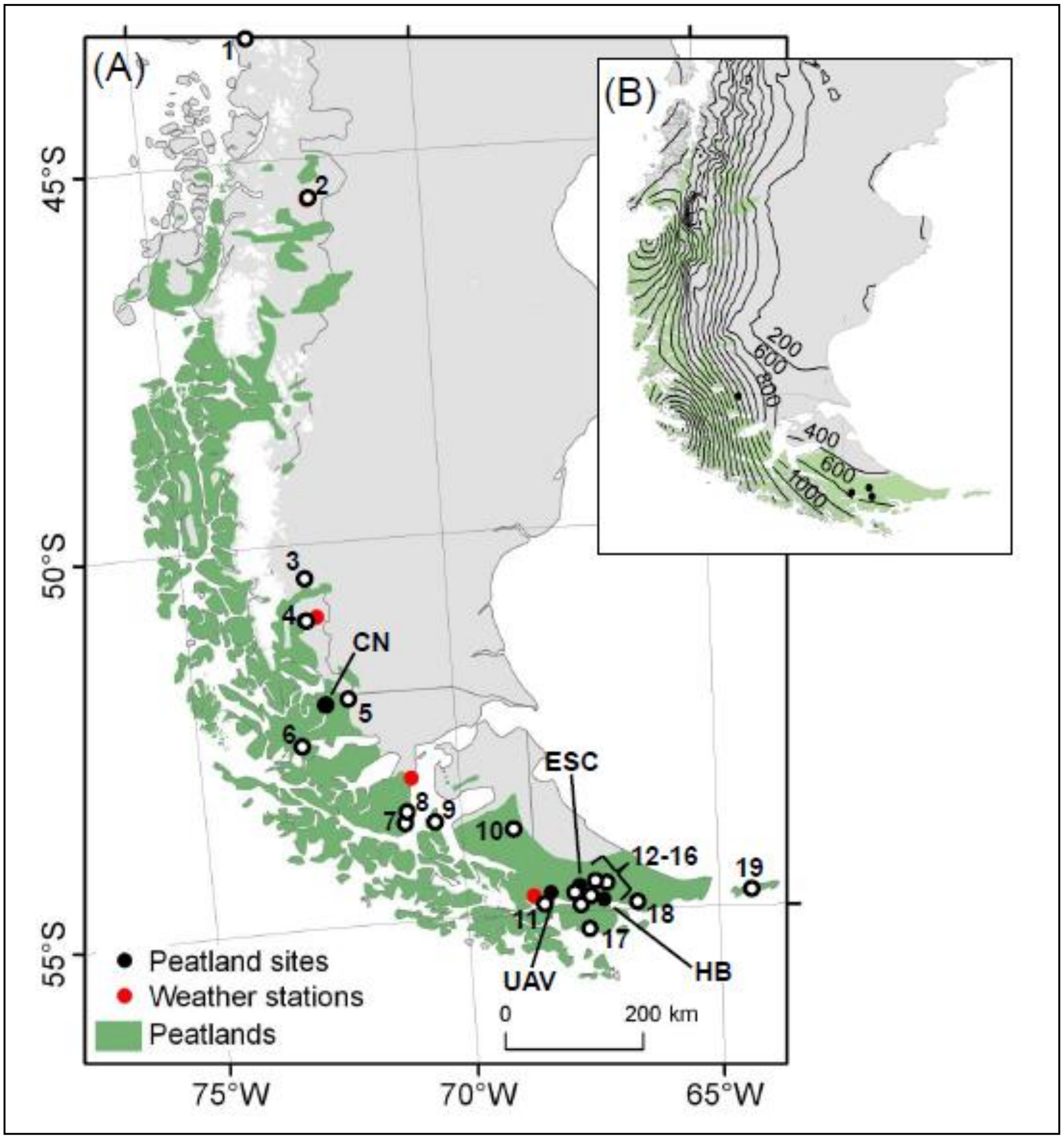

Figure 4.1. Location maps and study sites. **(A)** Map of southern Patagonia, South America, showing the distribution of southern peatlands (green area; from Yu et al., 2010), as well as the location of weather stations (red dots), our 4 new study sites (black dots), and the 19 sites from the literature review (white dots; site ID is the same as in Table 4.3). **(B)** Map of southern Patagonia showing mean annual precipitation isohyets for the period 1961-1990. (Data from New et al., 2002).

Cushion peatland ecosystems constitute about 50% of the Magellanic moorland ecozone (Arroyo et al., 2005), where cool, stormy, windy, and very wet conditions (annual precipitation can reach 7000 mm in the Chilean fjords region; Schneider et al., 2003) occur year-round due to the proximity to the ocean (Fig. 4.1; Godley, 1960). These peat-accumulating systems are dominated by *Donatia fascicularis* and *Astelia pumila*, two vascular plants capable of holding on to water and resist stormy weather by forming dense cushions or carpets (Tuhkanen, 1992; Squeo et al., 2006). Isolated cushions can also be found at high elevation (close to the tree line) in the Patagonian Mountains, where high winds occur (Markgraf and Huber, 2010). Cushion peat is generally highly decomposed, with bulk density values three to five times higher than *Sphagnum* peat (Kleinebecker et al., 2007; Fritz et al., 2011). The biodiversity, development, and C dynamics of these unique ecosystems are very limited at the moment, largely because they only occur in very remote areas of South America (but see Ashworth et al., 1991; Heusser, 1995; Fesq-Martin et al., 2004; Fritz et al., 2011).

Sphagnum-dominated peat bogs (Fig. 4.2a) are mostly embedded within the cool-temperate deciduous forest and evergreen rainforest ecoregions of Patagonia, where annual precipitation exceeds potential evapotranspiration (Pisano, 1983; Arroyo et al., 2005; Grootjans et al., 2010). In these regions, the annual temperature regime is cool, and characterized by a low seasonality as well as rare frost (Schneider et al., 2003; Arroyo et al., 2005). The ground layer of these peatlands is almost exclusively covered by *Sphagnum magellanicum*, and these peat mosses extend from high hummocks (>1 m in height) to pool margins (Fig. 4.2b and 4.2c; Kleinebecker et al., 2007). *Sphagnum cuspidatum* and *Drepanocladus* spp. are found in shallow pools (Fig. 4.2c). Linear string patterning was also observed in these peatlands and these features are perpendicular to the peatland surface slope. The main vascular species include *Nothofagus antarctica* (stunted tree), *Empetrum rubrum* (low shrub) and *Marsippospermum grandiflorum* (rush), which are found at the drier end of the hydrological gradient and on strings, and *Tetroncium magellanicum* (rush) along the pool margins (Fig. 4.2c). A few *Carex* species (*C. magellanica*, *C. curta*, and *C. banksii*) are also present. Generally speaking, these peatlands are characterized by thick and poorly decomposed peat deposits (Fig. 4.2d; Auer, 1965; Rabassa et al., 1989; Kleinebecker et al., 2007), and their surface water is acidic (pH ~ 4.0).

Herbaceous fens are found in the steppe region, to the east and north of the *Sphagnum* bog zone. As annual precipitation is low (< 400 mm; Pisano, 1983) and summer months are typically characterized by a large water balance deficit, these peatlands rely on temporary surface runoff as well as groundwater inputs (Grootjans et al., 2010). The vegetation communities are dominated by grasses, sedges (*Carex* spp.), rushes (*Marsippospermum grandiflorum*), and few shrubs. Patches of *Sphagnum* spp. and other mosses can be found (Pisano, 1983; Rydin and Jeglum, 2006; Grootjans et al., 2010). Herbaceous peat deposits are usually highly decomposed (Arroyo et al., 2005).

Patagonian peatland stratigraphy has first been studied by Bonarelli (1917), followed by extensive peat-core surveys conducted by Auer (1958, 1965). These authors have noticed that most peatlands started developing as herbaceous-rich fen ecosystems and, in today's bog ecoregion, these fens switched to *Sphagnum*-dominated bogs during the mid- to late-Holocene (Auer, 1965; Loisel et al., in review). This hydroseral succession is similar to that of northern peatlands (Hugues, 2000; Charman, 2002).

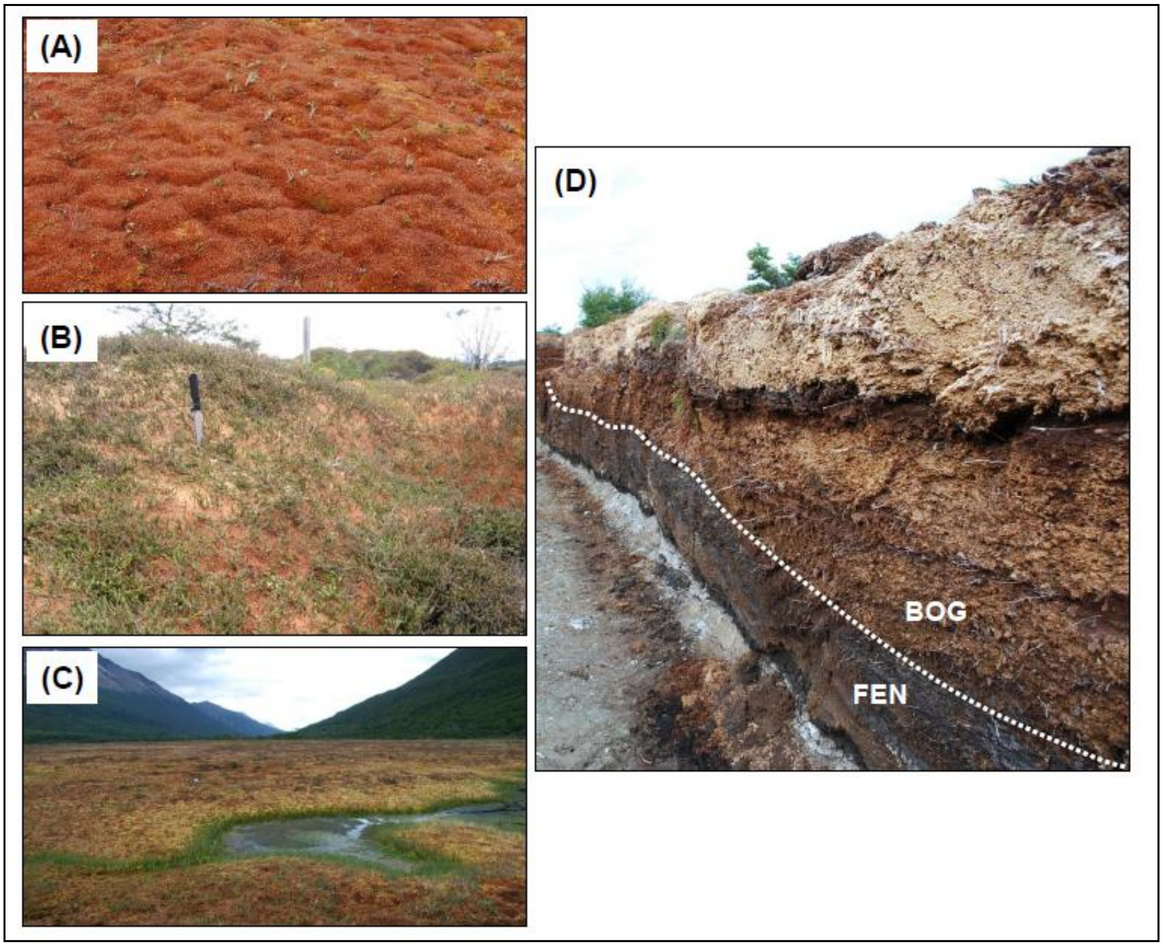

Figure 4.2. Photographs showing some Patagonian peatlands. **(A)** *Sphagnum magellanicum* carpet, Upper Andorra Valley peatland. **(B)** High hummock (> 60 cm) formed by *Sphagnum magellanicum* and colonized by *Empetrum rubrum* shrubs, Escondido peatland. **(C)** Wet depression (pool) colonized by *Sphagnum cuspidatum* and *Drepanocladus* spp. and surrounded by a narrow ring of *Tetroncium magellanicum* (rush), Upper Andorra Valley peatland. The pool is embedded in a large *Sphagnum magellanicum* carpet. **(D)** Peatland cross-section showing the fen-to-bog transition (dashed line), Escondido peatland. Herbaceous fen peat is dark brown, dense, and highly decomposed, whereas *Sphagnum* bog peat is reddish brown and poorly decomposed.

Although many paleoecological studies have been performed in Patagonian peat bogs over the past 30 years, they have almost exclusively focused on general Holocene vegetation and climate histories using pollen analysis (e.g., Heusser, 1989; Ashworth et al., 1991; Borromei, 1995; Mancini, 2009). Notable exceptions include the well-dated, high-resolution, multi-proxy reconstructions published by Pendall et al. (2001), Huber and Markgraf (2003), Mauquoy et al. (2004), and Chambers et al. (2007). Still, the scarcity of plant macrofossil records limits our understanding of Patagonian peatland formation and developmental history. Similarly, very few peat bulk density and carbon measurements are available from peat records, hampering the quantification of regional peat-C dynamics. On another note, basal peat ages from all Patagonian peatland studies (n = 54) were recently compiled to infer the timing, frequency, and probability of new peatland initiation (Yu et al., 2010). These authors also estimated Holocene peat-C accumulation rates for a subset of these sites (n = 17), where at least three radiocarbon (^{14}C) dates were available from each site. The main conclusions from Yu et al. (2010) are: (1) Patagonian peatlands mostly initiated between 17 and 12 ka, with a notable reduction during the Antarctic Cold Reversal (13 ka; Barker et al., 2009); (2) peat-C accumulation rates show a gradual increase, from 15 g C m^{-2} yr^{-1} in the early Holocene to ~ 30 g C m^{-2} yr^{-1} in the late Holocene, possibly due to changes in incoming solar radiation; (3) the mean Holocene peat-C sequestration rate is 22 g C m^{-2} yr^{-1}, and (4) Patagonian peatlands currently contain 15 ± 3 GtC.

4.2.2. Holocene boundary conditions and climate history

Due to the Earth’s orbital parameters, incoming solar radiation (insolation) in the high latitudes of the southern hemisphere is almost completely out of phase with insolation at the high northern latitudes (Fig. 4.3; Berger and Loutre, 1991; Vandergoes et al., 2005). Of particular interest here is the asynchrony of solar insolation maxima between the two hemispheres, which is mostly attributable to the precession of the equinoxes (Huybers, 2007; Drysdale et al., 2009). At about 10 ka, for example, a time when the Earth was closest to the Sun during northern hemisphere summers (perihelion), the Earth was farthest away from the Sun during southern hemisphere summers (aphelion). As a result, the intensity of the summer insolation peak was greater in the northern hemisphere than in the southern hemisphere (Fig. 4.3). During this time period, northern peatlands were rapidly spreading over the landscape and accumulating large quantities of organic C (MacDonald et al., 2006; Yu et al., 2010). Evidence from Alaska (Jones and Yu, 2010) and northern peatlands as a whole (Yu et al., 2009) suggest that this very positive C balance was induced by increased plant production during warmer-than-today summers, and by limited peat decomposition during colder-than-today winters. Conversely, the Earth was closest to the Sun during the southern hemisphere summer around 4 ka, meaning that incoming solar energy peaked in the high southern latitudes during this time (Fig. 4.3). Therefore, as each precession cycle progresses through time, the insolation intensity is almost anti-phase between the hemispheres. Given that, in terms of incoming solar energy (W m^{-2}), precession is the most important of all orbital parameters (Huybers, 2007), this asynchrony can be used as a ‘natural experiment’ to evaluate the long-term, large-scale role of summer insolation (and associated climate) on peatland functioning in both hemispheres and at different times since peatland inception.

In southern Patagonia, oceanic and atmospheric circulation patterns have important influences on the regional distribution of ecosystems, as well as on their structure and dynamics (Paruelo et al., 1998; Grootjans et al., 2010). Despite the proximity of the ocean, annual precipitation is rather low in the peatland-rich region of southern Patagonia, and is equable to the precipitation regime experienced by continental peatlands of North America and Eurasia (Wieder et al., 2006; Yu et al., 2009). Conversely, the temperature regime is similar to the oceanic conditions under which blanket bogs are found in the British Isles. The unique combination of precipitation and temperature regimes that characterizes Patagonian peatlands (e.g., Fig. 4.4), which was first pointed out by Smith and Clymo (1984) in their study of a peat deposit from the Falkland Islands, can be used to link peatland dynamics and climatic regimes beyond the northern peatland climate domain.

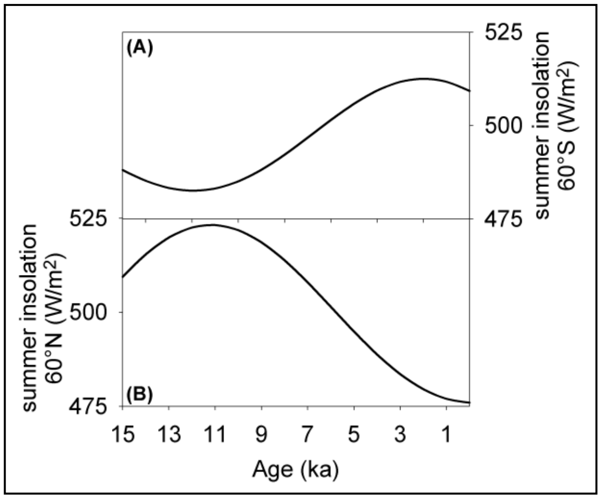

Figure 4.3. Summer insolation during the Holocene. Insolation at 60°S peaks around 4ka **(A)**, whereas maximum insolation occurred around 11 ka at 60°N **(B)**. These two curves show opposite trajectories. Data: Berger and Loutre (1991).

4.3. Materials and Methods

4.3.1. Climate envelope analysis

We used a global gridded climate data set (New et al., 2002) with a spatial resolution of 10x10’ (latitude/longitude) to generate bioclimatic information for the Patagonian peatland domain, as defined by Yu et al. (2010; Fig. 4.1). Mean monthly precipitation, temperature, and relative humidity for the period 1961-1990 were extracted for each grid that was covered by at least 50% peatlands (sources for the peatland map: Pisano, 1983; Heusser, 1995). Using these monthly values, mean annual temperature

(MAT), mean annual precipitation (MAP), mean annual relative humidity (RH), and a seasonality index (mean January T minus mean July T) were calculated.

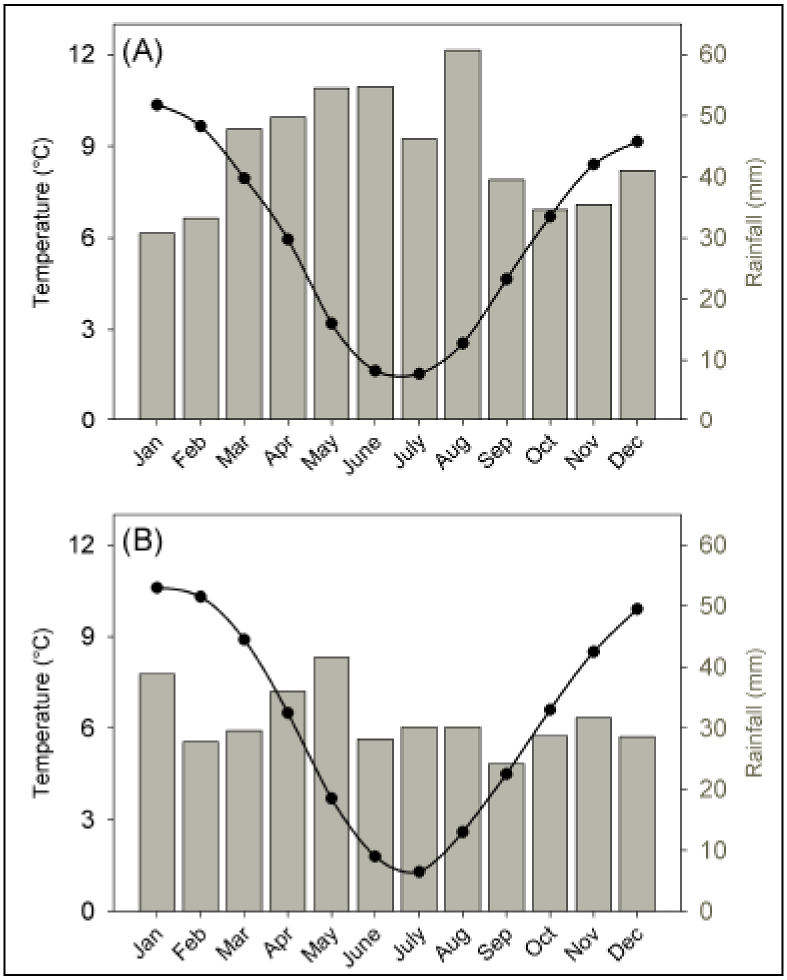

Figure 4.4. Mean monthly temperature and precipitation values for the period 1961-1990. Similar temperature regimes characterize Ushuaia in Argentina **(A)** and Punta Arenas in Chile **(B)**, though Punta Arenas receives less precipitation annually than Ushuaia. Data: Servicio Meteorológico Nacional (2012) and Dirección Meteorológica de Chile (2012), respectively.

4.3.2. New study sites and field sampling

All four study sites (Table 4.1) are raised bogs dominated by *Sphagnum magellanicum*, and surface vegetation is as described in section 4.2.1. Surface patterning is apparent in parts of these peatlands (Fig. 4.5). Upland vegetation surrounding these sites is dominated by *Nothofagus antarctica* and *N. pumilio*. Peat cores were collected in January 2010 using a 50 cm-long Russian-type corer. To minimize compaction of the surface layers, a box corer was used to retrieve the top meter of peat. The collected cores were wrapped in plastic films, secured in PVC pipes, transported to the laboratory, and stored at 4 °C in a cold room at Lehigh University.

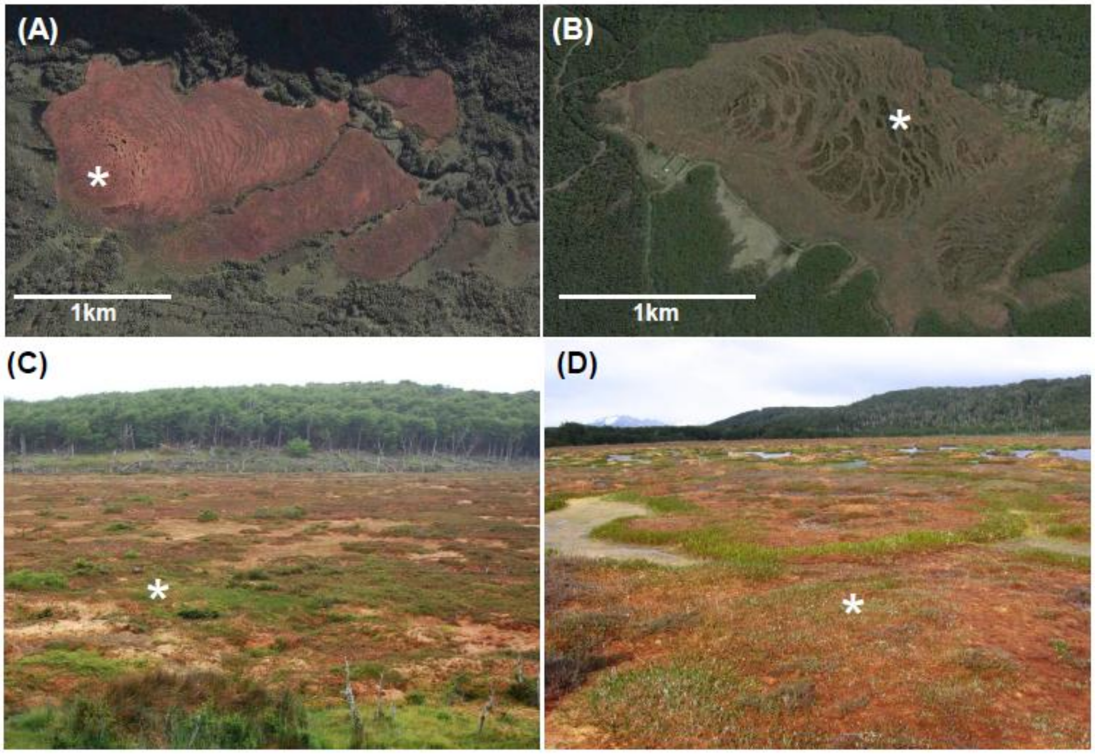

Figure 4.5. Study sites and peat core location (white stars) in Patagonia. **(A)** Spot image of Andorra Valley peatland. **(B)** Spot image of Escondido peatland. **(C)** Ground photograph of Harberton Bog. **(D)** Ground photograph of Cerro Negro peatland. Spot images: © 2012 Google, © 2012 DigitalGlobe GeoEye, © 2012 Inav/Geosistemas SRL.

Three of the four studied peatlands are located in the vicinities of Ushuaia, Argentina (54°47’ S, 68°14’ W). The climate in Ushuaia is cool temperate, with a 30-year mean annual temperature of 6.0 °C, ranging from 1.6 °C in July to 10.3 °C in January (monthly means), and mean annual precipitation is 528 mm (Fig. 4.4a; Servicio Meteorológico Nacional, 2012). The fourth site is located on the lee side of the Andes, about 150 km north of Punta Arenas in Chile (53°10' S, 70°56' W). Although this region is relatively dry with mean annual precipitation in Punta Arenas of 376 mm, the temperature regime is very similar to that of Ushuaia, with mean January temperature of 10.6 °C, mean July temperature of 1.3 °C, and mean annual temperature of 6.3 °C (Fig. 4.4b; Dirección Meteorológica de Chile, 2012).

Table 4.1. Summary information for the four new peatland study sites in Patagonia.

	Upper Andorra Valley (UAV)	Escondido (ESC)	Harberton Bog (HB)	Cerro Negro (CN)
Latitude	-54.75	-54.62	-54.87	-52.07
Longitude	-68.33	-67.77	-67.28	-72.03
Elevation (m)	200	127	11	217
Peatland type	*Sphagnum* bog	*Sphagnum* bog	*Sphagnum* bog	*Sphagnum* bog
Peat depth (cm)	715	450	525	445
Peat inception age (ka)	10823	6929	1866	9205
Mean annual temperature (°C)	4.2	4.8	3.4	6.4
Mean annual precipitation (mm)	542	469	507	1322
Mean relative humidity (%)	77	77	77	70
Seasonality (°C)	8.3	9.0	8.5	9.7

The Andorra peatland (54°45' S, 68°20' W, 200 m above mean sea level (a.m.s.l.)) is located in the Andorra Valley, about 6 km to the north-west of Ushuaia in Argentina (Fig. 4.5a). This peatland complex has developed over glacial clay and consists of four raised bogs and a fen, all of which are confined between glacier-covered mountains (e.g., Glaciar Vinciguerra, 1300 a.m.s.l.). Our peat core (715 cm-long) was collected in the Upper Andorra Valley bog (UAV), the highest and largest (about 0.5 km^2 in area) of these raised bogs (Fig. 4.5a). Recent studies have been conducted at these bogs, including nutrient loading experiments (Fritz et al., 2012), peat-CH_4 fluxes (Fritz et al., 2011), paleoecological reconstructions (Mauquoy et al., 2004; Chambers et al., 2007), and hydrological surveys and analyses (Baumann, 2006; Grootjans et al., 2010).

Escondido peatland (ESC; 54°37’ S, 67°46’ W, 127 m a.m.s.l.) is located just north of Lago Escondido, about 40 km to the north-east of Ushuaia (Fig. 4.5b). This site is about 1 km^2 in area, and its southernmost portion is being drained and mined. Our peat core (450 cm-long) was extracted from the highest and central area of the peat basin.

Harberton bog (HB; 54°52’ S, 67°17’ W, 11 m a.m.s.l.) is located near Estancia Harberton, a farm about 60 km east of Ushuaia (Fig. 4.5c). The peatland (about 0.5 km^2 in area) has an elongated shape and was the object of many studies over the past 20 years (e.g., Rabassa et al., 1989; Markgraf, 1991; Pendall et al., 2001; Huber et al., 2004; Markgraf and Huber, 2010). Our peat core (525 cm-long) was collected from the highest and central portion of the peat basin.

Cerro Negro peatland (CN; 52°04’ S, 72°02’W, 217 m a.m.s.l.) is located about 150 km north of Punta Arenas and 100 km south of Torres del Paine National Park in Chile (Fig. 4.5d). This peatland complex consists of two raised bogs; our peat core (445 cm-long) was collected in the highest but smallest (about 0.7 km^2 in area) of these raised bogs. Cerro Negro peatland is located approximately 12 km west of the Rio Rubens peatland that was studied by Huber and Markgraf (2003) and Huber et al. (2004).

4.3.3. Laboratory analysis of new peat cores

Major changes in peat stratigraphy were identified on the basis of visual examination of the peat core photographs (Fig. 4.6). Plant macrofossil samples were also analyzed at every centimeter along the CN core (from 0 to 445 cm) and at 2 cm increments along the UAV core (from 0 to 300 cm) following standard procedures (Mauquoy and van Geel, 2007). Peat sub-samples (2 cm^3) were gently boiled and rinsed with distilled water through a 150-µm sieve. For each sample, Sphagnaceae, Amblystegiaceae, herbaceous, ligneous and unidentifiable organic matter (UOM) material were quantified as a percentage of the total sample by volume.

Peat core chronology was established using AMS radiocarbon (^{14}C) dating method (Table 4.2). For each peatland, at least 10 ^{14}C dates were used to constrain the chronology. Dating material was hand-picked and cleaned with distilled water and was

Figure 4.6. Peat core photographs. **(A)** Herbaceous fen peat is dark brown, highly decomposed, and has a high density (mean = 0.07g OM cm^{-3}) as well as a low water content (mean = 89%). Peat core from the Escondido site (350-400 cm). **(B)** *Sphagnum* bog peat is reddish brown, poorly decomposed, and has a low density (mean = 0.05 g OM cm^{-3}) as well as a high water content (mean = 94%) Peat core from Harberton (top m).

Table 4.2. AMS radiocarbon (^{14}C) dating results from the four new peat cores in Patagonia.

Core ID	Sample depth (cm)	Dated material	^{14}C age (yr BP)	Calibrated 2σ range (cal yr BP)	Median age (cal yr BP)	Most probable age (cal yr BP)[*]	Lab ID (UCIAMS[**])
PAT-UAV (2010)	29.5	*Sphagnum* stems	-3365 ± 15	-12, -22	-17	60	94443
	47.5	*Sphagnum* stems	155 ± 15	0-282	140	194	94444
	77.5	*Sphagnum* stems	175 ± 15	0-283	140	277	88647
	113.5	*Sphagnum* stems	930 ± 15	795-911	850	860	82708
	135.5	*Sphagnum* stems	1050 ± 20	928-1046	990	1032	88648
	159.5	*Sphagnum* stems	1530 ± 15	1358-1513	1440	1402	79133
	183.5	*Sphagnum* stems	1620 ± 15	1418-1555	1490	1525	88649
	231.5	*Sphagnum* stems	1965 ± 15	1875-1949	1910	1946	82709
	319.5	root-free bulk peat	2270 ± 110	1995-2700	2350	2209	79134
	349.5	*Drepanocladus* stems	2365 ± 15	2341-2453	2400	2327	82704
	373.5	*Drepanocladus* stems	2480 ± 20	2464-2714	2590	2562	82705
	399.5	*Drepanocladus* stems	2450 ± 25	2359-2701	2530	2694	82706
	439.5	*Drepanocladus* stems	4020 ± 20	4427-4526	4480	4278	82707
	479.5	*Sphagnum* stems	4865 ± 15	5587-5642	5610	5558	79141
	519.5	*Drepanocladus* stems	5330 ± 20	6001-6190	6100	6168	89805
	559.5	ligneous fragment	6670 ± 15	7508-7580	7540	7540	97978
	639.5	*Drepanocladus* stems	7410 ± 110	8012-8404	8210	8214	79142
	714.5	root-free bulk peat	9480 ± 25	10604-11060	10830	10823	78207
PAT-ESC (2010)	33.5	*Sphagnum* stems	125 ± 15	0-268	130	136	94435
	53.5	*Sphagnum* stems	190 ± 15	0-287	140	207	94436
	73.5	*Sphagnum* stems	235 ± 15	154-304	230	289	94437
	111.5	*Sphagnum* stems	405 ± 15	344-507	430	484	97979
	149.5	*Sphagnum* stems	410 ± 15	466-508	490	607	94438
	209.5	*Sphagnum* stems	2785 ± 20	2801-2952	2880	2851	94439
	245.5	*Sphagnum* stems	3240 ± 15	3401-3548	3470	3448	97980
	279.5	*Sphagnum* stems	3570 ± 20	3783-3960	3870	3861	94440
	349.5	*Sphagnum* stems	4190 ± 15	4649-4832	4740	4791	94441
	399.5	*Drepanocladus* stems	4740 ± 15	5333-5581	5460	5504	94442
	450.5	root-free bulk peat	6250 ± 80	6944-7412	7180	6929	78212

PAT-HB (2010)	35.5	*Sphagnum* stems	-1375 ± 15	-9, -35	-22	4	94445
	51.5	*Sphagnum* stems	-2125 ± 15	-12, -28	-19	13	94446
	79.5	*Sphagnum* stems	65 ± 15	0-251	120	55	77124
	158.5	*Sphagnum* stems	185 ± 15	0-285	140	174	77125
	239.5	*Sphagnum* stems	265 ± 15	286-422	350	300	77126
	319.5	*Drepanocladus* stems	390 ± 15	335-503	420	479	77127
	349.5	*Drepanocladus* stems	650 ± 15	562-664	610	569	97976
	398.5	*Sphagnum* leaves	880 ± 15	735-898	820	762	77128
	429.5	root-free bulk peat	995 ± 15	832-956	890	919	97977
	479.5	ligneous fragment	1210 ± 15	1067-1177	1120	1164	77129
	525.5	Sedge stem bases	1985 ± 15	1891-1987	1940	1866	77131
PAT-CN (2010)	21.5	*Sphagnum* stems	-2405 ± 15	-13, -17	-15	4	97975
	79.5	*Sphagnum* stems	220 ± 20	0-304	150	298	76272
	119.5	*Sphagnum* stems	460 ± 15	501-524	510	511	79135
	159.5	*Sphagnum* stems	730 ± 20	660-690	680	654	76273
	211.5	*Sphagnum* stems	1465 ± 15	1311-1383	1350	1310	79136
	239.5	root-free bulk peat	1900 ± 20	1744-1917	1830	2111	77132
	245.5	*Sphagnum* stems	2465 ± 15	2366-2704	2540	2339	97974
	255.5	*Sphagnum* stems	2730 ± 15	2780-2857	2820	2704	79140
	295.5	*Sphagnum* stems	3100 ± 15	3265-3374	3320	3364	82710
	319.5	root-free bulk peat	3435 ± 15	3638-3813	3730	3644	77133
	349.5	*Sphagnum* stems	3805 ± 20	4095-4246	4170	4150	77134
	357.5	root-free bulk peat	4100 ± 15	4527-4799	4660	4327	79139
	365.5	root-free bulk peat	4720 ± 20	5326-5580	5450	4677	79137
	389.5	root-free bulk peat	7680 ± 90	8320-8647	8480	8205	79138
	405.5	root-free bulk peat	7745 ± 25	8452-8588	8520	8660	77135
	445.5	root-free bulk peat	8215 ± 20	9039-9275	9160	9205	77136

Table 4.3. Synthesis of available information from Patagonian peatland sites (n = 19). Site ID is the same as on Fig. 4.1. FBT: fen-to-bog transition; ka: thousands of years cal. BP; OM: organic matter; C/N ratio: carbon-to-nitrogen ratio; [C]: carbon concentration.

ID	**Reference**	**site**	**coordinates Y, X**	**peatland type**			**stratigraphic information**			
					peat types	**FBT (ka)**	**lithology**	**others**	**basal age (ka)**	**number of ^{14}C dates**
1	Heusser, 1992	Cuesta Moraga	-43.42, -73.83	*Sphagnum*	Y	-	OM content	-	14.41	6
2	Markgraf, 2007	Mallín Pollux	-45.52, -71.83	herbaceous	Y	-	-	-	18.66	17
3	Mancini, 2009	Cerro Frías	-50.4, -72.7	*Sphagnum*	Y	-	-	-	11.95	5
4	Villa-Martinez, 2007	Vega Ñandú	-51.13, -73.12	herbaceous	Y	2.26	OM content	-	12.57	10
5	Huber, 2003	Rio Rubens	-52.13, -71.88	*Sphagnum*	Y	3.55	-	Macrofossils	12.62	12
6	Fesq-Martin, 2004	Gran-Campo 2	-52.80, -72.92	herbaceous	Y	-	-	-	10.94	5
7	McCulloch, 2001	Puerto Hambre II	-53.60, -70.97	*Sphagnum*	N	-	OM content	-	17.36	6
8	Biester, 2003	Pbr2	-53.63, -70.97	*Sphagnum*	N	1.34	Bulk density	C/N, [C]	17.56	7
9	McCulloch, 2001	Est. Esmeralda II	-53.28, -72.55	*Sphagnum*	N	-	OM content	-	12.34	5
10	Heusser, 1993	Onamonte 1	-53.90, -68.95	*Sphagnum*	Y	1.10	-	-	9.82	5
11	Heusser, 1998	Ushuaia 2	-54.78, -69.30	*Sphagnum*	Y	4.57	-	-	13.98	6
12	Heusser, 2003	Lago Fagnano	-54.57, -67.62	*Sphagnum*	Y	3.82	-	-	12.80	5
13[*]	Borromei, 2010	Las Cotorras	-54.68, -68.05	*Sphagnum*	N	-	-	-	7.82	8
14[*]	Markgraf, 2010	Paso Garibaldi	-54.69, -67.85	*Sphagnum*	Y	0.56	-	-	12.61	6
15	Pendall, 2001	Harberton	-54.88, -67.33	*Sphagnum*	Y	6.46	-	-	15.87	23
16	Heusser, 1989	Caleta Róbalo	-54.93, -67.63	*Sphagnum*	Y	3.80	OM content	-	3.8	4
17	Saptoka, 2007	Oreste	-55.22, -67.62	*Sphagnum*	N	-	Bulk density	-	13.07	9
18	Heusser, 1995	Bahía Moat	-54.90, -66.73	cushion	Y	2.74	OM content	-	7.82	5
19	Unkel, 2008, 2010	Galvarne	-54.5, -64.0	*Sphagnum*	Y	-	OM content	C/N	16.09	6

[*] Site not included in Yu et al. (2010)

exclusively composed of non-aquatic plant macrofossil remains (e.g., *Sphagnum* stems and leaves, seeds, sedge stem bases). In horizons that lacked plant macrofossil dating material, root-free bulk peat samples were analyzed. The ^{14}C samples were submitted to Keck AMS Carbon Cycle Lab at University of California, Irvine. Results were calibrated using the program Bacon, a flexible Bayesian age-depth modeling approach (Blaauw and Christen, 2011) that was used in conjunction with the INTCAL09 calibration data set (Reimer et al., 2009). Post-modern ^{14}C dates were calibrated using CALIBomb and a concatenation of the Levin's Vermunt and Schauinsland calibration datasets (Levin and Kromer, 2004).

Bulk density and organic matter content were determined for all four peat cores at 1 cm increments following standard procedures (Dean, 1974). Contiguous peat sub-samples (1 cm^3) were dried overnight at 105 °C, weighed, and burned at 550 °C for two hours. Peat-C content was assumed to be 50% of the organic matter density (Turunen et al., 2002). Peat-C accumulation rates (in g C m^{-2} yr^{-1}) were calculated by multiplying the C mass of each depth increment (organic matter density x C content) by the interpolated deposition rate of each sample as inferred from the age-depth models.

Peat lithological differences (bulk density, organic matter content, organic matter density, and water content) between *Sphagnum* peat, herbaceous peat, and highly decomposed peat were tested using one-way analysis of variance (ANOVA). Tukey's HSD post-hoc tests were also performed to show which group means were significantly different from one another. Finally, we used a cluster analysis (Ward's method) to identify the main peat types (clusters) along our new peat cores on the basis of the plant macrofossil samples from cores CN and UAV (n = 588). These clusters will be used to infer stratigraphic changes along cores ESC and HB, for which plant macrofossil analysis was not performed. Ward's (1963) method is a 'bottom-up' hierarchical cluster analysis where each observation starts in its own cluster, and pairs of clusters are progressively merged to build the hierarchy. The criterion for choosing the pair of clusters to merge at each step is based on the minimum distance between each cluster.

4.3.4. Data synthesis of published peat records

We used the compilation of peat-C accumulation records (n = 17) from Yu et al. (2010) and 2 additional records (Borromei et al., 2010; Markgraf and Huber, 2010) for our data synthesis and C dynamics analysis (Table 4.3). These peat cores all had at least four ^{14}C dates to constrain their chronology. An age-depth model was established for each site using the program Bacon (Blaauw and Christen, 2011) on the basis of the uncalibrated ^{14}C dates that were presented in the form of published figures or tables in the original publications. Peat depth was converted to cumulative mass using organic matter (OM) density values of 0.05 g OM cm^{-3} for *Sphagnum* peat, 0.06 g OM cm^{-3} for fibrous peat, and 0.07 g OM cm^{-3} for herbaceous and decomposed peat types (mean values as derived from 438 peat-core samples; see section 4.4.2). When stratigraphic information was not available, an overall mean value of 0.06 g OM cm^{-3} was used (Table 4.3).

4.3.5. Calculating and modeling Holocene peat accumulation

The soil C density (in kg C m^{-2}), or accumulated C mass since peat inception, was directly obtained by summing the peat mass of each depth increment (OM g cm^{-3} X cm) along each peat core independently. This value was then multiplied by the assumed peat C content (50%). Long-term apparent rate of peat accumulation (in g C m^{-2} yr^{-1}) was then obtained for each core by dividing the soil C density by the peat basal age ("LORCA" *sensu* Turunen et al., 2002).

As these peat-C accumulation rates decrease over time in the catotelm because of the slow but continuous decay that takes place in the deeper peat layers (Clymo, 1984; Turunen et al., 2002), it is challenging to compare PCAR values between sites of different ages. Therefore, peat accumulation was also calculated using the exponential decay model developed by Clymo (1984). In this model, a proportional decay function (eq. 1, 2) is used to represent long-term peat decomposition, assuming (1) a constant peat addition rate (*PAR*) at the top of the catotelm in the peat column, and (2) a constant peat proportional decay coefficient (α) in the catotelm. The exponential decay has the form of

$$\frac{dM}{dt} = PAR - \alpha * M \,, \qquad \text{(eq. 1)}$$

which has the analytical solution of

$$M = \left(\frac{PAR}{\alpha}\right) * (1 - e^{-\alpha * t}) \,. \qquad \text{(eq. 2)}$$

This model was applied to the 19 sites from the data synthesis as well as to our 4 new peat cores. In brief, eq. 2 was fitted to each peat core-derived age-depth relationship, where depth was presented as cumulative peat mass (*M*). For our new peat cores, this value was directly calculated as indicated in section 4.3.3, whereas organic matter density was assumed to range from 0.05 to 0.07 g OM cm^{-3} for sites from the data synthesis, depending on the peat type (see section 4.3.4).

4.4. Results

4.4.1. Climate domain for Patagonian peatlands

Southern peatlands typically occur where mean annual temperatures (MAT) are between 3 and 9°C, and mean annual precipitation (MAP) is between < 300 and > 4000 mm (Fig. 4.7a). Most of the peatlands that are being analyzed in the present study (new peat cores and data synthesis) were found in the middle portion of the MAT distribution (mean = 4.7 ± 0.3 °C (S.E.)), and toward the lower end of the MAP range (mean = 820 ± 113 mm) since they are not found in the coastal Magellanic moorland ecozone (Fig. 4.1; section 2.1). Mean annual relative humidity ranges between 60 and 85%, and temperature seasonality values are between 5 and 15°C (Fig. 4.7b). Mean annual relative humidity is negatively correlated with seasonality ($R^2 = 0.289$, $p < 0.0001$), such that lower relative humidity is found in conjunction with higher seasonality. This pattern could relate to continentality, with lowest seasonality and higher relative humidity characterizing oceanic sites vs. highest seasonality and lower relative humidity characterizing continental sites. Finally, mean precipitation and mean temperature of the warmest (January) and coldest (July) months are plotted in Fig. 4.7c and 4.7d, respectively. January mean precipitation ranges from 26 to 388 mm, and July mean precipitation is between 10 and 377 mm. Mean temperatures range between 5 and 15°C in January, and from -4 to 6°C in July. Mean precipitation of the coldest and warmest months follow a 1:1 line ($R^2 = 0.945$, $p < 0.0001$), suggesting that precipitation is equally distributed throughout the year in this region (Fig. 4.7c; see also Fig. 4.4). Mean temperature of the coldest and warmest months are also positively correlated ($R^2 = 0.305$, $p < 0.0001$), though there is a wide spread of data that is likely due to the continentality effect (Fig. 4.7d). Our 23 peatland sites are characterized by a mean January precipitation of 70 ± 10 mm, a mean July precipitation of 66 ± 10 mm, a mean January temperature of 8.9 ± 0.3°C, and a mean July temperature of 1.0 ± 0.7°C.

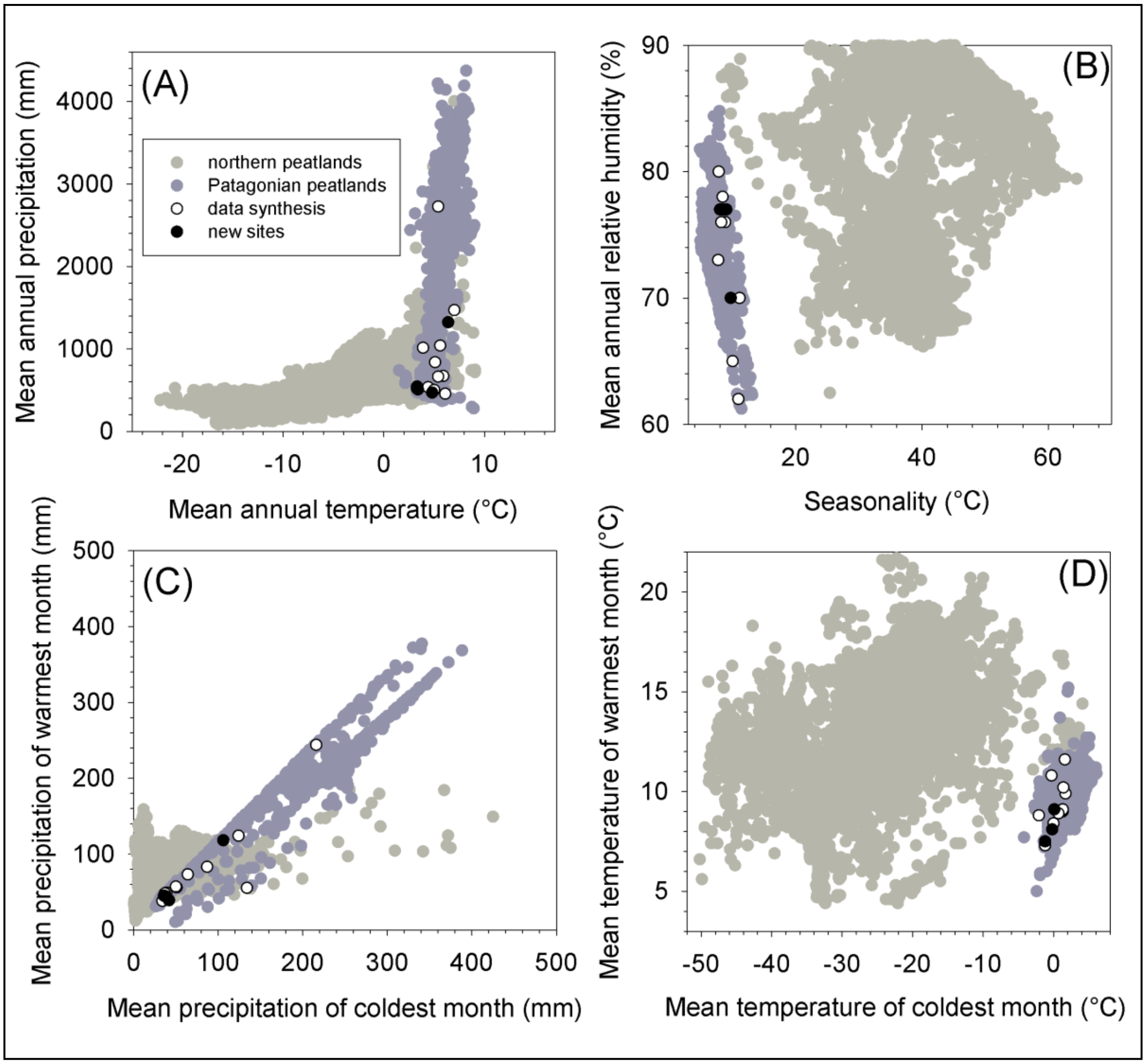

Figure 4.7. The climate space of Patagonian peatlands (dark gray) based on 10x10' (lat/long) gridded instrumental climate data for the period 1961-1990 (data from New et al., 2002). The location in the climate space of our new study sites (black) and of the published sites (white) is shown. The climate space of northern peatlands (light gray) as shown in Yu et al. (2009), but using a different gridded climate data set is also presented for comparison. **(A)** Mean annual temperature vs. precipitation. **(B)** Temperature seasonality (warmest minus coldest month) vs. mean annual relative humidity. **(C)** Mean precipitation of the coldest vs. warmest month. **(D)** Mean temperature of the coldest vs. warmest month.

4.4.2. Peat types, bulk density, and organic matter content

The stratigraphic record of all four new cores showed a clear and sharp switch from herbaceous-dominated fen peat to *Sphagnum*-dominated bog peat over time, similar to Bonarelli's (1917) and Auer's (1958, 1965) descriptions of peat deposits across southern Patagonia. The stratigraphic analysis of plant macrofossil samples along CN and UAV cores (n = 588) were condensed into three main peatland types on the basis of a cluster analysis (Ward's method; Fig. 4.8): (1) *Sphagnum* peat, (2) herbaceous peat (including brown moss *Drepanocladus* spp.), and (3) decomposed peat (with high unidentifiable organic matter (UOM) percentage). The cluster analysis also indicated that herbaceous and decomposed peat types were similar, probably related to their common litter sources (i.e., herbaceous plants).

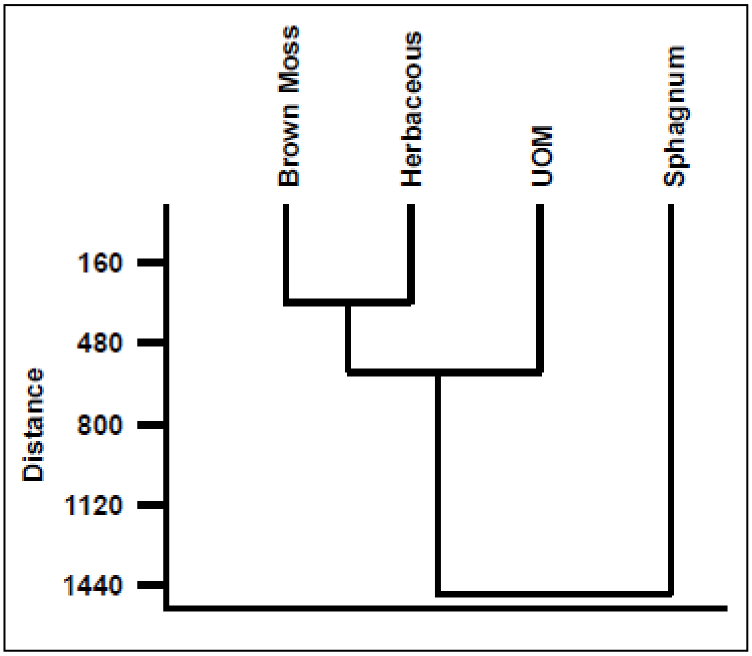

Figure 4.8. Cluster analysis (Ward's method) of plant macrofossil samples from Cerro Negro and Upper Andorra Valley cores (n = 588). Three main peatland types are identified: *Sphagnum* peat, herbaceous peat (including brown moss *Drepanocladus* spp.), and highly decomposed peat (with high unidentifiable organic matter (UOM)). The cluster analysis also indicates that herbaceous and decomposed peat types are closely related.

Our loss-on-ignition measurements (n = 2133) revealed that bulk density in our four peat cores varied between 0.01 and 0.20 g cm^{-3}, with an overall mean value of 0.07 g cm^{-3} ± 0.7% (standard error (S.E.)). Peat organic matter (OM) content had a mean value of 95.8 ± 0.1% by dry weight, and organic matter density values ranged from 0.01 to 0.18 g OM cm^{-3}, with a mean value of 0.06 g OM cm^{-3} ± 0.8%. On average, peat water content was 92.5 ± 0.1%. These datasets are presented in Fig. 4.9a.

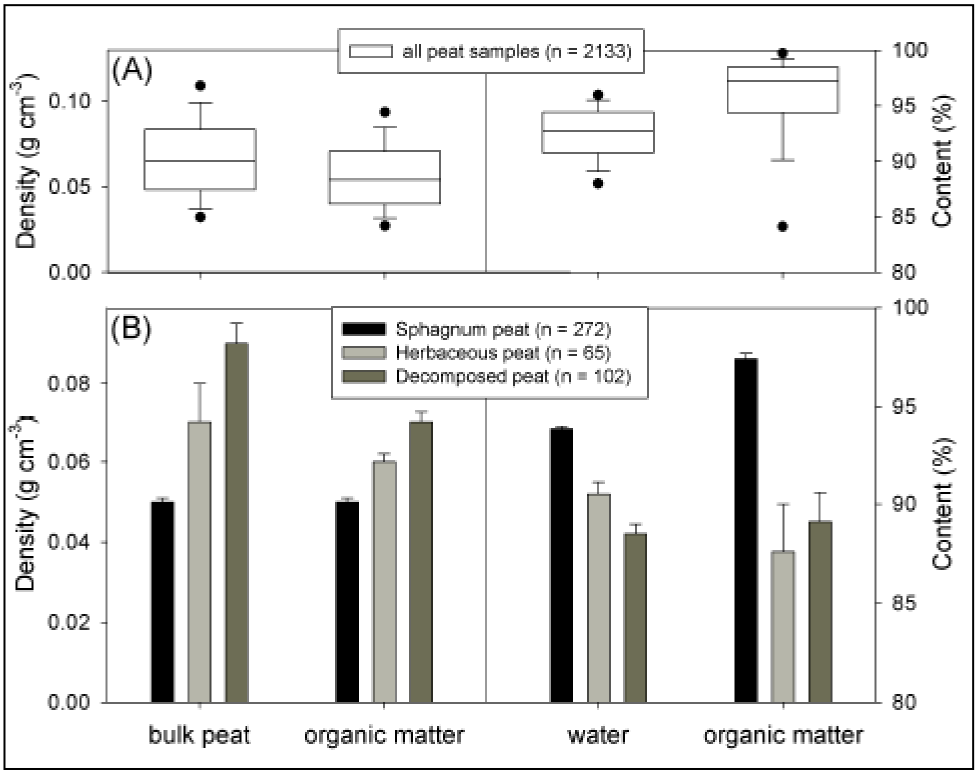

Figure 4.9. Peat lithological properties. **(A)** Box plots of peat bulk density, organic matter density, water content and organic matter content for all peat samples from our 4 new peat cores (n = 2133). Mean values are represented by the middle lines, the boxes indicate the 25th and 75th percentiles, the whiskers above and below the boxes represent the 10th and 90th percentiles, and the circles represent the 5th and 95th percentiles. **(B)** Bar charts of peat bulk density, organic matter density, water content and organic matter content for *Sphagnum*, herbaceous, and decomposed peat types for all peat samples from the Cerro Negro core (n = 438). Mean values and standard error are presented.

Relationships between peat type (*Sphagnum*, herbaceous, and highly decomposed) and peat lithology variables (bulk density, organic matter content, organic matter density, and water content) along the CN core (n = 438) were described using

ANOVAs (Fig. 4.9b and Table 4.4). Results indicate that peat lithological properties were significantly different amongst all three peat types ($p < 0.0001$ for all four ANOVAs; Table 4.4). In addition, post-hoc Tukey's HSD tests revealed that *Sphagnum* peat was statistically distinct from herbaceous and decomposed peat in terms of water content, OM content, bulk density, and OM density ($p < 0.0001$ for all eight HSD tests; Table 4.4). Similarly, herbaceous and highly decomposed peat were characterized by statistically different bulk density ($p = 0.026$), OM density ($p < 0.0001$), and water content ($p = 0.001$). However, herbaceous and decomposed peat could not be distinguished on the basis of their OM content ($p = 0.643$). As water content exhibited the most significant variability between peat types ($F (2,436) = 112.37$, $p < 0.0001$; Table 4.4), this property was used to infer changes in peat type along our new cores without detailed macrofossil analysis (Fig. 4.10).

Table 4.4. Results of one-way ANOVA of peat lithology (bulk density, organic matter (OM) content, organic matter density, and water content) predicted by peat type (*Sphagnum* (Sph), herbaceous (Herb), and highly decomposed (Dec)). Tukey's HSD post-hoc tests show which group means were significantly different from one another. df: degree of freedom (the comma separates the number of df for the numerator and denominator); p: probability.

				Tukey's HSD		
	df	F	p	Sph vs. Herb	Sph vs. Dec	Herb vs. Dec
Bulk density	2, 436	66.58	< 0.0001	< 0.0001	< 0.0001	0.026
OM density	2, 436	80.48	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Water content	2, 436	112.37	< 0.0001	< 0.0001	< 0.0001	0.001
OM content	2, 436	26.29	< 0.0001	< 0.0001	< 0.0001	0.643

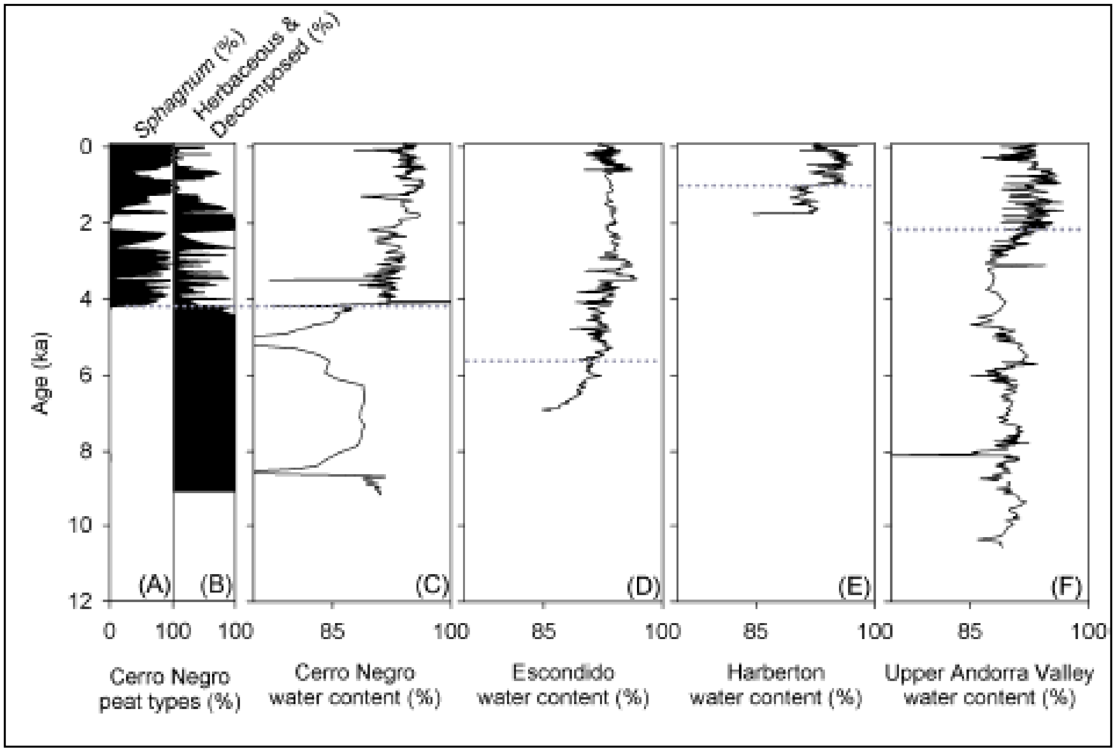

Figure 4.10. Water content profiles for the four new peat cores from Patagonia. Plant macrofossil analysis at Cerro Negro **(A)** was used to establish characteristic water content values for *Sphagnum* (> 92%) vs. non-*Sphagnum* (< 92%) peat types along cores Cerro Negro **(B)**, Escondido **(C)**, Harberton **(D)**, and Upper Andorra Valley **(E)**. These percentages are based on the mean water content value of *Sphagnum* peat (94 ± 2% (S.D.)) and that of non-*Sphagnum* peat (89 ± 4%). Grey dashed lines represent the non-*Sphagnum* (fen) to *Sphagnum* (bog) peat transition. Ages (ka) are presented in calibrated thousands of years before present.

4.4.3. Peat accumulation dynamics

Total peat-core lengths ranged from 4.45 to 7.15 m at our new study sites, and from 1.71 to 11.77 m in the synthesis data set. Once converted to cumulative mass (see section 4.4.2), these values ranged from 24 to 50 g OM cm^{-2} at the new sites, and from 12 to 76 g OM cm^{-2} in the data synthesis. There was a non-linear correlation between peat depth and cumulative OM mass (Fig. 4.11); $R^2 = 0.880$, $p < 0.0001$) that is likely due to the fact that older peat gets increasingly denser over time due to compaction, but also because it tends to contain high percentages of herbaceous and highly decomposed peat types, which have high OM densities than *Sphagnum* peat. Assuming a C content of 50% (Turunen et al., 2002), these values are equivalent to a mean soil C density of 168 kg C m^{-2} ± 10%, though there is a large range among sites from 60 to 381 kg C m^{-2}. A significant proportion of this carbon has accumulated over the past 4 ka, with a mean value of 68 kg C m^{-2} ± 11% (range from 17 to 142 kg C m^{-2}).

Age-depth relationships for our new four peat cores are presented in Fig. 4.12, with ^{14}C dates and corresponding calibrated ages in Table 4.2. All four sites followed a general concave pattern that is typical of peat bogs due to the differential decay experienced by old and young peat layers (Clymo, 1984; Yu et al., 2001). Long-term apparent rates of peat accumulation for all four new cores ranged from < 1 g C m^{-2} yr^{-1} in the catotelm to > 500 g C m^{-2} yr^{-1} in the acrotelm. The HB site had the highest mean value (57 g C m^{-2} yr^{-1}) over the last 1870 years, followed by 23 g C m^{-2} yr^{-1} at UAV (last 10,820 years), 16 g C m^{-2} yr^{-1} at CN (last 9205 years), and 13 g C m^{-2} yr^{-1} at ESC (last 6930 years; Table 4.5). Our data synthesis indicated a mean peat-C accumulation rate of 14 g C m^{-2} yr^{-1}. This value is significantly lower than the mean value of 22 g C m^{-2} yr^{-1} obtained by Yu et al. (2010), probably because the latter authors assumed a bulk density of 0.1 g OM cm^{-3} for all peat types. The time-weighted mean rate of peat accumulation for all 23 sites during the Holocene was 16.0 g C m^{-2} yr^{-1}.

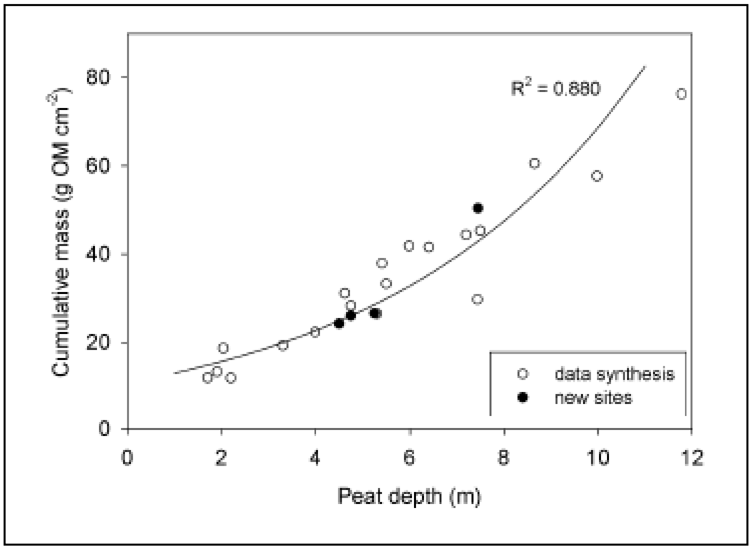

Figure 4.11. Relationship between peat depth and cumulative organic matter (OM) mass in Patagonian peatlands. Exponential function: f(x) = $10.837e^{0.1846x}$.

Holocene mean rates of peat accumulation were inversely correlated with peat inception age in a non-linear manner ($R^2 = 0.288$, $p = 0.001$), such that younger sites were characterized by higher rates because less cumulative decay has occurred at these sites than at the older ones (Fig. 4.13a). There was no significant relationship between mean annual temperature, precipitation, and peat-C accumulation rates (Fig. 4.13a). Similarly, peat-C accumulation since 4 ka was not correlated to peat inception age, MAT, or MAP (data not shown). On average, our sites show a 20% increase in the rate of peat-C accumulation since 4 ka compared to the Holocene average at these same sites (Fig. 4.14; Table 4.5). This trend is probably attributable to the differential long-term decay and succession from herbaceous to *Sphagnum* peat at most sites.

Peat addition rates (*PAR*), as calculated from curve fitting using Clymo's (1984) model (eq. 2), ranged from 40 g OM m^{-2} yr^{-1} at the ESC site, followed by 80 g OM m^{-2} yr^{-1} at CN, 100 g OM m^{-2} yr^{-1} at UAV, and finally to 320 g OM m^{-2} yr^{-1} at HB (Fig. 4.12), all for the entire length of the records. Overall, a mean value of 140 g OM m^{-2} yr^{-1} was obtained for our four new Patagonian sites. Decomposition coefficients (α) ranged from 0.0002 yr^{-1} to 0.0013 yr^{-1}, with a mean value of 0.0004 yr^{-1}(Fig. 4.12). Our data synthesis indicated lower values for both parameters (Fig. 4.12e), with a mean *PAR* of 50 g OM m^{-2} yr^{-1} ± 12% (ranging from 20 to 90 g OM m^{-2} yr^{-1}) and a mean α of 0.0002 yr^{-1} (ranging from 0.00001 to 0.0008 yr^{-1}). We only analyzed 14 peat cores that exhibited a 'concave-shaped' age-depth relationship (see Table 4.3). These values are summarized in Table 4.5. Neither *PAR* nor α was correlated with climatological parameters (Fig. 4.14b, c). Instead, non-linear relationships between peat inception and *PAR* ($R^2 = 0.510$, $p < 0.0001$) as well as between peat inception and α ($R^2 = 0.411$, $p = 0.004$) were found, suggesting that long-term autogenic peatland dynamics are important in explaining Holocene rates of peat accumulation across this region (Fig. 4.14b, c). Vegetation succession could also play an important role in controlling peat accumulation. In an attempt to minimize these age effects, *PAR* and α were also calculated for the past 4 ka of these records. These computations yielded a mean *PAR* of 80 g OM m^{-2} yr^{-1} ± 11% (ranging from 30 to 130 g OM m^{-2} yr^{-1}) and a mean α of 0.0006 yr^{-1} (ranging from 0.00004 to 0.001 yr^{-1}). These values are presented in Table 4.5. Once again, however, peat addition rate and decay were neither correlated with temperature nor precipitation (data not shown).

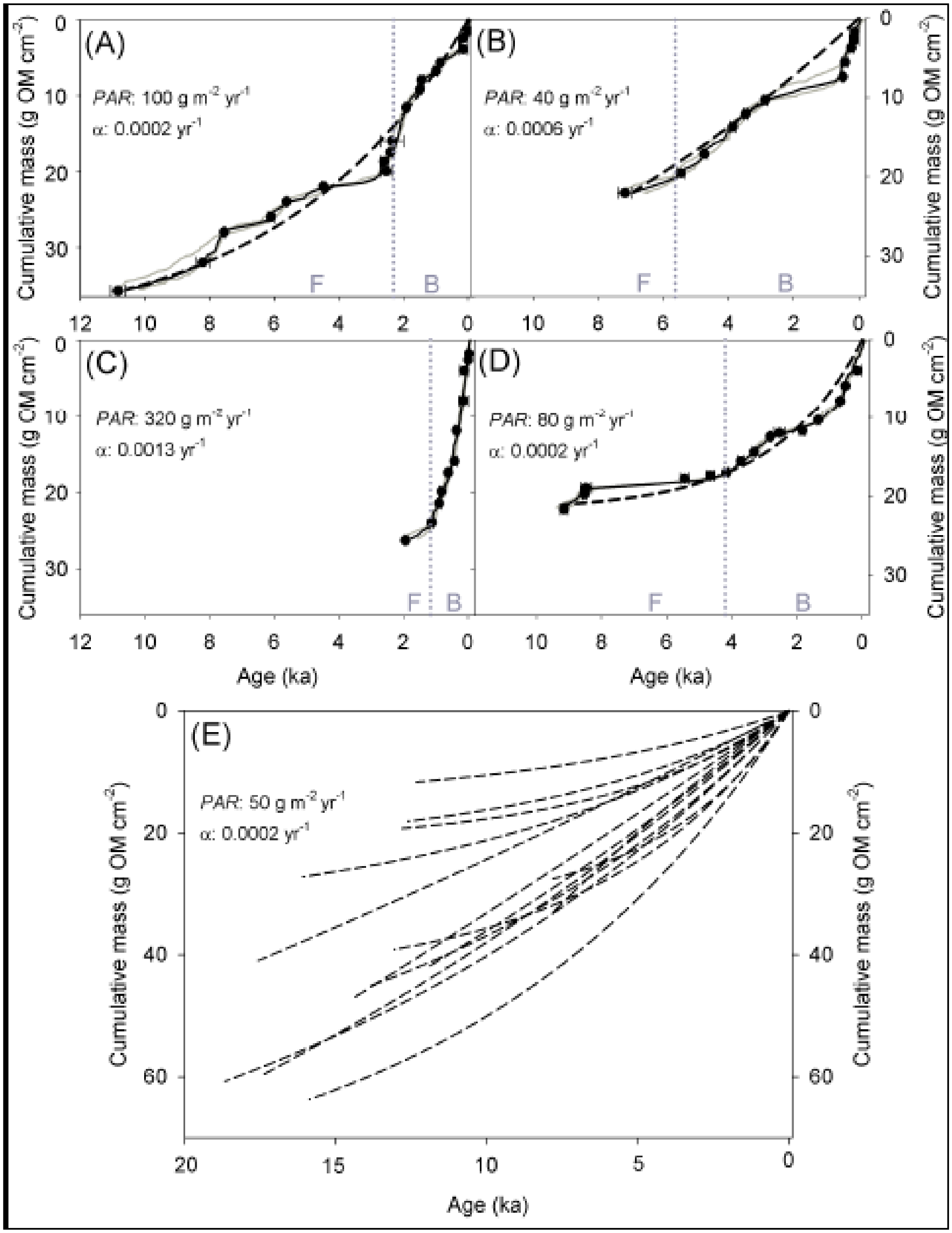

Figure 4.12. Age-depth (cumulative mass) relationships and exponential decay curves for Patagonian peat cores. The median age (black dots) and calibrated 2 σ range (error bars) of each ^{14}C date are presented, along with the most probable age-depth model (solid black lines) and associated error range (grey lines) from the program Bacon (Blaauw and Christen, 2011). The Clymo (1984) decay curves (black dashed lines) are also presented,

Table 4.5. Mean peat-carbon accumulation rates (PCAR), as well as peat addition rates (PAR) and peat decay (α) coefficients as derived from Clymo's (1984) exponential decay model. Holocene and late-Holocene (4 ka) results are shown separately. For the data synthesis, peat depth was converted to cumulative mass using organic matter density values of 0.05 g OM cm^{-2} for *Sphagnum* peat, 0.06 g OM cm^{-2} for herbaceous peat, and 0.07 g OM cm^{-2} for decomposed peat types (mean values as derived from our measurements; see Table 4.4 and Fig. 4.9). When stratigraphic information was not available, an overall mean density value of 0.06 g OM cm^{-2} was used.

ID	Since peat inception			Last 4 ka		
	PCAR	PAR	α	PCAR	PAR	α
UAV	22.6	0.0100	0.0002	34.8	-	-
ESC	15.9	0.0040	0.0006	15.6	0.0133	0.0013
HB	57.4	0.0320	0.0013	-	-	-
CN	13.4	0.0080	0.0002	20.3	0.0131	0.0009
1	15.4	0.0034	0.00001	14.9	-	-
2	20.3	0.0052	0.00006	34.2	0.0124	0.0003
3	17.4	0.0042	0.00003	19.4	0.006	0.0002
4	10.2	-	-	5.8	-	-
5	12.3	-	-	4.9	0.0032	0.0009
6	6.1	-	-	4.2	-	-
7	17.4	0.0044	0.00003	-	-	-
8	11.8	0.0026	0.00001	12.9	0.0078	0.0007
9	4.8	0.0018	0.0001	-	-	-
10	5.8	0.0087	0.0008	11.2	0.0110	0.0012
11	16.1	0.0053	0.0008	20.4	0.0081	0.0004
12	7.5	0.0036	0.0002	12.4	0.0046	0.0004
13	16.8	0.0075	0.0002	23.5	0.0082	0.0003
14	6.5	0.0028	0.0001	10.4	0.0088	0.0010
15	20.5	0.0077	0.00009	21.0	0.0043	0.00004
16	34.3	-	-	-	-	-
17	14.2	0.0071	0.0002	24.2	0.0062	0.0001
18	21.2	-	-	21.2	-	-
19	12.8	0.0033	0.00009	-	-	-

(Fig. 4.12 continued) along with their associated peat addition rate (*PAR)* and decay coefficient (α). The fen-to-bog transition is depicted by vertical light grey dashed lines (F = fen; B = bog) for Upper Andorra Valley **(A)**, Escondido **(B)**, Harberton **(C)**, and Cerro Negro **(D)**. **(E)** Exponential decay curves from the data synthesis (n = 14) as well as mean *PAR* and α parameters.

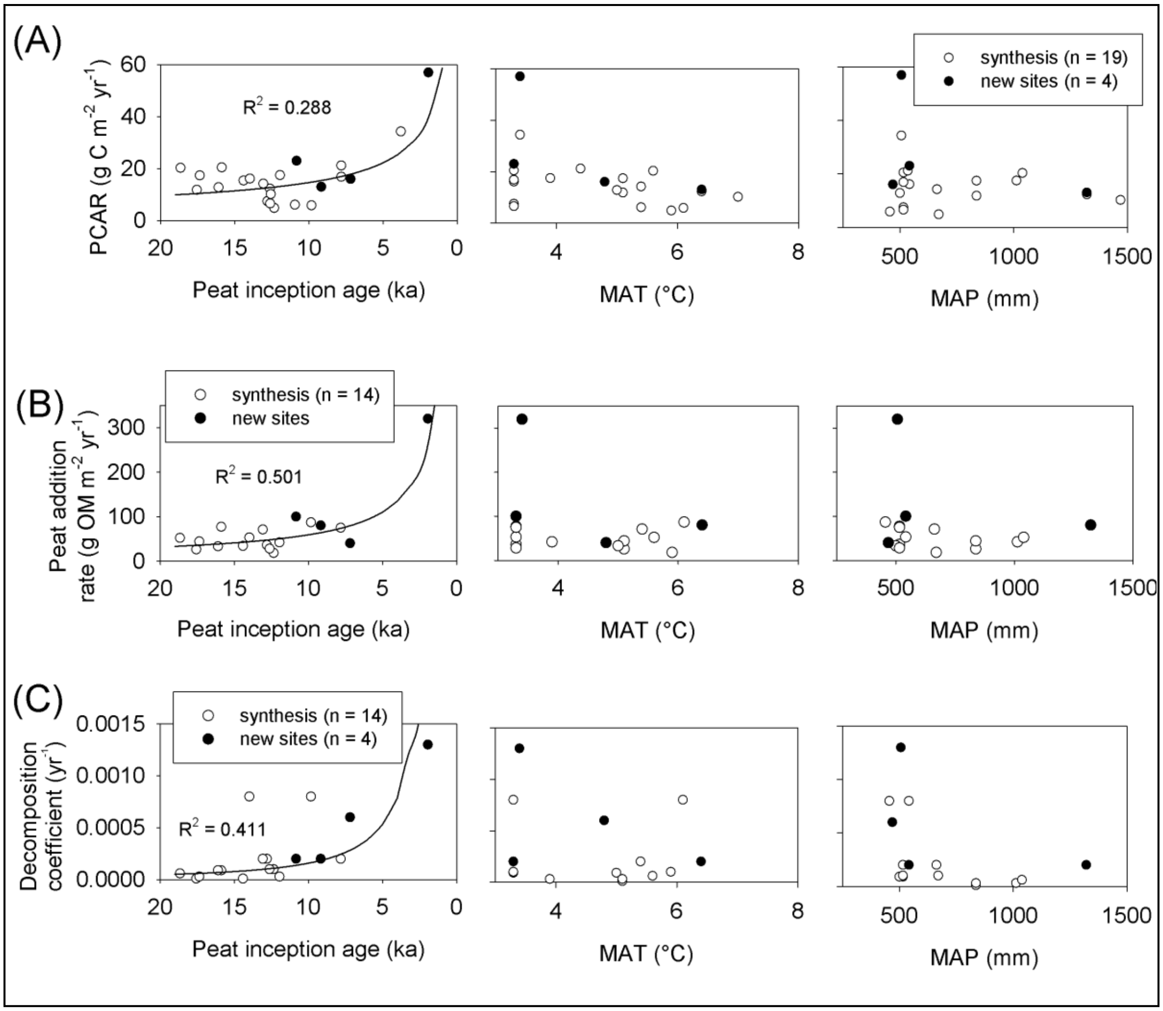

Figure 4.13. Relationships between peat inception age, climatological parameters (mean annual temperature (MAT), mean annual precipitation (MAP)), and peat accumulation parameters. Climate data from New et al. (2002). New study sites (solid circles) and sites from the data synthesis (open circles) are shown. **(A)** Holocene peat-carbon accumulation rate (PCAR), **(B)** peat addition rate (*PAR*; from Clymo's (1984) exponential decay model), and **(C)** peat decay coefficient (α; from Clymo's (1984) exponential decay model). Power function for PCAR: $f(x) = 58.74x^{-0.604}$; for *PAR*: $f(x) = 0.0468x^{-0.899}$; for α: $f(x) = 0.0088x^{-1.744}$.

4.5. Discussion

4.5.1. Patagonian peatlands: a distinct climate envelope

The Patagonian peatland domain is much different from its northern counterpart (Fig. 4.7). Its uniqueness is depicted in the following key observations. (1) Patagonian peatlands occupy the warmest portion of the mean annual temperature range for northern peatlands (Fig. 4.7a), and mean monthly temperatures in the Patagonian peatland climate space remain above 0°C throughout the year (Fig. 4.4; Fig. 4.7d). (2) Patagonian peatlands are characterized by lower temperature seasonality values than northern peatlands (Fig. 4.7b). They also experience milder conditions during the coldest month of the year as well as cooler conditions during the warmest month of the year than their northern counterparts (Fig. 4.7d). (3) Patagonian peatlands occupy wider ranges of annual precipitation and relative humidity than northern peatlands (Fig. 4.7a, b), although peatland sites presented in this study are mostly found at the lower end of the annual precipitation range. The monthly precipitation is evenly distributed throughout the year (Fig. 4.4; Fig. 4.7c), providing peatlands with a constant moisture supply.

This distinct temperature and precipitation space results in long growing seasons that potentially span the entire year. Such conditions should promote plant growth and associated carbon sequestration, as also suggested in a recent study where modern *Sphagnum* productivity was correlated with photosynthetically active radiation integrated over the growing season (Loisel et al., 2012). Cool summer conditions combined with an even distribution of precipitation also limit evapotranspiration, which should benefit *Sphagnum* growth and limit peat decomposition processes. Overall, the Patagonian peatland climatic regime corresponds to an end-member of the northern peatland climate domain. These southern peatlands can therefore be used for studying peatland-carbon-climate linkages under a novel set of climatic conditions.

4.5.2. Unusually high rates of peat addition during the Holocene

Patagonian peatlands have accumulated, on average, 168 kg C m^{-2} ± 10% (S.E.) since their initiation. A significant proportion of this carbon has accumulated over the past 4 ka (68 kg C m^{-2} ± 11%). Scaling up this Holocene value to the Patagonian peatland area (45,000 km^2) yields a total C sink of 7.6 GtC (ranging from 6.8 to 8.4 GtC), where 1 Gt = 10^{15} g. This estimate is cabout half the value of 15 GtC that was reported by Yu et al. (2010). Again, the discrepancy is likely due to their use of a bulk density of 0.1 g OM cm^{-3} for all peat types, which is an overestimate. Overall, these soil C density values are higher than the mean values that were calculated for northern peatlands by Oechel (1989; 113.6 kg C m^{-2}), Gorham (1991; 130 kg C m^{-2}), Lappalainen (1992; 61 kg C m^{-2}) and Turunen et al. (2002; 55 kg C m^{-2}), but Patagonian peatland C density values are close to estimates by Sheng et al. (2004) for Western Siberia (180 kg C m^{-2}).

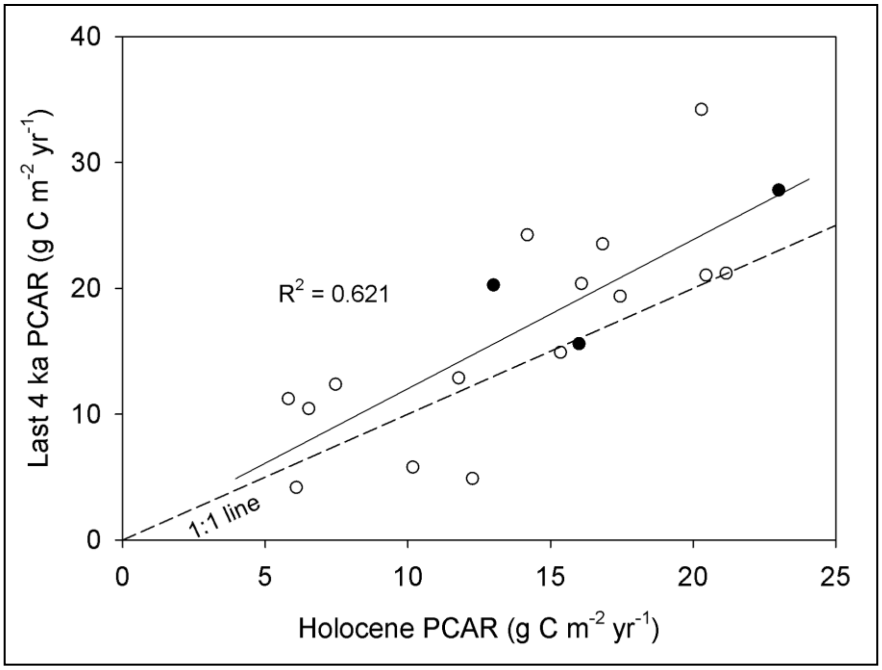

Figure 4.14. Relationship between mean apparent peat-carbon accumulation rates during the Holocene and since 4 ka.

High peat addition rates (*PAR*) were modeled for Patagonian peatlands using Clymo's (1984) model (eq. 2). Values from our four new sites (from 40 to 320 g OM m^{-2} yr^{-1}) as well as the mean from our data synthesis (50 g OM m^{-2} yr^{-1} ± 12%) were higher than what has been reported for northern sites (Fig. 4.15a). These results suggest efficient transfer and burial of peat into the catotelm, leading to high rates of peat-C sequestration. Two possible mechanisms can explain this high efficiency: (1) high plant growth and peat production at the surface, and (2) low decay in the acrotelm. We speculate that the very weak temperature seasonality combined to the lack of moisture deficit due to evenly distributed rainfall optimizes peat accumulation in Patagonia: while mild growing seasons enhance plant productivity by allowing plants to grow year-round, cool summers limit peat decay in the acrotelm. The very low nitrogen (0.45%; unpublished data) and phosphorus (< 0.023%; Godoy et al., 2003) concentration that characterizes Patagonian peat deposits could also be limiting microbial activity in the acrotelm, promoting an efficient peat transfer down into the catotelm. However, these low nutrient concentrations would also limit plant growth.

Alternatively, high *PAR* values could be an artifact of peat inception age: a young peatland should be characterized by a steeper cumulative mass-to-age slope than an old peatland, thereby exhibiting a high *PAR*. This process likely explains the very high *PAR* value that was recorded at the HB site (320 g OM m^{-2} yr^{-1}; Fig. 4.15a). But despite its young age, the HB site has accumulated a significant amount of peat (525 cm in less than 2 ka), illustrating the high efficiency of peat transfer into the catotelm in this region. On the other hand, basal ages from all three other sites (UAV, ESC and CN) are similar to those from northern peatlands, allowing inter-hemispheric comparison of *PAR* values. In addition, peatlands from both high-latitude regions exhibit comparable α values (Fig. 4.15b), suggesting that long-term peat decay affects the model curvatures in a similar way. Therefore, our study indicates that Patagonian peatlands are characterized by higher peat addition rates than northern peatlands, probably because of favorable climatic conditions for high *Sphagnum* growth and low surface peat decay, causing peat transfer to the deep catotelm at a greater rate than in northern peatlands.

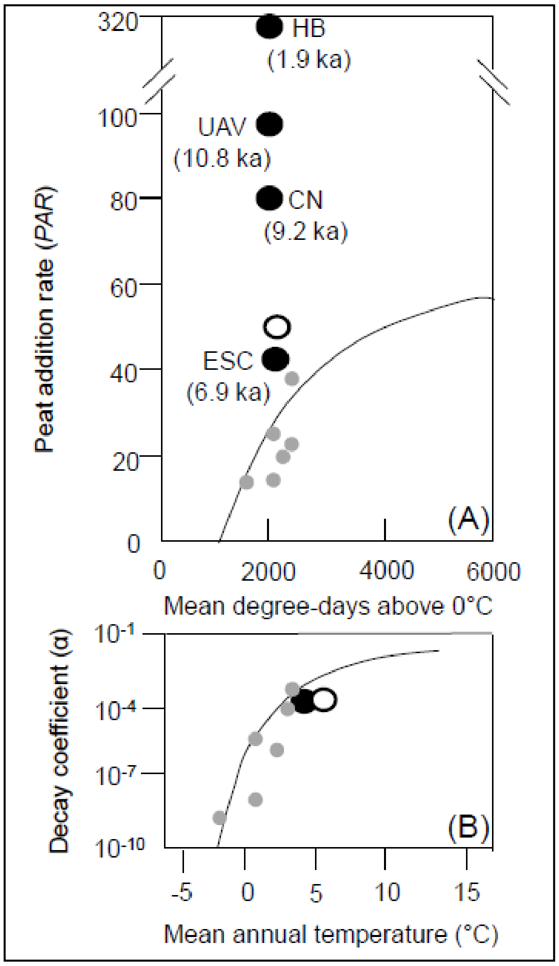

Figure 4.15. Peat accumulation parameters for northern and southern peatlands. Mean values from our new study sites (black circles, along with basal ages), our data synthesis (white dots), as well as from Canada and Finland (grey circles) are presented (figure modified from Clymo et al., 1998, on results from Finland and Canada). **(A)** Peat addition rates (*PAR*), and **(B)** peat decay coefficients (α).

4.5.3. Controls of carbon accumulation in peatlands of Patagonia

Our results suggest that Patagonian peatlands experience optimal climatic conditions for plant growth and long-term peat accumulation (see sections 4.5.1 and

4.5.2). However, the lack of correlation between climatic parameters (temperature and precipitation) and peat accumulation indices (PCAR, *PAR*, and α) across the region (Fig. 4.13) suggests that other controlling factors might be at play. In the northern hemisphere, Clymo et al. (1998) found a clear relationship between degree-days, mean annual temperature and long-term peat-C accumulation in Finland and Canada. Similarly, peat-C accumulation rates over the last millennium were positively correlated with photosynthetically active radiation and growing season length across the circum-arctic region of the northern hemisphere (Charman et al., in review). However, northern peatlands are distributed across a wide range of temperature and precipitation (Fig. 4.7). It is thus possible that the lack of correlations in Patagonia is simply due to a too narrow range of climatic conditions.

Alternatively and more likely, the lack of correlation between climate and peat accumulation is caused by the strong influence of local factors on peatland development. It is well known that local-scale autogenic mechanisms such as vegetation succession and peatland self-regulation mechanisms might mediate the role of climate on carbon accumulation. As such, recent theoretical studies indicate that peatland self-organization entails complex ecohydrological feedbacks that can disconnect ecosystem behavior from external climatic influence (Belyea and Baird, 2006; Belyea, 2007, 2009; Swindles et al., in review). For example, surface patterning was shown to be a means to reach ecosystem stability as it provides diverse habitats at many levels of spatial scales (Rietkerk et al., 2004). In peatlands, it possibly provides a way to increase peat accumulation when the conditions for accumulating peat are optimal or are above a threshold. In an analysis of four Patagonian peatlands (HB, CN, UAV, and ESC), Loisel (2012) provides empirical evidence for explaining the linkages between cyclic vegetation succession, peat-C sequestration rates, and regional climatic changes. In her study, long-term rates of peat accumulation are influenced by regional climatic conditions, but vegetation structure and succession are regulated by local-scale peatland dynamics. Reconstructions show that, under favorable climatic conditions, high peat accumulation rates co-occurred with fast shifts between wet and dry vegetation communities. Conversely, lower peat accumulation rates were correlated with much longer periodicities. Loisel (2012) postulates that these recurring wet and dry intervals along the peat cores are indicative of changing peatland surface patterning at the coring sites. Therefore, it can be argued that the complex adaptivity of peatlands directly influences peat accumulation rates in Patagonia, explaining the weak correlation between peat formation indices and climatic parameters. It is possible that self-organization exerts more fundamental controls in Patagonian peat bogs than in the northern hemisphere due to the simple vegetation structure of these systems coupled with rapid peat accumulation rates.

Recent studies have indicated that northern peatlands were rapidly accumulating large quantities of organic C during the early Holocene due to maximum incoming solar radiation and associated warm summer temperatures and strong seasonality (Yu et al., 2009; Jones and Yu, 2010). In light of these results, it was hypothesized that Patagonian peatlands would show an increase in peat-C sequestration around 4 ka. Results from Cerro Negro lend support to this hypothesis (Fig. 12d), with a three-fold increase in PCAR around 4.2 ka that is simultaneous to the fen-to-bog transition (Loisel et al., in review). However, important changes in precipitation variability that were induced by changes in the strength and latitudinal position of the southern westerly winds have been reconstructed across the study region around this time (Whitlock et al., 2007; Moy et al., 2009; Moreno et al., 2009). Such changes in effective moisture could have triggered the fen-to-bog transition and the associated increase in peat accumulation rate (Hugues, 2000). The volcanic fallout and sulfur dioxide release from Mount Burney, a stratovolcano situated in the southern Andes that erupted around 4.2 ka (Stern, 2008), could also have facilitated the fen-to-bog transition by causing intense peatland acidification (Kilian et al., 2006). A tephra layer from this eruption was identified along several peat profiles (> 40) throughout southern Patagonia, including at Cerro Negro, indicating that the volcanic plume effectively affected the entire study region (Loisel et al., in review). Overall, the synchronicity between the maximum solar insolation, the changing regional precipitation regime, and the volcanic eruption at 4.2 ka challenges our ability to test the hypothesis that the orbitally-induced temperature increase controlled peat-C sequestration in Patagonia, as observed in the northern hemisphere. Additional paleoecological work such as testate amoebae-inferred water table reconstructions and stable isotope-inferred temperature reconstructions is needed to further test this hypothesis.

4.6. Conclusions and Future Research

Patagonia provides a unique opportunity to study peatland-carbon-climate linkages under a climatic regime that is different from the northern peatland domain. Our results show that Patagonian peatlands are distributed under cool summer conditions, very weak temperature seasonality (extended growing seasons), and an even distribution of precipitation throughout the year. As modeled peat addition rate (*PAR*) values from

Patagonian peatlands are higher than what has been reported for northern peatlands, we speculate that the unique climatic conditions in Patagonia promote long-term peat accumulation by enhancing *Sphagnum* growth and minimizing aerobic peat decay, causing peat transfer to the deep catotelm at a greater rate than in northern peatlands. Overall, our new peat-core analysis combined with our data synthesis indicates that Patagonian peatlands have been an important regional carbon sink, with an average soil C density of 168 kg C m^{-2} ± 10%. A significant proportion of this carbon has accumulated over the past 4 ka (68 kg C m^{-2} ± 11%). Scaling up this Holocene value to the Patagonian peatland area (45,000 km^2) yields a total C sink of 7.6 GtC (ranging from 6.8 to 8.4 GtC).

Contrary to what has been observed in the northern high latitudes, peat accumulation across Patagonia does not correlate to climatic parameters (temperature and precipitation), suggesting that local-scale controls might mediate the influences of climate on peat accumulation. We propose that self-organization mechanisms exert fundamental controls in Patagonian peat bogs due to the simple vegetation structure of these systems coupled with rapid peat accumulation rates. For example, the ecohydrological feedbacks between peat formation and hydrology that create surface patterning in peatlands might disconnect ecosystem behavior from external climatic influence (Loisel, 2012).

Our study has shown that Patagonian peatlands can be used to test hypotheses on peatland development and carbon sequestration due to their unique climate envelope, simple structure, and rapid vertical accumulation. For example, the development, persistence and spatio-temporal dynamics of surface patterning could be analyzed in detail on the basis of paleoecological tools, hydrological monitoring, modeling, and surface metric analyses (Belyea and Baird, 2006; Belyea, 2007; 2009; Loisel 2012; Swindles et al., in review). Patagonian peat deposits are also ideally suited for paleoecological work such as high-resolution stable isotope-inferred temperature reconstructions due to their dominance by a single *Sphagnum* species (Pendall et al., 2001; Daley et al., 2012). Finally, the rapid vertical peat accumulation provides an opportunity to investigate short-term peat decomposition rates and litter breakdown processes.

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4.8. References

Aaby, B. 1976. Cyclic climatic variations in climate over the past 5,500 yr reflected in raised bogs. Nature. 263: 281-284.

Arroyo, M.T.K., Mihoc, M., Pliscoff, P. Arroyo-Kalin, M. 2005. The Magellanic moorland. In: Fraser, L.H., Keddy, P.A. (Eds.), The world's largest wetlands: ecology and conservation. Cambridge University Press, Cambridge, UK, pp. 424-445.

Ashworth, A.C., Markgraf, V., Villagran, C. 1991. Late Quaternary climatic history of the Chilean Channels based on fossil pollen and beetle analyses, with an analysis of the modern vegetation and pollen rain. Journal of Quaternary Science. 6(4): 279-291.

Auer, V. 1958. The Pleistocene of Fuego- Patagonia. Part II: the history of the flora and vegetation. Anales Academiae Scientiarum Fennicea, Series A III, Geologica-Geographica 50, Helsinki, Finland, 239 p.

Auer, V. 1965. The Pleistocene of Fuego- Patagonia. Part IV: bog profiles. Anales Academiae Scientiarum Fennicea, Series A III, Geologica-Geographica 80, Helsinki, Finland, 165 p.

Barber, K.E. 1981. Peat stratigraphy and climatic change: a palaeoecological test of the theory of cyclic peat bog regeneration. A.A. Balkema, Rotterdam, The Netherlands, 219 p.

Barker, S., Diz, P., Vautravers, M.J., Pike, J., Knorr, G., Hall, I.R., Broeker, W.S. 2009. Interhemispheric Atlantic seesaw response during the last deglaciation. Science. 457: 1097-1103.

Baumann, M. 2006. Water flow, spatial patterns, and hydrological self-regulation of a raised bog in Tierra del Fuego (Argentina). M.Sc. thesis, University of Greifswald, Germany.

Belyea, L.R. 2007. Revealing the Emperor's new clothes: niche-based palaeoenvironmental reconstruction in the light of recent ecological theory. The Holocene. 17(5): 683-688.

Belyea, L.R. 2009. Non-linear dynamics of peatlands and potential feedbacks on the climate system. In: Baird, A., Belyea, L., Comas, X., Reeve, A., Slater, L. (Eds.), Northern peatlands and carbon cycling, American Geophysical Union Monograph Series, Washington D.C., USA, pp. 5-18.

Belyea, L.R., Baird, A.J. 2006. Beyond 'The limits to peat bog growth': cross-scale feedback in peatland development. Ecological Monographs. 76(3): 299-322.

Berger, A., Loutre, M.-F. 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews. 10: 297-317.

Biester, H., Martinez-Cortizas, S., Birkenstock, S., Kilian, R. 2003. Effect of peat decomposition and mass loss on historic mercury records in peat bogs from Patagonia. Environmental Science and Technology. 37(1): 32-39.

Blaauw, M. Christen, J.A. 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis. 6(3), 457-474.

Bonarelli, G. 1917. Tierra del Fuego y sus turberas. Anales del Ministerio de Agricultura de la Nación, Sección Geologíca Mineralogía y Minería, Buenos Aires, Argentina, 119 p.

Borromei, A.M., Coronato, A., Franzén, L.G., Ponce, J.F., López Sáez, J.A., Maidana, N., Rabassa, J., Candel, M.S. 2010. Multiproxy record of Holocene paleoenvironmental change, Tierra del Fuego, Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology. 286: 1–16.

Borromei, A.M. 1995. Análisis polínico de una turbera holocénica en el Valle de Andorra, Tierra del Fuego, Argentina. Revista Chilena de Historia Natural. 68: 311-319.

Chambers, F.M., Charman, D.J. 2004. Holocene environmental change: contributions from the peatland archive. The Holocene. 14(1): 1-6.

Chambers, F.M., Mauquoy, D., Brain, S.A, Blaauw, M., Daniell, J.R.G. 2007. Globally synchronous climate change 2800 years ago: Proxy data from peat in South America. Earth and Planetary Science Letters. 253, 439-444.

Charman, D., Beilman, D., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F., Christen, J.A., Gallego-Sala, A.V., Harrison, S.P., Hughes, P.D.M., Jackson, S., Korhola, A., Mauquoy, D., Mitchell, F., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z., Alm, J., Bauer, I.E.,McCorish, Y., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D., Zhao, Y. In review. Climate-driven changes in peatland carbon accumulation during the last millennium. Proceedings of the National Academy of Sciences of the USA. Manuscript 2011-19956.

Charman, D.J. 2002. Peatlands and environmental change. John Wiley and Sons, Chichester, UK, 301 p.

Clapperton, C. 1993. Quaternary geology and geomorphology of South America. Elsevier, Amsterdam, The Netherlands, 779 p.

Clymo, R.S. 1984. The limits to peat growth. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences. 303(1117): 605-654.

Clymo, R.S., Turunen, J., Tolonen, K. 1998. Carbon accumulation in peatlands. Oikos. 81(2), 368-388.

Collantes, M., Faggi A.M. 1999. Los Humedales del Sur de Sudamérica. In: A.I. Malvárez (Ed.), Tópicos sobre humedales templados y subtropicales de Sudamérica. UNESCO, Montevideo, Uruguay, pp. 15-25.

Coronato, A., Roig, C., Collado, L., Roig, F. 2006. Geomorphologic emplacement and vegetation characteristics of Fuegian peatlands, southernmost Argentina, South America. In: Martini, I.P., Martinez Cortizas, A., Chesworth, W. (Eds), Peatlands: evolution and records of environmental and climate changes. Elsevier, Amsterdam, The Netherlands, pp. 111-128.

Daley, T.J., Mauquoy, D., Chambers, F.M. 2012. Investigating late Holocene variations in hydroclimate and the stable isotope composition of precipitation using southern South American peatlands: a hypothesis. Climate of the Past Discussions. 8: 595-620.

Dean Jr, W.E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Petrology. 44(1): 242-248.

Dirección Meteorológica de Chile. 2012. http://www.meteochile.gob.cl/

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., Aerts, R. 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature. 460: 616-620.

Drysdale, R.N., Hellstrom, J.C., Zanchetta, G., Fallick, A.E., Sánchez Goñi, M.F., Couchoud, I., McDonald, J., Maas, R., Lohmann, G., Isola, I. 2009. Evidence for obliquity forcing of glacial termination II. Science. 325: 1527-1531.

Fenner, N., Freeman, C. 2011. Drought-induced carbon loss in peatlands. Nature Geosciences. 4: 895-900.

Fesq-Martin, M., Friedmann, A., Peters, M., Kilian, R. 2004. Late-glacial and Holocene vegetation history of the Magellanic rain forest in southwestern Patagonia, Chile. Vegetation, History and Archaeobotany. 13: 249-255.

Fritz, C., Pancotto, V.A., Elzenga, J.T.M., Visser, E.J.W., Grootjans, A.P., Pol, A., Iturraspe, R., Roelofs, J.G.M., Smolders, A.J.P. 2011. Zero methane emission bogs: extreme rhizosphere oxygenation by cushion plants in Patagonia. New Phytologist. 190: 398-408.

Fritz, C., van Dijk, G., Smolders, A.J.P., Pancotto, V.A., Elzenga, T.J.T.M., Roelofs, J.G.M., Grootjans, A.P. 2012. Nutrient additions in pristine Patagonian Sphagnum bog vegetation: can phosphorus addition alleviate (the effects of) increased nitrogen loads. Plant Biology. doi:10.1111/j.1438-8677.2011.00527.x

Frolking, S., Roulet, N.T. 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Global Change Biology. 13: 1-10.

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.-S., Roulet, N. 2011. Peatlands in the Earth’s 21st century coupled climate-carbon system. Environmental Reviews. 19: 371-396.

Godley, E.J. 1960. The Botany of Southern Chile in Relation to New Zealand and the Subantarctic. Proceedings of the Royal Society of London. Series B, Biological Sciences. 152 (949): 457-475.

Godoy, R., Paulino, L., Oyarzun, C., Boeckx, P. 2003. Atmospheric N deposition in central and southern Chile: an overview. Gayana Botánica. 60(1): 47-53.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications. 1: 182-195.

Grootjans, A, Iturraspe, R, Lanting, A, Fritz, C, Joosten, H. 2010. Ecohydrological features of some contrasting mires in Tierra del Fuego, Argentina. Mires and Peat. 5(8): 1-14.

Heusser, C.J. 1989. Late Quaternary vegetation and climate of southern Tierra del Fuego. Quaternary Research. 31: 396-406.

Heusser, C.J., Heusser, L.E., Hauser, A. 1992. Paleoecology of Late Quaternary deposits in Chiloé continental, Chile. Revista Chilena de Historia Natural. 65: 235-245.

Heusser, C.J. 1993. Late-Glacial of southern South America. Quaternary Science Reviews. 12: 345-350.

Heusser, C.J. 1995. Paleoecology of a *Donatia-Astelia* cushion bog, Magellanic Moorland-Subantarctic evergreen forest transition, southern Tierra del Fuego, Argentina. Review of Paleobotany and Palynology. 89: 429-440.

Heusser, C.J. 1998. Deglacial paleoclimate of the American sector of the Southern Ocean: Late Glacial-Holocene records from the latitude of Canal Beagle (55°S), Argentine Tierra del Fuego. Palaeogeography, Palaeoclimatology, Palaeoecology. 141: 277-301.

Heusser, C.J. 2003. Ice age southern Andes: a chronicle of paleoecological events. Elsevier, Amsterdam, The Netherlands, 240 p.

Huber, U.M. 2003. Linkages among climate, vegetation and fire in Fuego-Patagonia during the Late-Glacial and Holocene. PhD dissertation, University of Colorado, USA.

Huber, U.M., Markgraf, V. 2003. Holocene Fire Frequency and Climate Change at Rio Rubens Bog, Southern Patagonia. In: Whitlock, C., Anderson, R.S. (Eds.), Fire and climatic Change in temperate ecosystems of the western Americas. Ecological Studies vol. 160 (3), Springer, New York, USA, pp. 357-380.

Huber, U.M., Markgraf, V., Schabitz, F. 2004. Geographical and temporal trends in Late Quaternary fire histories of Fuego-Patagonia, South America. Quaternary Science Reviews. 23: 1079-1097.

Hugues, P.D.M. 2000. A reappraisal of the mechanisms leading to ombrotrophy in British raised mires. Ecology Letters. 3: 7-9.

Huybers, P. 2007. Glacial variability over the last two million years: an extended depth-derived agemodel, continuous obliquity pacing, and the Pleistocene progression. Quaternary Science Reviews. 26: 37-55.

Ise, T., Dunn, A.L., Wosfy, S.C., Moorcroft, P.R. 2008. High sensitivity of peat decomposition to climate change through water-table feedback. Nature Geoscience. 1: 763-766.

Jones, M.C., Yu, Z. 2010. Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proceedings of the National Academy of Sciences. 107(16): 7347-7352.

Kilian, R., Biester, H., Behrmann., J, Baeza., O, Fesq-Martin, M., Hohner, M., Schimpf, D., Friedmann, Mangini, A. 2006. Millennium-scale volcanic impact on a superhumid and pristine ecosystem. Geology. 34(8): 609-612.

Kleinebecker, T., Holzel, N., Vogel, A. 2007. Gradients of continentality and moisture in South Patagonian ombrotrophic peatland vegetation. Folia Geobotanica. 42: 363-382.

Lappalainen, E. 1996. General review on world peatlands and peat resources. International Peat Society, Jyska, Finland.

Levin I., Kromer, B. 2004. The tropospheric $^{14}CO_2$ level in mid-latitudes of the Northern Hemisphere. Radiocarbon. 46: 1959-2003.

Loisel, J. 2012. Autogenic and allogenic controls on carbon dynamics in peatlands from Alaska and Patagonia. PhD Dissertation, Lehigh University, USA.

Loisel, J., Gallego-Sala, A.V., Yu, Z. 2012. Global-scale pattern of peatland *Sphagnum* growth driven by photosynthetically active radiation and growing season length. Biogeosciences Discussion. 9: 1-28.

Loisel, J., Yu, Z., D’Odorico, P. In review. Peatland dynamics in Patagonia: abrupt mid-Holocene fen-to-bog transition and carbon sequestration implications. Proceedings, 14th International Peat Congress, Stockholm, Sweden. Abstract 201/54.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L.C., Valichko, A.A. 2006. Rapid early development of circumarctic peatlands and atmospheric CH_4 and CO_2 variations. Science. 314: 285-288.

Mancini, M.V. 2009. Holocene vegetation and climate changes from a peat pollen record of the forest – steppe ecotone, Southwest of Patagonia (Argentina). Quaternary Science Reviews. 28: 1490-1497.

Markgraf, V. 1991. Younfer Dryas in southern South America. Boreas. 20: 63-69.

Markgraf,V. Huber, U.M. 2010. Late and postglacial vegetation and fire history in Southern Patagonia and Tierra del Fuego. Palaeogeography, Palaeoclimatology, Palaeoecology. 297: 351-366.

Markgraf, V., Whitlock, C. and S. Haberle. 2007. Vegetation and fire history during the last 18’000 cal yr B.P. in Southern Patagonia: Mallin Pollux, Coyhaique, Province Aisen (45°41’30’’ S, 71°50’30’’ W, 640 m elevation). Palaeogeography, Palaeoclimatology, Palaeoecology. 254: 492-507.

Martini, I.P., Martinez Cortizas, A., Chesworth, W. 2006. Peatlands: evolution and records of environmental and climate changes. Elsevier, Amsterdam, The Netherlands, 587 p.

Mauquoy, D., van Geel, B. 2007. Mire and Peat Macros. In: Elias S.A. (Ed.), Encyclopedia of Quaternary Science, vol. 3. Elsevier, Amsterdam, The Netherlands, pp. 2315-2336.

Mauquoy, D., Blaauw, M., van Geel, B., Borromei, A., Quattrocchio, M., Chambers, F.M., Possnert, G. 2004. Late Holocene climatic changes in Tierra del Fuego based on multiproxy analyses of peat deposits. Quaternary Research. 61: 148-158.

McCulloch, R.D., Davies, S.J. 2001. Late-Glacial and Holocene palaeoenvironmental change in the central Strait of Magellan, southern Patagonia. Palaeogeography, Palaeoclimatology, Palaeoecology. 173: 143-173.

Moreno, P.I., François, J.P., Villa-Martınez, R.P., Moy, C.M. 2009. Millennial-scale variability in Southern Hemisphere westerly wind activity over the last 5000 years in SW Patagonia. Quaternary Science Reviews. 28: 25-38.

Moy, C.I., Moreno, P.I., Dunbar, R.B., Kaplan, M.R., Francois, J.P., Villalba, R., Haberzettl, T. 2009. Climate change in southern South America during the last two millennia. In: Vimeux, F., Sylvestre, F., Khodri, M. (Eds.), Past climate variability in South America and surrounding regions, Springer, Amsterdam, The Netherlands, pp. 353-393.

New, M., Lister, D., Hulme, M., Makin, I. 2002. A high-resolution data set of surface climate over global land areas. Climate Research. 21: 1-25.

Oechel, W.C. 1989. Nutrient and water flux in a small arctic watershed: an overview, Holarctic Ecology, 12, 229-237.

Paruelo, J.M., Beltrán, A., Jobbágy, E.G., Sala, O.E., Golluscio, R.A. 1998. The climate of Patagonia: general patterns and controls on biotic processes. Ecologia Austral. 8, 85–101.

Pendall, E., Markgraf, V., White, J.W.C., Dreier, M. 2001. Multiproxy record of Late Pleistocene-Holocene climate and vegetation changes from a peat bog in Patagonia. Quaternary Research. 55: 168-178.

Pisano, E. 1983. The Magellanic tundra complex. In: Gore, A.J.P. (Ed.), Mires: swamp, bog, fen and moor, vol. 2, Elsevier, Amsterdam, The Netherlands, pp. 295-329.

Rabassa, J., Heusser, C.J., Coronato, A. 1989. Peat-bog accumulation rate in the Andes of Tierra del Fuego and Patagonia (Argentina and Chile) during the last 43,000 years. Pirineos. 133: 113-122.

Rabassa, J., Coronato, A., Roig, C. 1996. The peat bogs of Tierra del Fuego, Argentina.

In: Lappalainen, E. (Ed.), Global Peat Resources. International Peat Society, Saarijärven Offset Oy, Saarijärvi, Finland, pp. 129-145.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Bertrand, C., Blackwell, P.G., Buck, C.E., Burr, G., Cutler, K.B., Damon, P.E., Edwards, R.L., Fairbanks, R.G., Friedrich, M., Guilderson, T.M., Hughen, K.A., Kromer, B., McCormac, F.G., Manning, S., Bronk Ramsey, C., Reimer, R.W., Remmele, S., Southon, J.R., Stuiver, M., Talamo, S., Taylor, F.W., van der Plicht, J., Weyhenmeyer, C.E. 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. Radiocarbon. 51(4): 1111-1150.

Rietkerk, M., Dekker, S.C., de Ruiter, P.C., van de Koppel, J. 2004. Self-organized atchiness and catastrophic shifts in ecosystems. Science. 305: 1926-1929.

Rydin, H., Jeglum, J. 2006. The biology of peatlands. Oxford University Press, Oxford, UK, 343 p.

Saptoka, A., Cheburkin, A.K., Bonani, G., Shotyk, W. 2007. Six millennia of atmospheric dust deposition in southern South America (Isla Navarino, Chile). The Holocene. 17(5): 561-572.

Schneider, C, Glaser, M, Kilian, R, Santana, A, Butorovic, N, Casassa, G. 2003. Weather observations across the Southern Andes at 53°S. Physical Geography. 24(2): 97-119.

Sheng, Y., Smith, L.C., MacDonald, G.M., Kremenetski, K.V., Frey, K.E., Velichko, A.A., Lee, M., Beilman, D.W., Dubinin, P. 2004. A high-resolution GIS-based inventory of the west Siberian peat carbon pool. Global Biogeochemical Cycles. 18. GB3004, doi:10.1029/ 2003GB002190.

Servicio Meteorológico Nacional. 2012. http://www.smn.gov.ar/

Smith, R.I.L., Clymo, R.S. 1984. An extraordinary peat-forming community on the Falkland Islands. Nature. 309: 617-620.

Squeo, F.A., Warner, B.G., Aravena, R., Espinoza, D. 2006. Bofedales: high altitude peatlands of the central Andes. Revista Chilena de Historia Natural. 79: 245-255.

Stern, C.R. 2008. Holocene tephrochronology record of large explosive eruptions in the southernmost Patagonian Andes. Bulletin of Volcanology. 70:435–454.

Swindles, G.T., Morris, P.J., BNaird, A.J., Blaauw, M., Plunkett, G. Ecohydrological feedbacks confound peat-based climate reconstructions. Geophysical Research Letters. Manuscript 2012-GL-051500.

Tuhkanen, S. 1992. The climate of Tierra del Fuego from a vegetation geographical point of view and its ecoclimatic counterparts elsewhere. Acta Botanica Fennica. 145: 1-64.

Turunen, J., Tomppo, E., Tolonen, K., Reinikainen, A. 2002. Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. The Holocene. 12(1): 69-80.

Unkel, I., Björk, S., Wohlfarth, B. 2008. Deglacial environmental changes on Isla de los Estados (54.41°S), southeastern Tierra del Fuego. Quaternary Science Reviews. 1541-1554.

Unkel, I., Fernandez, M., Björk, S., Ljung, K., Wohlfarth, B. 2010. Records of environmental changes during the Holocene from Isla de los Estados (54.4°S), southeastern Tierra del Fuego. Global and Planetary Change. 74(3-4): 99-113.

Vandergoes, M.J., Newnham, R.M., Preusser, F., Hendy, C.H., Lowell, T.V., Fitzsimons, S.J., Hogg, A.G., Kasper, H.U., Schlüchter, C. 2005. Regional insolation forcing of late Quaternary climate change in the Southern Hemisphere. Nature.436: 242-245.

Villa-Martínez, R., Moreno, P.I. 2007. Pollen evidence for variations in the southern margin of the westerly winds in SW Patagonia over the last 12,600 years. Quaternary Research. 68: 400-409.

Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association. 58(301): 236–244.

Whitlock, C., Moreno, P.I., Bartlein, P. 2007. Climatic controls of Holocene fire patterns in southern South America. Quaternary Research. 68: 28-36.

Wieder, R.K., D.H. Vitt, Benscoter, B.W. 2006. Peatlands and the boreal forest. In: Wieder, R.K., Vitt, D.H. (Eds.), Boreal peatland ecosystems, Ecological Studies, vol. 188, Springer, New York, USA, pp. 1-8.

Yu, Z. In review. Northern peatland carbon stocks and dynamics: a review. Biogeosciences Discussions.

Yu, Z. 2011. Holocene carbon flux histories of the world's peatlands: global carbon-cycle implications. The Holocene. 21(5): 761-774.

Yu, Z., Beilman, D.W., Jones, M.C. 2009. Sensitivity of northern peatland carbon dynamics to Holocene climate change. In: Baird, A., Belyea, L., Comas, X., Reeve, A., Slater, L. (Eds.), Northern peatlands and carbon cycling, American Geophysical Union Monograph Series, Washington D.C., USA, pp. 55-69.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J. 2010. Global peatland dynamics since the Last Glacial Maximum. Geophysical Research Letters. 37. L13402. doi:10.1029/ 2010GL043584.

Yu, Z., Turetsky, M.R., Campbell, I.D., Vitt, D.H. 2001. Modeling long-term peatland dynamics. II. Processes and rates inferred from litter and peat-core data. Ecological Modelling. 145: 159-173.

CONCLUSIONS

Over the past 20 years, considerable efforts have been put towards better understanding peatland spatio-temporal development, conceptualizing peatland structure and functioning, quantifying past and present peat-carbon fluxes, analyzing peatland sensitivity to climate change, and predicting the fate of northern peat-carbon stocks under global changes. However, a multitude of challenges still need to be addressed to strengthen our understanding of allogenic and autogenic controls on peatland dynamics. The conceptual, empirical, and modeling work presented in this dissertation represents small steps in filling these outstanding data and knowledge gaps.

In Chapter 1, a new modeling approach was proposed to link short- and long-term peatland dynamics. In addition, I showed that recent warming could trigger non-linear changes in peatland vegetation communities, inducing important changes in the peat-carbon sink capacity. Although peatlands have long been viewed as stable ecosystems where the successional change from fen to bog vegetation occurs as a result of slow, internal processes that lead to the gradual accumulation of peat above the groundwater influence, my results indicated that a rapid transition from *Carex* fen peat to *Sphagnum* mosses has occurred over large portions of the study site (Petersville peatland, Alaska) over the past 100 years. There is increasing recognition that peatland ecosystems exhibit such non-linear, step-like transitions from one stable state to another.

In Chapter 2, photosynthetically active radiation (PAR) integrated over the growing season was shown to be the most important variable explaining *Sphagnum* growth on the basis of a meta-analysis of a global database. These results suggest that broad-scale controls on *Sphagnum* growth are significant despite the effect of local or site-specific factors such as nutrient influx or depth to water table. This analysis also showed that, although adequate effective moisture is necessary for peatland development and peat moss growth, moisture availability might only play a secondary role when compared to growing season length, temperature, and PAR on *Sphagnum* growth over large spatial scales. These results imply increased peat production under warming climates if there is no moisture stress, in agreement with the idea that warming could lead to a negative feedback from terrestrial ecosystems as a result of increased net primary production and subsequent increased carbon storage.

In Chapter 3, I demonstrated that slope gradient and basin topography exert deterministic controls on peatland development on the basis of peat-core analysis and a ground penetrating radar survey. I found that lateral expansion in basins with slopes greater than ~ 0.5° is slope-limited, whereas lateral expansion in basins with less than ~ 0.5° are peat growth-limited. In addition, I showed that lateral expansion rate and slope follow a non-linear relationship (power-law). Overall, peatlands have the tendency and ability to smooth out basin irregularities and generate a gentler slope for themselves. This self-generated slope shallowing and stabilizing mechanism reduces water flow and increases water storage, further promoting peat formation through positive feedback loops.

In Chapter 4, I showed that Patagonian peatlands occupy a distinct climatological niche that corresponds to an end-member of the northern peatland climate domain, with a mild mean annual temperature and very weak temperature seasonality. I also found that Patagonian peatlands have been efficient land carbon sinks since their initiation and that modeled peat addition rates to the catotelm were significantly higher than what has been reported for northern peatlands, despite similar decomposition coefficients between these peatland regions. These results support the idea that long, mild growing seasons promote peat accumulation. Finally and contrary to what has been observed in the northern high latitudes, peat accumulation across Patagonia did not correlate to climatic parameters (temperature and precipitation), suggesting that local-scale controls might mediate the influences of climate on peat accumulation. I proposed that self-organization mechanisms exert fundamental controls in Patagonian peat bogs due to the simple vegetation structure of these systems coupled with rapid peat accumulation rates.

A recurrent theme across these chapters (and appendixes) is the non-linearity of peatland behavior: vegetation shifts, threshold values, power-law behaviors, and self-regulation mechanisms are good examples. There is a growing body of theoretical, empirical, and modeling evidence suggesting that peatland dynamics are, indeed, non-linear: rather than displaying gradual structural and functional changes that match the frequency of external forcing, these ecosystems show long periods of little change that are punctuated with step-like transitions to alternative states. From a theoretical standpoint, therefore, peatlands can be considered ‘complex adaptive systems’. This non-linear behavior is mostly induced by ecohydrological feedbacks that involve interactions between the biota (plant growth, peat decomposition) and the physical environment (basin morphology, hydrology). These self-regulating mechanisms tend to attenuate, through negative feedback loops, externally-driven changes in an attempt to maintain ecosystem status quo (i.e., reactive homeostasis). Alternatively, peatlands can also exhibit rapid, non-linear, and disproportionally large responses to external forcing mechanisms.

Such abrupt transitions from one steady state to another are described as bifurcations (or tipping points), and they occur once the stability properties of the ecosystem are suddenly lost to the expense of a new (or alternative) stable state. Once in place, the alternative ecosystem state may be maintained by a new set of self-regulating feedbacks. In addition, even in the absence of an environmental trigger, regular patterns may emerge in peatland ecosystems where positive and negative feedbacks occur at different spatial scales. For these reasons, the interplay between localized interactions and regional climatic forcing may lead to ecosystem responses that are context-sensitive rather than climate-sensitive, and it is especially challenging to tease apart internal vs. external controls when both interact on similar timescales. In my opinion, a better understanding and reappraisal of peatland internal dynamics constitutes today's most important challenge for the peatland scientific community.

APPENDIX I

Peatland dynamics in Patagonia: abrupt mid-Holocene fen-to-bog transition and carbon sequestration implications

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Summary

We use peatlands from southern Patagonia as model examples to investigate the role of regional-scale allogenic controls on the fen-bog transition, an important regime shift that had occurred throughout high-latitude regions of both hemispheres and that likely impacted the global carbon cycle through a major change in the rate of methane emissions and peat-carbon sequestration. In addition to documenting the mid-Holocene fen-bog transition in Patagonia, our goals are: (1) to identify and describe key fen and bog stability properties, and (2) to integrate these mechanisms into conceptual and process-based models. We argue that peatlands are ‘complex adaptive systems’, and that a reappraisal and better understanding of fundamental and important peatland processes such as the fen-bog transition under this view is critical to better assess the role of external forcing such as climate change on peatland structure and functioning.

Rationale

Over the past 12,000 years, peatlands have played a significant role in the global carbon (C) cycle by acting as long-term carbon dioxide (CO_2) sinks and as the most important natural sources of methane (CH_4) to the atmosphere (MacDonald *et al*., 2006; Yu, 2011). These ecosystems have had a net cooling effect on the global climate throughout the Holocene, as they have sequestered up to about 550 gigatons of C, which accounts for roughly 1/3 of all organic soil C and represents as much as to 2/3 of the present atmospheric C pool (Yu *et al*., 2010). There is a growing body of evidence suggesting that peatland dynamics are non-linear: rather than displaying gradual structural and functional changes that match the frequency of external forcing, these ecosystems show long periods of little change that are punctuated with step-like transitions to alternative states (Belyea and Baird, 2006; Belyea, 2009). From a theoretical standpoint, therefore, peatlands can be considered ‘complex adaptive systems’ (Levin, 1998). As abrupt changes in peatland dynamics may directly impact peat-C sequestration rates, profound effects on the global C cycle and the climate system can result from such a non-linear behavior.

Peatlands as complex adaptive systems

There is increasing recognition that ecosystems often exhibit non-linear, step-like responses to external forcing mechanisms (Andersen *et al*., 2009). Such abrupt transitions from one steady state to another are described as bifurcations (or tipping points), and they occur once the stability properties of an ecosystem are suddenly lost to the expense of a new (or alternative) stable state (Scheffer *et al*., 2001). Once in place, the alternative ecosystem state may be maintained by self-regulating physical, biological, and/or chemical positive feedbacks, making it difficult or impossible to reverse (Scheffer and Carpenter, 2003). The difficulty to foresee these non-linear responses is concerning because changes in ecosystem structure may lead to critical shifts in ecosystem function and associated services.

Most high-latitude peatlands start their development as fens. As peat accumulates over time, fen surfaces progressively get farther away from the mineral groundwater, and a shift to bog vegetation occurs (Foster and Wright, 1990). Here, the expression 'bog' represents *Sphagnum*-dominated peatlands and therefore includes poor fens. This transition is usually thought of being strictly governed by the plant community itself through peat accumulation: as peat thickness progressively increases, groundwater inputs diminish until precipitation becomes the sole water source to the peatland surface (Zobel, 1988). In nature, however, an 'intermediate' stage between the fen and bog states does not exist, suggesting that the transition from fen to bog is unstable, or transient (Fig. A.1).

Here we hypothesize that both the bog and fen phases possess specific stability properties that promote their own self-maintenance, explaining the abruptness of the fen-bog transition. We speculate that, over time, fens lose their resilience due to increasing peat thickness and, as a result, they become more sensitive to perturbations (Fig. A.1). Under this scenario, we argue that the ecosystem reaches a tipping point where the bog state becomes more attractive than the fen domain, inducing a rapid fen-bog transition via positive feedback loops. We also predict that, over time, changes in climate (moisture and temperature) and stochastic disturbance events (e.g., drought, flood, volcanic eruption, fire) get increasingly important in facilitating the fen-bog transition (i.e., the fen state becomes less stable over time). Specifically, our goals are: (1) to identify and describe key fen and bog stability properties, and (2) to integrate these mechanisms into a conceptual model (Fig. A.1) as well as a process-based model. The latter is being developed as a bimodal model that is capable of simulating peat accumulation and self-maintaining mechanisms for two alternative states using simple ‘fen’ and ‘bog’ vegetation functions and feedback loops.

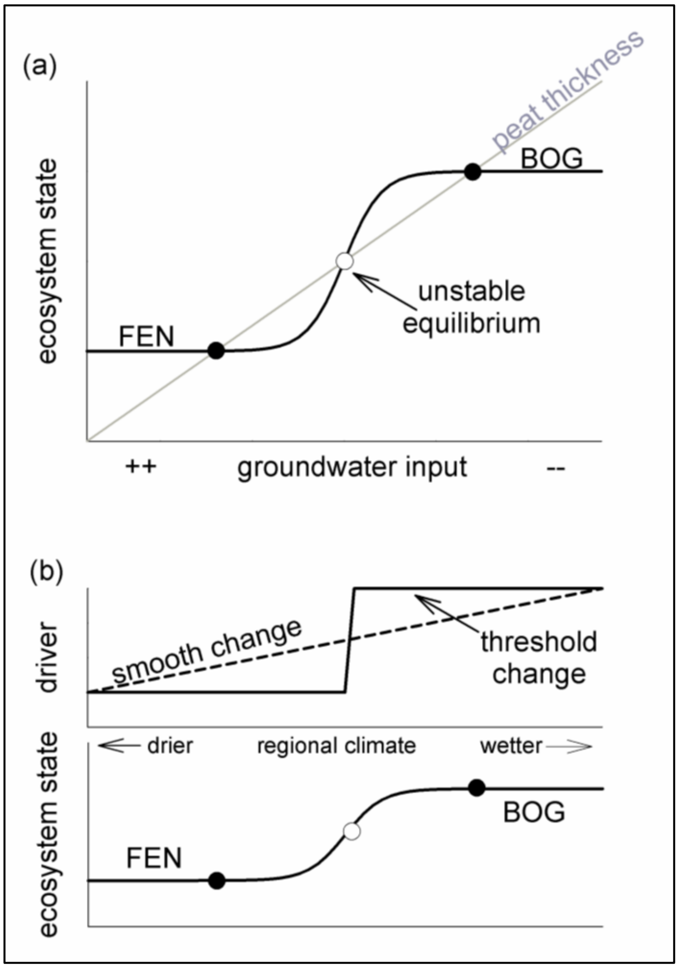

Figure A.1. Conceptual models for the fen-bog transition. (a) autogenic bistable system: increasing peat depth leads to a lower nutrient level, itself leading to a weakening of the fen resilience until the ecosystem jumps to the alternative state. (b) driver-threshold: the ecosystem shift is induced after an external driver (e.g., climate) exceeds a threshold. Adapted from Andersen et al. (2009).

Case study: fen-bog transition in southern Patagonia

Patagonian peatlands (Fig. A.2) are strikingly similar to their northern counterparts in terms of structure and functioning, but these ecosystems have developed under very different boundary conditions, including unique climatic settings, landscape features, and disturbance regimes. Therefore, these southern ecosystems provide a unique opportunity to test hypotheses about local- and regional-scale controls on peatland dynamics.

We present peat-core evidence for abrupt, three-fold increases in peat-carbon accumulation rates in Patagonian peatlands around 4200 years ago (Fig. A.2). This sudden increase in C sequestration is coincident with a rapid transition from groundwater-fed minerotrophic fens to precipitation-fed ombrotrophic bogs, as shown by our high-resolution plant macrofossil analysis. Our data synthesis from 46 sites similarly indicates a large-scale switch from fens to bogs across southern Patagonia at the same time, pointing towards a regional-scale, 'driver threshold-type' control on the fen-bog transition and associated peat-C dynamics (Fig. A.1). We use this transition as a 'natural experiment' to explicitly test and evaluate the following two important, non-exclusive hypotheses.

(1) Increasing precipitation and flushing reduced the influence of mineral-rich groundwater and allowed the pioneer bog genus *Sphagnum* to establish, which rapidly led to the fen-bog transition and to increased C sequestration around 4200 years ago (Granath *et al*., 2010). Under this scenario, climatic conditions facilitated *Sphagnum* establishment and growth. In the study region, precipitation constitutes a key control on ecosystem dynamics (Tuhkanen, 1992). Paleoecological evidence from peat and lake cores indicates

major millennial- and centennial-scale changes in the regional fire regime, forest extent, and lake productivity around 5000 years ago (Moy *et al*., 2009). These ecosystem shifts have been linked to important precipitation variability that was induced by changes in the strength and latitudinal position of the southern westerly winds (Moreno *et al*., 2009).

(2) A catastrophic disturbance around 4200 years ago induced an abrupt acidification of the peatland surface that facilitated *Sphagnum* establishment, which led to the fen-bog transition. We hypothesize that volcanic fallout and sulfur dioxide (SO_2) release from Mount Burney, a stratovolcano situated in the southern Andes that erupted 4200 ± 900 years ago (Stern, 2008), has caused intense peatland acidification because of fens weak buffering capacity (Gorham *et al*., 1984), which led to nutrient seepage and an abrupt ecosystem shift. A tephra layer from this eruption was identified along several peat profiles (> 40) throughout southern Patagonia, indicating that the volcanic plume effectively affected the entire study region. In addition, major, long-lasting damage to forest, aquatic and peatland ecosystems caused by Mount Burney's eruption have previously been reported, though they were restricted to the vicinity of the volcano (Kilian *et al*., 2006). Our scenario implies a much broader, regional-scale impact for this eruption.

Implication

Since fens emit 10 to 100 times more CH_4 than bogs (Laine and Vasander, 1996), and bogs possess a greater C sequestration capacity than fens (Granath *et al*., 2010), the fen-to-bog transition has clear implications for soil-atmosphere C exchanges at a regional to global scale. For instance, the progressive decrease in atmospheric CH_4 concentration that has been occurring between 8000 and 4000 years ago might relate to the fen-to-bog transition across the boreal biome (MacDonald *et al*., 2006). The processes leading to this ecosystem shift, however, remain poorly understood (Hugues, 2000).

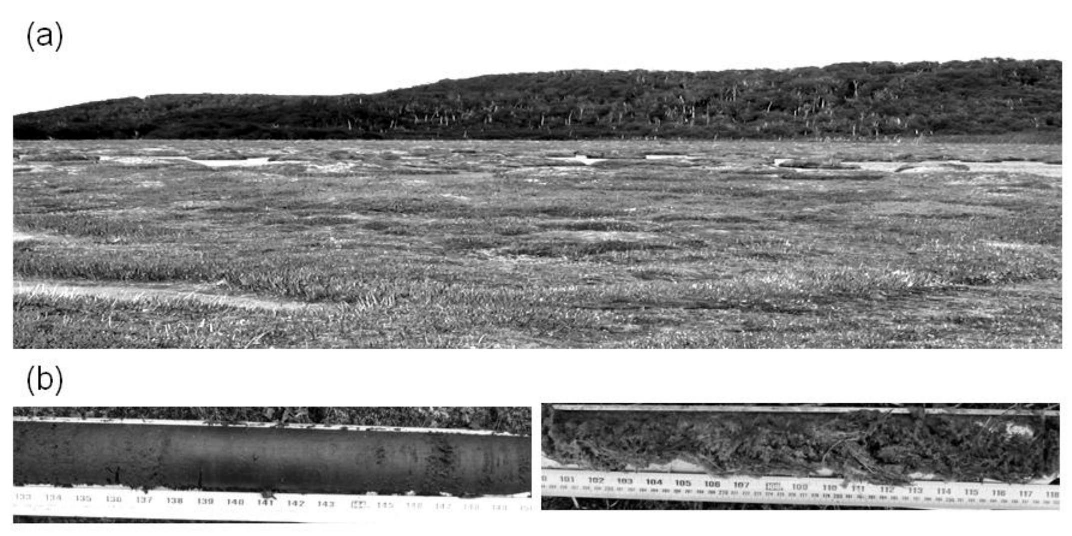

Figure A.2. Cerro Negro peatland, southern Chile. (a) photo of the study site; (b) peat cores showing highly decomposed fen peat (left) and fresh-looking bog peat (right).

Overall, a reappraisal and better understanding of fundamental and important peatland processes such as the fen-bog transition is critically needed to better assess the role of allogenic factors on peatland change and carbon sequestration ability. In addition to documenting the mid-Holocene fen-bog transition in Patagonia, our conceptual and process-based models clearly represent a step forward in reducing the complexity of peatland dynamics by identifying the key variables and quantifying the interactions that control non-linear behavior in peatlands.

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References

Andersen, T., Carstensen, J., Hernández-Garcia, E., Duarte, C.M. (2009). Ecological thresholds and regime shifts: approaches and identification. *Trends in Ecology and Evolution* **24**(1): 49-57.

Belyea, L.R. (2009). Non-linear dynamics of peatlands and potential feedbacks on the climate system. In Baird, A., Belyea, L., Comas, X., Reeve, A., Slater, L. (eds.) *Northern Peatlands and Carbon Cycling*. American Geophysical Union Monograph Series.

Belyea, L.R., Baird, A.J. (2006). Beyond "The limits to peat bog growth": cross-scale feedback in peatland development. *Ecological Monographs* **76**(3): 299–322.

Foster, D., Wright, H.E. Jr. (1990). Role of ecosystem development and climate change in bog formation in central Sweden. *Ecology* **71**: 450-463.

Gorham, E., Bayley, S.E., Schindler, D.W. (1984). Ecological effects of acid rain deposition upon peatlands: a neglected field in 'acid-rain' research. *Canadian Journal of Fisheries and Aquatic Science* **41**: 1256-1268.

Granath, G., Strengbom, J., Rydin, H. (2010). Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology* **91**(10): 3047-3056.

Hugues, P.D.M. (2000). A reappraisal of the mechanisms leading to ombrotrophy in British raised mires. *Ecology Letters* **3**: 7-9.

Kilian, R., Biester, H., Behrmann., J, Baeza., O, Fesq-Martin, M., Hohner, M., Schimpf, D., Friedmann, Mangini, A. (2006). Millennium-scale volcanic impact on a superhumid and pristine ecosystem. *Geology* **34**(8): 609-612.

Laine J., Vasander, H. (1996). Ecology and vegetation gradients of peatlands. In Vasander, H. (ed.), *Peatlands in Finland*. Finnish Peatland Society.

Levin, S.A. (1998). Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* **1**: 431-436.

MacDonald, G.M., Beilman, D.W., Kremenetski, K.V., Sheng, Y., Smith, L., Valichko, A.A. (2006). Rapid early development of circumarctic peatlands and atmospheric CH_4 and CO_2 variations. *Science* **314**: 285-288.

Moreno, P.I., François, J.P., Villa-Martınez, R.P., Moy, C.M. (2009). Millennial-scale variability in Southern Hemisphere westerly wind activity over the last 5000 years in SW Patagonia. *Quaternary Science Reviews* **28**: 25-38.

Moy, C.I., Moreno, P.I., Dunbar, R.B., Kaplan, M.R., Francois, J.P., Villalba, R., Haberzettl, T. (2009). Climate change in southern South America during the last two millennia. In Vimeux, F., Sylvestre, F. and Khodri, M. (eds.), *Past climate variability in South America and surrounding regions*. Springer.

Scheffer, M. Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems : linking theory to observation. *Trends in Ecology and Evolution* **18**(12): 648-656.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* **413**: 591-596.

Stern, C.R. (2008). Holocene tephrochronology record of large explosive eruptions in the southernmost Patagonian Andes. *Bulletin of Volcanology* **70**:435–454.

Tuhkanen, S. (1992). The climate of Tierra del Fuego from a vegetation geographical point of view and its ecoclimatic counterparts elsewhere. *Acta Botanica Fennica* **145**: 1-64.

Yu, Z. (2011). Holocene carbon flux histories of the world's peatlands: global carbon-cycle implications. *The Holocene* **21**: 761-774.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters* **37**: L13402 doi:10.1029/ 2010GL043584.

Zobel, M. (1988). Autogenic succession in boreal mires – a review. *Folia Geobotanica et Phytotaxonomica* **28**: 417-445.

APPENDIX II

Patagonian testate amoebae transfer function for paleohydrological reconstructions in ombrotrophic peatlands

Database and preliminary transfer function

In preparation for *Journal of Quaternary Science*

We are currently developing the first testate ameobae - water table depth transfer function for Patagonian peatlands. The transfer function is based on 85 surface samples that were collected in January 2005 (collected by Prof. Dan Charman and analyzed by Loisel) and in 2010 (collected by Loisel and Yu). Environmental parameters such as pH, water table depth and water content (Fig. A.3) were measured in the field for each sample to quantify the tolerance range and optimum of each species. Preliminary results confirm that amoebae are sensitive to water table depth in Patagonia (Fig. A.4). The range of hydrologic variability for each species will be used to quantitatively reconstruct past changes in water table depth along peat cores. Sample preparation of modern and fossil samples follows standard techniques.

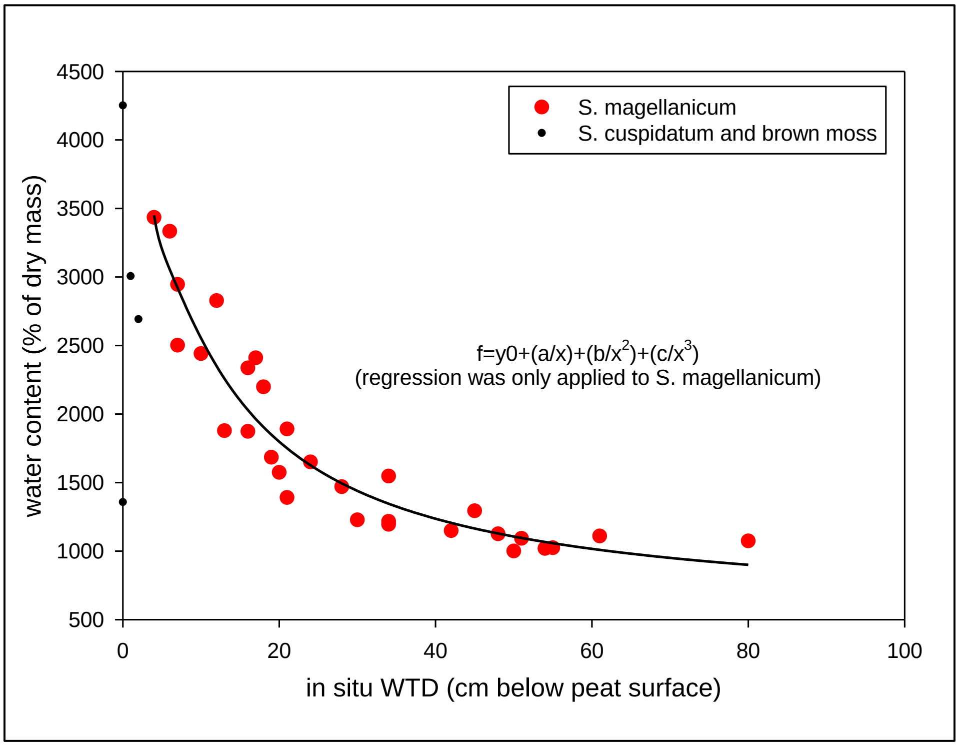


Figure A.3. Power-law behavior between water table depth and *Sphagnum magellanicum* water content.

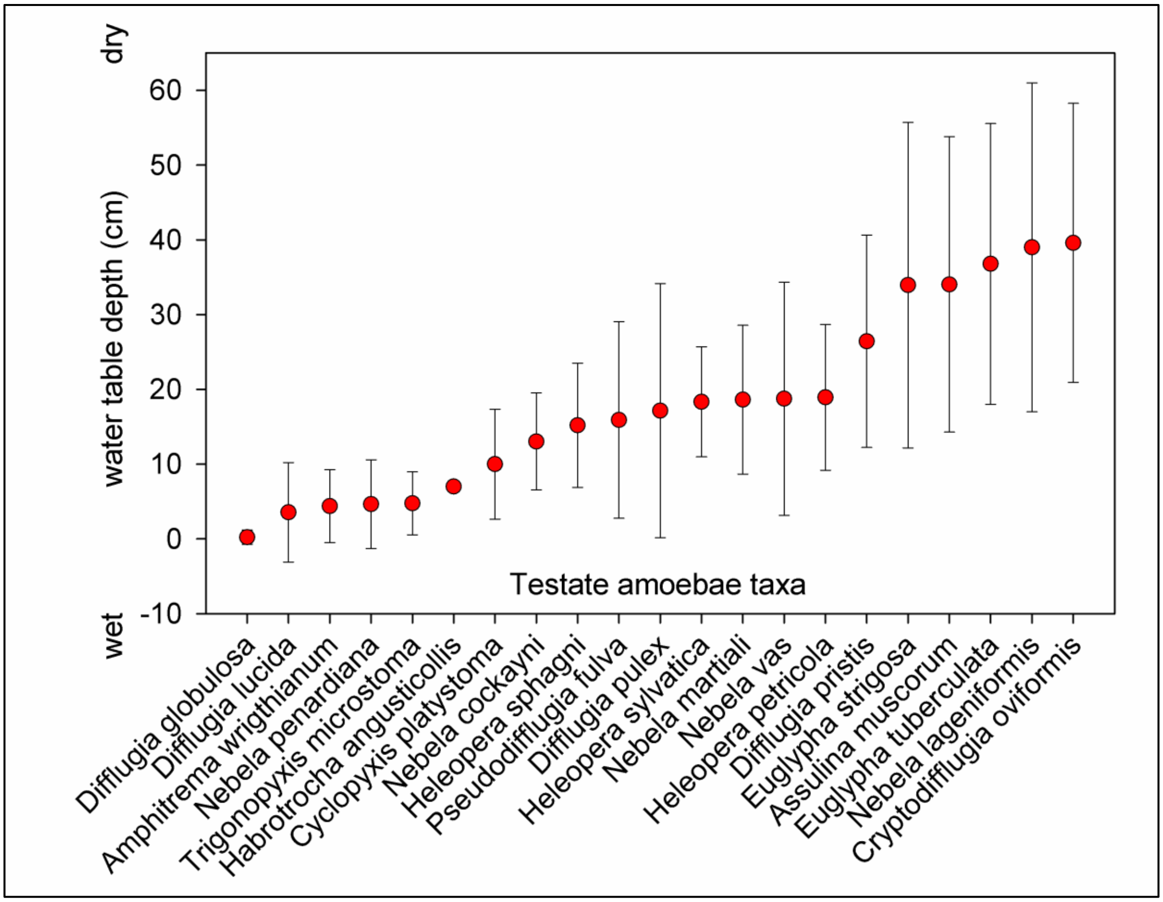


Figure A.4. Water table depth optima and tolerance ranges for testate amoebae species in southern Patagonia based on 35 surface samples. Additional surface samples will be added to this database to create a transfer function that will be applied to fossil samples found along peat cores. This is the first calibration dataset that is being done for South America, and it will be useful for future paleoecological studies by others.

APPENDIX III

Climate control of carbon sequestration in peatlands mediated by local-scale ecohydrological feedbacks

Dataset and Disussion

In prepration for *Nature Geosciences*

Observations

Here I present a detailed plant macrofossil analysis combined with long-term carbon accumulation estimates for a peat bog located near Puerto Natales, in southern Chile (Cerro Negro peatland: 52°04’ S, 72°02’W, 217 m a.s.l.). Results show that the fen-to-bog transition occurred around 4.2 ka (1 ka = 1000 calibrated years before present) at this site. During the bog phase, regular oscillations between light- and dark-colored peat layers were found on the basis of peat stratigraphy (Fig. A.5). While the light layers were composed of well-preserved *Sphagnum* macrofossils, the dark layers were composed of a highly decomposed organic matter matrix where monocotyledon plant remains (likely the rush *Tetroncium magellanicum*) and *Drepanocladus* spp. (brown moss) were identified (Fig. A.6). These alternating macrofossil assemblages along the peat core could represent distinct switches between hummocks (light peat) and hollows (dark peat), as observed in the field at the present. Preliminary testate amoebae analysis supports this interpretation (Fig. A.7), as wet-adapted species such as *Amphitrema wrightianum* and *Trigonopyxis microstoma* dominated the assemblages within the humified peat layers, and intermediate species including *Heleopera sphagni* and *Nebela martiali* were identified in the *Sphagnum*-rich layers (see transfer function in Appendix II, Fig. A.4). Plant macrofossils analysis is also being performed at three other peat bogs across the region (preliminary results presented in Fig. A.8).

These cyclic changes also followed clear regularity. At the Cerro Negro peatland, the dry to wet shifts showed a 150-year periodicity from 4.2 to 2.8 ka, and a 700-year periodicity during the last 2.8 ka (Fig. A.6). From 2.8 ka to today, three more cycles occurred, but at a much lower periodicity (700 years). Similar cyclical shifts between wet and dry vegetation communities were identified at the three additional peatland sites, though these cyclic changes were characterized by different periodicities (Fig. A.9).

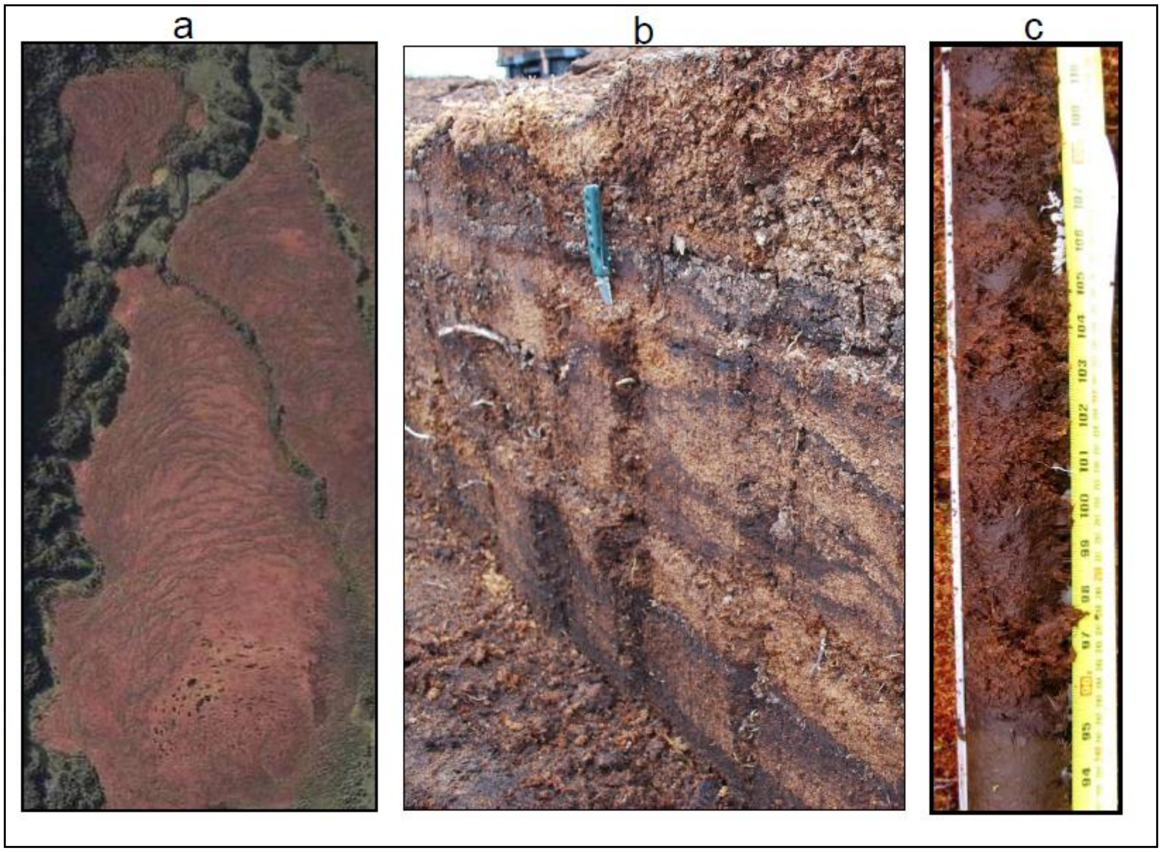


Figure A.5. Regular surface patterns in Patagonian peatlands. **(a)** Spot image of Upper Andorra Valley peatland (54°45’ S, 68°20’ W, 200 m a.s.l.) showing stripe orientation perpendicular to the slope and stripe aspect. © 2012 Google, © 2012 DigitalGlobe GeoEye, © 2012 Inav/Geosistemas SRL. **(b)** Cross-section of Escondido peatland (54°37’ S, 67°46’ W, 127 m a.s.l.) showing alternating horizontal layers of wet and dry plant community assemblages. Herbaceous peat is dark brown, dense, and highly decomposed, whereas *Sphagnum* peat is reddish brown and poorly decomposed. **(c)** Peat core (240-280 cm) from Cerro Negro peatland (52°04’ S, 72°02’W, 217 m a.s.l.) showing the rapidly alternating fossilized plant assemblages.

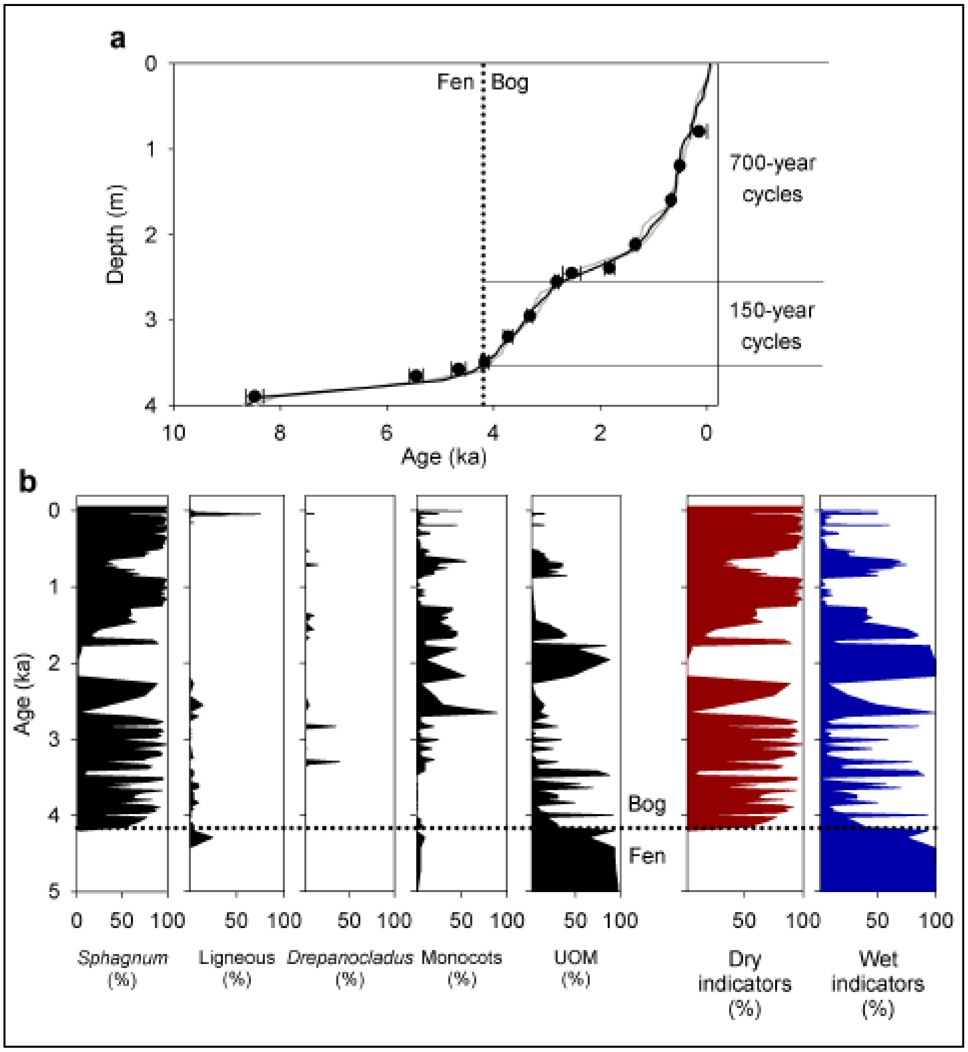


Figure A.6. Age-depth relationship and plant macrofossil analysis for Cerro Negro peatland, southern Patagonia. The fen-to-bog transition is depicted by black dashed lines. Age (ka) is presented in thousands of calibrated years before present. **(a)** Age-depth relationship. The median age (black dots) and calibrated 2 σ range (error bars) of each ^{14}C date are presented, along with the most probable age-depth model (solid black lines) and associated error range (grey lines) as estimated using the program Bacon. **(b)** Plant macrofossil analysis. Black areas represent the original percentages of each plant type. The summed *Sphagnum* and ligneous percentages are presented as 'dry indicators' (red area), whilst the summed *Drepanocladus*, monocots, and unidentifiable organic matter (UOM) percentages are presented as 'wet indicators' (blue area).

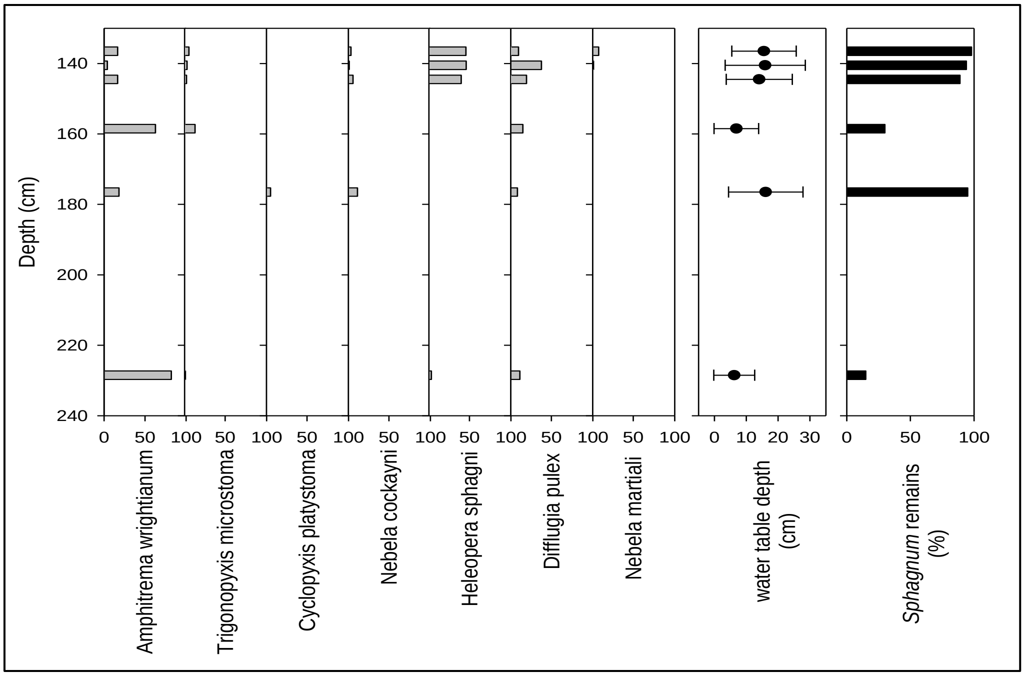


Figure A.7. Main testate amoebae taxa (percentages) found in 6 peat samples at the Cerro Negro peatland. Testate taxa are presented from wettest to driest. Reconstructed water table depth and standard error are based on a transfer function for Patagonian peatlands (Appendix II, Fig. A.4). Light peat layers (*Sphagnum*-rich) are characterized by different testate amoebae assemblages and drier conditions than dark (herbaceous, brown moss, and decomposed matter) peat layers.

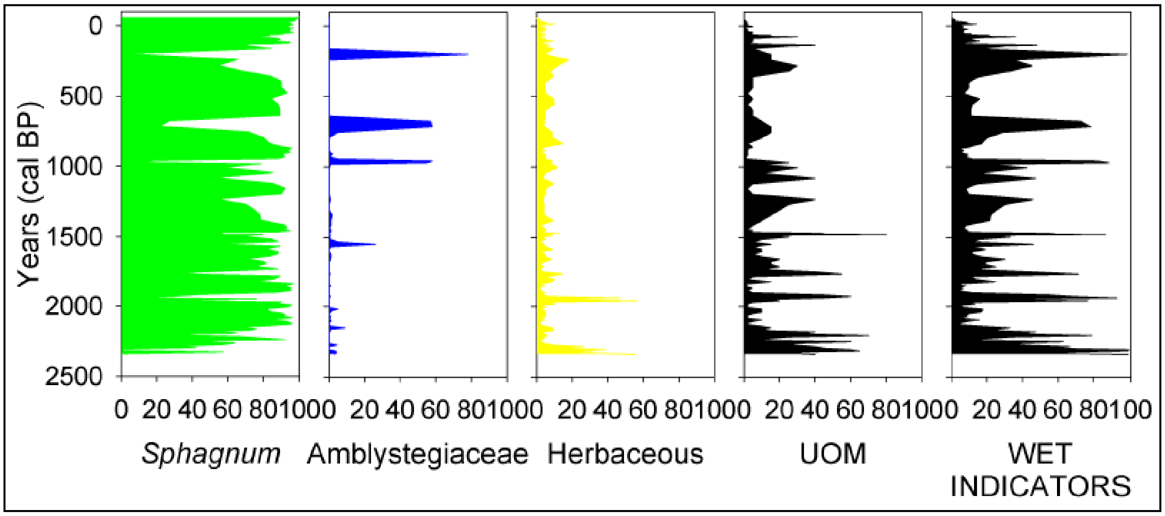
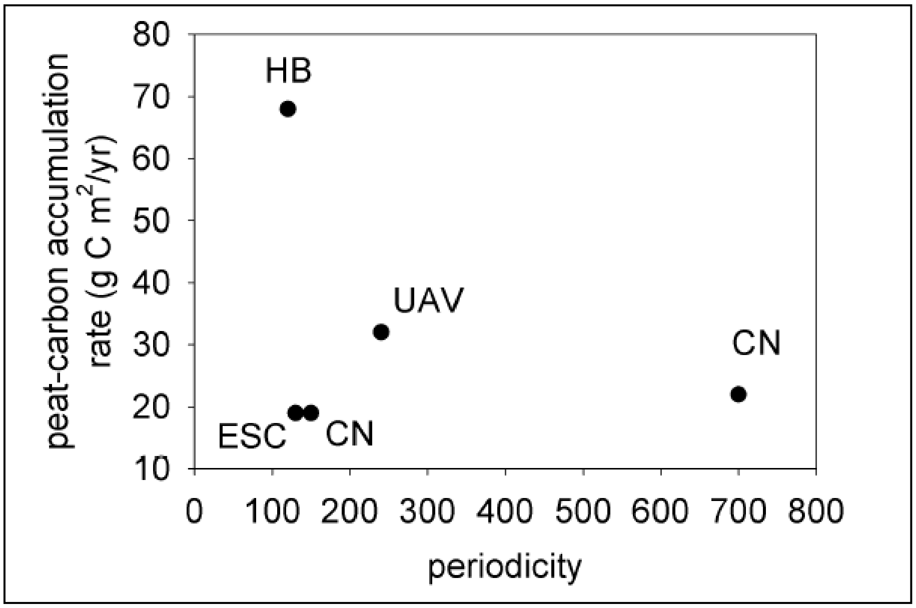


Figure A.8. Plant macrofossil analysis for Upper Andorra Valley peatland, southern Patagonia. Summed Amblystegiaceae, herbaceous, and unidentifiable organic matter (UOM) percentages are presented as 'wet indicators'.



	Depth interval (cm)	Time (years)	Time (ka)	Number of cycles	Periodicity (yrs/cycle)	PCAR (g C $m^{-2}yr^{-1}$)
CN*	245-350	1350	2.8-4.2	9	150	19
CN	0-245	2800	0-2.8	3	700	22
UAV	0-300	2400	0-2.4	10	240	32
ESC*	210-350	1850	2.8-4.6	14	130	19
HB	250-450	730	0.3-1.0	6	120	68

*PCARs from these sites cannot be directly compared with values from other sites because they integrate 2800 years of decomposition.

Figure A.9. Relationship between long-term apparent rate of peat-carbon accumulation (PCAR; g C m^{-2} yr^{-1}) and wet-dry cycle periodicity at four Patagonian peatland sites.

Discussion

The wet and dry phases of these successional sequences have occurred cyclically rather than unidirectionally, indicating that peatland development did not follow the simple hydroseral succession from wetter to drier plant communities. Two hypotheses can explain these stratigraphic changes: (1) climate (Barber, 1981), or (2) autogenic processes that promote the development of hummocks and hollows such as (i) evaporation-induced scale-dependent feedbacks between hummock vegetation and nutrient availability (Eppinga et al., 2008), (ii) positive feedback between the net rate of peat formation and acrotelm thickness (Belyea and Clymo, 2001), and (iii) pool formation and subsequent development of linear patterns (Foster et al., 1983).

It is unlikely that climatic changes alone have induced these wet and dry cycles because these periods were found to oscillate at different periodicities amongst sites, implying different climate histories. However, three of these sites (UAV, ESC, and HB) are located within 50 km and should be influenced by similar climatic conditions. Similarly, hypotheses regarding the formation of hummocks and hollows cannot explain our observations because three of the four coring sites are located in large lawn areas with minimal topography, tens of meters away from hummocks and ridges (see Chapter 4, Fig. 4.5), though pools that are colonized by *Drepanocladus* spp. and surrounded by *Tetroncium magellanicum* are found in close proximity to the coring sites (Fig. A.10).

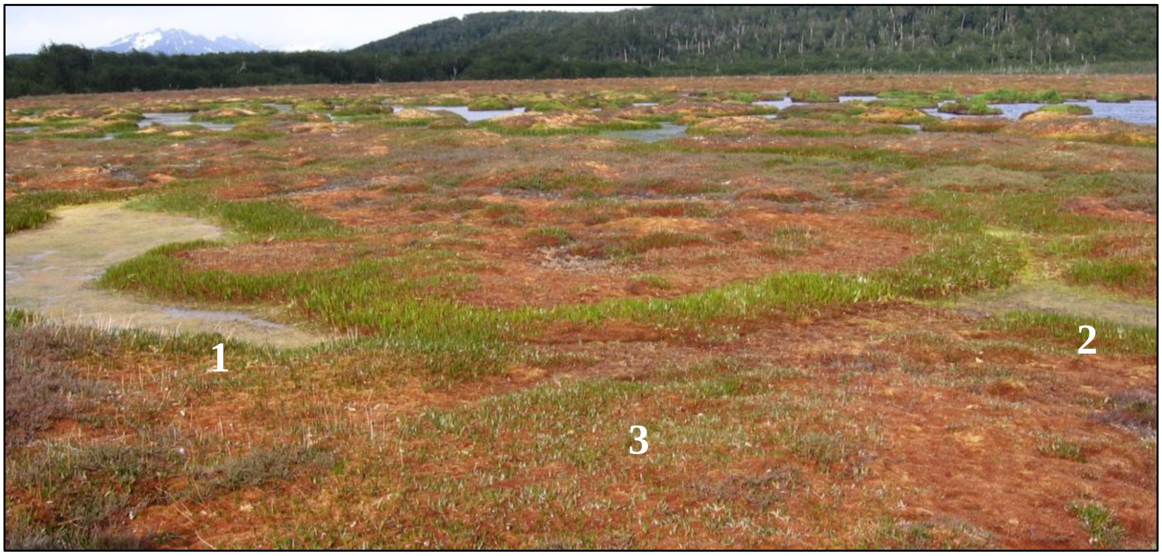


Figure A.10. Coring site, Cerro Negro peatland. Note that the *Sphagnum* lawn lacks high topographic features such as hummocks and ridges, but pools are abundant. (1) widest and deepest pool; (2) shallower and narrower pool; (3) old pool now colonized by *Sphagnum magellanicum*.

Therefore, we propose that positive feedbacks between the net rate of peat formation and acrotelm thickness (Belyea and Clymo, 2001) as well as scale-dependent feedbacks between hummock vegetation and nutrient availability (Eppinga et al., 2008) could both partly explain our observations, but modifications must be made. These two hypotheses stipulate that hummocks are elevated above hollows because they have a thicker acrotelm that promotes vascular plant growth (i.e., shrubs), which accumulate nutrients and increases acrotelm thickness, further traping nutrients and accentuating the hummock-hollow topography. As our study sites are flat *Sphagnum magellanicum* lawns with limited shrub vegetation, these ideas cannot be applied directly. Instead, we suggest that *Tetroncium magellanicum* (rush), which is characterized by deep root systems, acts as the nutrient and water pumps in the Patagonian peatlands (instead of shrubs). By doing so, it allows lawn-forming *Sphagnum* mosses, which possess greater water-holding capacity and are characterized by limited decomposition, to grow very close to the pool margins, creating a sharply bounded lawn-to-hollow topography. These *Sphagnum* plants grow over adjacent *Tetroncium*, which provides a hydrologically stable microhabitat for moss growth. Lateral *Sphagnum* growth was observed in the field, and is probably attributable to plant competition for space and water resources (Fig. A.11). As *Tetroncium* gets colonized by such *Sphagnum* ‘fronts’, we speculate that it migrates toward the center of the pool, followed by *Sphagnum*. Over time, while pools get completely colonized by *Sphagnum* and become lawns, new pools are formed elsewhere. This process is thought to be climate-sensitive, such that conditions that favor *Sphagnum* growth accelerate pool colonization. In summary, the dynamics of surface patterning is determined by the interplay between regional climate and local hydrological settings.

Figure A.11. *Sphagnum magellanicum* growing laterally in a lawn, Upper Andorra Valley.

Although we do not have specific topographic and hydrological information to evaluate the relative role of local factors in driving the reconstructed cyclic changes in peatland vegetation at the Cerro Negro site, it is assumed that these local controls remained the same over the past 4.2 ka. Therefore, only a major change in the regional climate can explain the shift in periodicities from 150 years to 700 years at 2.8 ka. Based on pollen analysis, southern beech (*Nothofagus*) woodlands expanded rapidly around 4.5 ka throughout the region, fire occurrence decreased, and glaciers advanced (Moreno et al., 2009; Huber and Markgraf, 2003). Peat bogs also started establishing at this time (Huber and Markgraf, 2003). These vegetation changes have been linked to increasing effective moisture due to millennial-scale changes in either the latitudinal position or the overall strength of the southern westerlies. Around 3 ka, a re-opening of the *Nothofagus* woodlands was reconstructed and associated to decreased precipitation (Mancini, 2009).

The relationship between periodicities and carbon accumulation at all four peatland sites (Fig. A.9) indicates the important role of surface patterning and its dynamics on carbon sequestration ability in peatlands. As we have shown, surface patterning is determined by the interplay between local factors (topography, hydrology) and the regional climate. Our results suggest that climate impacts on carbon accumulation are not direct, but strongly mediated by ecohydrological feedbacks at individual peatlands. Preserving peatland surface structure is essential for carbon sequestration capacity. Therefore, we propose that regional climatic conditions exert a fundamental control on peat accumulation rates. In turn, peat accumulation rates control the speed at which surface patterning develops, persists, and transits over the peatland surface (Fig. A.9). Site-specific landscape morphology and peatland developmental history could also partly explain the different periodicities that were reported at the Cerro Negro site, as well as the difference amongst sites.

It is generally assumed that regional climatic changes are recorded in peat bog stratigraphy, albeit with some level of distortion that may be introduced by internal peatland dynamics. This study suggests that long-term peat accumulation rates are indeed sensitive to external forcing mechanisms, but that local ‘noise’ might exert an important and underestimated control on vegetation succession and peatland development. Results show that peatland self-organization processes such as those responsible for surface patterning can disconnect, or at least mediate, ecosystem behavior from external climatic influence, which may lead to ecosystem behavior that is context-sensitive rather than climate-sensitive. Overall, a better understanding of fundamental and important peatland processes such as surface patterning is critically needed to better assess the role of allogenic factors on peatland change and carbon sequestration ability.

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References

Barber, K.E. *Peat stratigraphy and climatic change: a palaeoecological test of the theory of cyclic peat bog regeneration*. A.A. Balkema, Rotterdam, The Netherlands, 219 p. (1981).

Belyea, L.R. & Clymo, R.S. Feedback control on the rate of peat formation. *Proceedings: Biological Sciences*, **268**, 1315-1321 (2001).

Eppinga, M.B., Rietkerk, M., Borren, W., Lapshina, E.D., Bleuten, W. & Wassen, M.J.

Regular surface patterning of peatlands: confronting theory with field data. *Ecosystems*, **11**, 520-536 (2008).

Foster, D.R., King, G.A., Glaser, P.H. & Wright, H.E. Jr. Origin of string patterns in boreal peatlands. *Nature,* **306**, 256-258 (1983).

Huber, U.M., Markgraf, V. *Holocene Fire Frequency and Climate Change at Rio Rubens Bog, Southern Patagonia*. In: Whitlock, C., Anderson, R.S. (Eds.), Fire and climatic change in temperate ecosystems of the western Americas. Ecological Studies vol. 160 (3), Springer, New York, USA, pp. 357-380 (2003).

Mancini, M.V. Holocene vegetation and climate changes from a peat pollen record of the forest – steppe ecotone, Southwest of Patagonia (Argentina). *Quat. Sci. Rev.*, **28**, 1490-1497 (2009).

Moreno, P.I., François, J.P., Villa-Martínez, R.P. & Moy, C.M. Millennial-scale variability in Southern Hemisphere westerly wind activity over the last 5000 years in SW Patagonia. *Quat. Sci. Rev.*, **28**, 25-38 (2009).

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Education

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B.Sc. **Physical Geography**
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Teaching Experience

Adjunct Faculty (Fall 2011), **Terrestrial Ecosystem Ecology** (EES250)
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2005 Paleoecology, Lanoraie peatland complex (southern Québec)
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2004 Quaternary paleogeography, Lanoraie peatland complex (southern Québec)
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Peer-reviews

The Holocene (2), Water, Air and Soil Pollution (2), Journal of Quaternary Science (1)
Palaeogeogr., Palaeoclim., Palaeoecol. (1), Geophysical Research Letters (1)

Undergraduate student mentoring

2010-11: Trained and supervised an undergraduate (Greg Sills, Lehigh University) completing a senior project on the effects of fire and climate on peat-carbon accumulation in Patagonia. My work included lab training, supervising research grant proposal writing (3/3 proposals were funded) and thesis redaction, as well as preparing Greg for poster and oral presentations.

Internships

2012 **Modeling non-linear shifts in peatland ecosystems**
Mentor: Paolo D'Odorico
Department of Environmental Sciences, University of Virginia, USA

2011 **Cellulose extraction and isotopic analysis (C,H,O) of *Sphagnum***
Mentors: Tim Daley, Neil Loader, Alayne Street-Perrott
School of the Environment & Society, Swansea University, Swansea, Wales

2007 **Peat humification analysis**
Mentor: Frank Chambers
University of Goucestershire, England

2005 **Pollen analysis**
Mentor: Pierre Richard
Université de Montréal, Canada

Peer-Reviewed Publications

Published articles

Loisel, J., Gallego-Sala, A.V., Yu, Z. 2012. Global-scale pattern of peatland *Sphagnum* growth driven by photosynthetically active radiation and growing season length. *Biogeosciences-Discussions*, 9: 2169-2196. (PhD)

Yu, Z., **Loisel, J.**, Brosseau, D., Beilman, D., Hunt, S. 2010. Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters* 37, L13402, doi10.1029/2010GL043584 (PhD)
****Research spotlight article in EOS****

Loisel, J., Garneau, M. 2010. Late-Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: potential and limits of multi-proxy analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 291:493-533. (MSc)

Loisel, J., Garneau, M., Hélie, J.-F. 2010. *Sphagnum* δ^{13}C values as indicators of paleohydrological changes in a peat bog. *The Holocene* 20(2): 285-291. (MSc)

Loisel, J., Garneau, M., Hélie, J.-F. 2009. Modern *Sphagnum* δ^{13}C signatures follow a surface- moisture gradient in two boreal peat bogs, James Bay lowlands, Québec. *Journal of Quaternary Science* 24(3): 209-214. (MSc)

Ali, A.A., Ghaleb, B., Garneau, M., Asnong, H., **Loisel, J.** 2008. Recent peat accumulation rates in minerotrophic peatlands of Bay James region, Eastern Canada, inferred by ^{210}Pb and ^{137}Cs radiometric techniques. *Applied Radiation and Isotopes* 66: 1350-1358. (collaboration)

Submitted Manuscripts

Loisel, J., Yu, Z. Submitted. Recent acceleration of carbon accumulation in a boreal peatland, south-central Alaska. *Journal of Geophysical Research - Biogeosciences,* 2012-JG-001978. (PhD)

Loisel, J., Yu, Z., Parsekian, A., Nolan, J., Slater, L. Submitted. Quantifying landscape morphology influence on peatland lateral expansion using ground penetrating radar (GPR) and peat core analysis. *Journal of Geophysical Research - Biogeosciences*, 2012-JG-002015. (PhD)

Charman, D., Beilman, D., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F., Christen, J.A., Gallego-Sala, A.V., Harrison, S.P., Hughes, P.D.M., Jackson, S., Korhola, A., Mauquoy, D., Mitchell, F., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z., Alm, J., Bauer, I.E.,McCorish, Y., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., **Loisel, J.**, Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D., Zhao, Y. Submitted. Climate-driven changes in peatland carbon accumulation during the last millennium. *Proceedings of the National Academy of Sciences of the USA*, PNAS-2011-19956. (collaboration)

Yu, Z., **Loisel, J.**, Turetsky, M.R., Cai, S., Zhao, Y., Frolking, S., MacDonald, G.M., Bubier, J.L. Submitted. Evidence for elevated emissions from high-latitude wetlands causing high atmosphericCH_4 concentration in the early Holocene. *Global Biogeochemical Cycles*, 2011-GB-004222. (collaboration)

Manuscripts in Preparation

Loisel, J., Yu, Z. In Prep. Holocene peatland carbon dynamics in Patagonia. *Quaternary Science Reviews*. (PhD)

Loisel, J., Yu, Z. In Prep. Self-organized spatial vegetation patterning mediates long-term carbon sequestration rates in peatlands. *Nature Geosciences*. (PhD)

Loisel, J., Yu, Z., D'Odorico, P. In Prep. The fen-to-bog transition in peatlands: an important non-linear ecosystem shift. (collaboration)

Loisel, J., Charman, D.J., Booth, R.K., Yu, Z. In Prep. Patagonian testate amoebae transfer function for paleohydrological reconstructions on ombrotrophic peatlands. *Journal of Quaternary Science*. (collaboration)

Loisel, J., Daley, T., Yu, Z., Loader, N., Street-Perrott, F.A. In Prep. High-resolution climate and atmospheric circulation changes in southern Patagonia over the past 1000 years. *Geology*. (collaboration)

Loisel, J., Yu, Z., Turunen, J., Moore, T. In Prep. Peatland carbon accumulation in northern peatlands over the past 100 years: the role of warming and nitrogen deposition. *Global Change Biology*. (collaboration)

Most Relevant Conferences and Seminar Presentations

Loisel, J., Yu., Z., D'Odorico, P. 2012 (upcoming). Peatland dynamics in Patagonia: abrupt mid-Holocene fen-to-bog transition and carbon sequestration implications. Oral presentation, *14th International Peat Congress,* Stockholm, Sweden. (PhD)

Yu, Z., **Loisel, J.**, Hunt, S., Klein, E., Booth, R., Jones, M. 2012 (upcoming). Alaskan peatland carbon dynamics during past warm climate intervals. Oral presentation, *14th International Peat Congress,* Stockholm, Sweden. (PhD)

Loisel, J., Yu, Z. 2011. Recent acceleration of carbon accumulation rates in wet boreal peatlands. Poster presentation, *AGU Fall Meeting,* San Francisco, USA. (PhD)

Loisel, J., Yu, Z. 2011. Southern peatlands: a new perspective on Holocene carbon dynamics. Oral presentation, *GSA Annual Meeting,* Minneapolis, USA. (PhD)

Loisel, J. 2011. Recent- and long-term peat-carbon accumulation: rates, timing, and climatic controls. Oral presentation (invited), School of the Environment & Society Research Seminars, Swansea University, Swansea, Wales, UK. (PhD)

Loisel, J., Yu, Z. 2011. Post-Little Ice Age warming induces a state shift in peat-carbon accumulation rates in Alaska. Oral presentation, *41st Arctic Workshop*, Montreal, Canada. (PhD)

Loisel, J., Nolan, J., Yu, Z., Parsekian, A., Slater, L. 2010. The influence of landscape morphology on peatland dynamics and carbon accumulation inferred from ground penetrating radar (GPR) and peat core analysis. Poster presentation, *AGU Fall Meeting,* San Francisco, USA. (PhD)

Brosseau, D., Ramage, J.M., Yu, Z., Booth, R.K., Klein, E.S., **Loisel, J.**, Mark, B. 2010. Peatland distribution and characterization in the Susitna River basin, Alaska. Poster presentation, *AGU Fall Meeting*, San Francisco, USA. (collaboration)

Loisel, J., Yu, Z. 2010. Holocene peat-carbon dynamics in Patagonia: timing, rates, and potential causes. Oral presentation, *2nd International LOTRED-South America Symposium (PAGES)*, Valdivia, Chile. (PhD)

Loisel, J., Yu, Z., Jones, M. 2009. Expanding peatlands in south-central Alaska: a response to glaciers-climate feedbacks? Poster presentation, *2nd International Symposium: Peatlands in the Global Carbon Cycle*, Prague, Czech Republic. (PhD)

Yu, Z., **Loisel, J.**, Jones, M., Beilman, D. 2009. Peatland carbon dynamics in the Holocene: controls, relevance and implications. Oral presentation (invited), *2nd International Symposium: Peatlands in the Global Carbon Cycle*, Prague, Czech Republic. (collaboration)

Garneau, M., Asnong, H., van Bellen, S., Tremblay, L., Lamarre, A., **Loisel, J.**, Beaulieu-Audy, V. 2009. The Holocene carbon dynamics of boreal and sub-arctic peatlands following a nordic gradient in Québec: a synthesis for northeastern Canada. Poster presentation, *2nd International Symposium: Peatlands in the Global Carbon Cycle*, Prague, Czech Republic. (MSc)

Loisel, J., Yu, Z., Jones, M. 2009. Expanding peatlands in Alaska caused by accelerated glacier melting under a warming climate. Oral presentation, *AGU Joint Assembly*, Toronto, Canada. (PhD)

Loisel, J., Yu, Z., Jones, M., Booth, R.K. 2008. Expanding sloping bog systems under a continental climate in south-central Alaska: possible causes and carbon-cycle implications. Poster presentation, *AGU Fall Meeting,* San Francisco, USA. (PhD)

Loisel, J., Garneau, M. 2008. The effects of moisture, climate and vegetation on long-term carbon sequestration rates in a boreal peatland, James Bay, Québec, Oral presentation, *GAC-MAC Annual Meeting*, Québec, Canada. (MSc)

Pelletier, L., **Loisel, J.**, Garneau, M. 2008. Reconstitution des flux de méthane locaux durant l'Holocène récent dans 2 tourbières boréales à l'aide des assemblages de rhizopodes, Baie James, Québec. Oral presentation, *ACFAS Annual Meeting,* Québec, Canada. (collaboration)

Loisel, J., Garneau, M., Hélie, J.-F. 2007. *Sphagnum* δ^{13}C values as potential indicators of palaeohydrological changes in boreal peat bogs. Poster presentation, *AGU Fall Meeting,* San Francisco, USA. (MSc)

Pelletier, L., **Loisel, J.**, Garneau, M. 2007. Late-Holocene reconstruction of methane fluxes based on testate amoebae assemblages: application to a boreal peat bog. Oral presentation, *AGU Fall meeting,* San Francisco, USA. (collaboration)

Garneau, M., Turunen, J., Ali, A.A., Asnong, H., Pelletier, L., **Loisel. J.**, Beaulieu-Audy, V. 2007. The understanding of past and present-day carbon dynamics of boreal peatlands, James Bay lowlands, Québec, Canada. Poster presentation, *AGU Fall meeting,* San Francisco, USA. (MSc)

Loisel, J., Garneau, M., Hélie, J.-F. 2007. Testate amoebae, *Sphagnum* carbon isotopic composition and other proxy data as palaeoindicators of surface-moisture changes in two boreal peatlands during the late Holocene: preliminary results. Oral presentation, *CANQUA Conference*, Ottawa, Canada. (MSc)

Ali, A.A., **Loisel, J.**, Ghaleb, B., Garneau, M., Asnong, H. 2007. ^{210}Pb radiometric dating of peat accumulation and environmental changes during the last centuries in taiga and boreal forests, Québec, Canada. Poster presentation, *CANQUA Conference*, Ottawa, Canada. (collaboration)

Loisel, J., Garneau, M., Hélie, J.-F. 2007. Carbon accumulation in boreal peatlands estimated by *Sphagnum* carbon isotopic composition and proxy indicators. Poster presentation, *1st International Symposium: Peatlands in the Global Carbon Cycle*, Wageningen, The Netherlands. (MSc)

Loisel, J., Garneau, M. 2007. Can palaeohydrological changes in peat bogs be inferred by *Sphagnum* $\delta^{13}C$ values? Poster, *ACUNS Student Conference*, Saskatoon, Canada. (MSc)

Loisel, J. 2007. Carbon accumulation in Canadian boreal peatlands: Can climatic information be inferred from *Sphagnum* $\delta^{13}C$ values? Oral presentation (invited), *Centre for Environmental Change and Quaternary Research Seminars*, University of Gloucestershire, Cheltenham, England. (MSc)

Loisel, J., Garneau, M., Rosa, E. 2006. Paléogéographie et reconstitution de la succession végétale du complexe tourbeux de la région de Lanoraie, Québec. Oral presentation, *AQQUA Conference*, Montréal, Canada. (BSc)

Funded Research Proposals

Doctoral Dissertation Improvement Grant (07/2011-12/2012)
US National Science Foundation
Impacts of temperature and precipitation on peat-carbon dynamics in Alaska and Patagonia (PhD)
**** My proposal was ranked 'Outstanding' by all four reviewers; only three proposals received that ranking*

Graduate Research Grant (09/2011-04/2012)
Department of Earth and Environmental Sciences, Lehigh University
Peatland dynamics in Patagonia: abrupt mid-Holocene fen-to-bog transition and carbon sequestration implications (PhD)

Graduate Research Grant (09/2010-04/2011)
Department of Earth and Environmental Sciences, Lehigh University
Abrupt shifts of the Southern Hemisphere westerlies during the Holocene thermal maximum (PhD)

Faculty Innovation Grant (09/2009-09/2010)
College of Arts and Sciences, Lehigh University (PI: Zicheng Yu)
Exploring Holocene carbon dynamics of peatlands in Patagonia: toward a global synthesis of high-latitude peatlands (PhD)

Graduate Research Grant (09/2009-04/2010)
Department of Earth and Environmental Sciences, Lehigh University
Late Pleistocene and Holocene peatland development in southeastern Patagonia: an important data and knowledge gap (PhD)

Kerry Kelt Research Award (09/2009-09/2010)
Limnogeology Division, Geological Society of America
Expanding peatlands in south-central Alaska: a response to glaciers-climate feedbacks? (PhD)

Northern Scientific Training Program (05/2007-05/2008)
Indian and Northern Affairs Canada
Paléoécologie des tourbières de la Baie James, Québec (MSc)

Fellowships and Competitive Scholarships

Dean's Fellowship, College of Arts and Sciences (08/2011-07/2012)
Lehigh University, tuition & stipend (PhD)

Alexander Graham Bell Canada Postgraduate Scholarship (08/2008-08/2011)
NSERC, stipend (PhD)

Quebec Research Scholarship B2 (08/2008-08/2011) - declined -
Fonds québécois de recherche sur la nature et les technologies, stipend (PhD)

College of Arts and Sciences Scholarship (08/2008-06/2011)
Lehigh University, tuition (PhD)

Quebec Research Scholarship B1 (06/2007-06/2008)
Fonds québécois de recherche sur la nature et les technologies, stipend (MSc)

Alexander Graham Bell Canada Postgraduate Scholarship (06/2006-06/2007)
NSERC, stipend (MSc)

Fairfax Financial Holdings Ltd Scholarship (09/2004-09/2006)
Association of Universities and Colleges of Canada, stipend (BSc)

Excellence in Research Scholarship (02/2006-05/2006)
Université du Québec à Montréal Foundation, stipend (BSc)

Student Exchange Program Scholarship (03/2006-06/2006) - declined -
Ministère de l'éducation, Loisir et Sport du Québec (for U. Lausanne), stipend (BSc)

Atmospheric and Meteorological Science Award (05/2005-08/2005)
NSERC and Environment Canada, stipend (BSc)

Undergraduate Student Research Award (05/2005-08/2005)
NSERC, stipend (BSc)

Undergraduate Student Research Award (05/2004-08/2004)
NSERC, stipend (BSc)

Canada Excellence Award for Leadership (09/2004-09/2005)
Canada Millennium Scholarship Foundation, stipend (BSc)

Workshops and Technical Course Attendance

2012 **Preparing for an academic career in the geosciences**
Cutting Edge, NSF and National Association of Geoscience Teachers
Chapel Hill, USA (PhD)

2012 **Science and policy conference**
American Geophysical Union
Washington D.C., USA (PhD)

2012 **Science communication**
National Geographic society
Washington D.C., USA (PhD)

2010 **Teacher development series**
Lehigh University
Bethlehem, USA (PhD)

2009 **Acquisition, visualization, and interpretation of lidar-derived DEMs**
Geological Society of America
Portland, USA (PhD)

2008 **4th international workshop on the ecology and identification of *Sphagnum***
PeatNet (Dale Vitt and John Shaw)
Anchorage, USA (PhD)

2007 **Testate amoebae as paleohydrological proxies in peatlands**
GEOTOP-UQÀM
Montreal, Canada (MSc)

2006 **Peatland ecology and bryophyte identification**
Université Laval
Québec, Canada (BSc)

Field courses

2011 Big Island (Hawai'i, USA), Lehigh University (PhD)

2009 Northern Apennines (Italy), Lehigh University (PhD)

2005 Mobil-UQ program, northern Québec (Canada), Université du Québec à Rimouski (BSc)

Main field research experience

2010 Southern Patagonia (Chile and Argentina) (PhD)

2008-10 Alaska (south-central, south-east and the interior) (PhD)

2006-07 Northern Québec (James Bay lowlands) (MSc)

Organizational Memberships

Ecological Society of America (ESA) since 2010
Geological Society of America (GSA) since 2009
American Geophysical Union (AGU) since 2007
Peatland Ecosystem Analysis and Training Network (PeatNet) since 2007
Canadian Quaternary Association (CANQUA) since 2007
Association Québécoise pour l'Étude du Quaternaire (AQQUA) since 2006
Palaeo-peatlands Research Group (PalPeat) since 2006
Geochemistry and Geodynamics Research Center (GEOTOP) since 2006
Canadian Association of Palynologists (CAP) since 2005

Service

2011-12 Student representative, Advisory Council
College of Arts and Sciences, Lehigh University

2010-11 Student representative, GIC (Graduate Instruction Committee)
Dept. of Earth & Environmental Sciences, Lehigh University

2009-10 Co-organized the annual departmental research symposium
Dept. of Earth & Environmental Sciences, Lehigh University

2008-11 Organized the Friday Seminars Series (weekly dept. seminars)
Dept. of Earth & Environmental Sciences, Lehigh University

2007-08 Secretary, Graduate Student Association
Département de Géographie, Université du Québec à Montréal

Media

2009 Interviewed by Discovery News on my research on Alaskan peatlands (PhD)