Pollen-Derived Paleovegetation Reconstruction and Long-Term Carbon Accumulation at a Fen Site in the Attawapiskat River Watershed, Hudson Bay Lowlands, Canada

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Abstract

The Hudson Bay Lowlands (HBL) constitute a globally significant carbon pool; the paleo-ecological record provides an opportunity to investigate long-term drivers of change in carbon accumulation and related changes in vegetation. We present a Holocene record from the Victor Fen site (VM-3-3) in Ontario's HBL to reconstruct vegetation history, quantify rates of carbon accumulation, and determine the role of paleoclimatic drivers. Pollen analysis indicates initiation of peat accumulation over a mineral substrate, accompanied by relatively rapid rates of carbon accumulation, following emergence from the Tyrrell Sea ~6900 yrs BP. The earliest vegetation assemblage consisted of a tidal marsh, quickly succeeding to a *Typha* marsh, then a poor fen dominated by *Sphagnum* and Cyperaceae by 6400 yrs BP. Rapid rates of isostatic uplift at the time likely contributed to these changes. Once established, this fen community persisted without major vegetation change until the most recent century, when the abundance of shrub and Cyperaceae pollen increased, suggesting increasingly minerotrophic conditions. Average rate of long-term carbon accumulation (LORCA) for the whole record (mean = 22.8 g C m^{-2} yr^{-1}) is similar to other northern peatlands, and higher than the Holocene average for an adjacent bog. Increased precipitation after ~2400 yrs BP may have contributed to the higher LORCA reconstructed for the late Holocene, but the increased precipitation did not coincide with any apparent changes in vegetation as inferred from pollen assemblages.

Introduction

The Hudson Bay Lowlands (HBL) is a vast, low-relief landscape of which >90% is a saturated peatland ecosystem with organic deposits ranging from <0.3 m to upwards of 4 m in thickness (Sjörs, 1959; Martini, 2006). The HBL peatlands have been developing since the middle Holocene following emergence of the underlying flat Paleozoic limestone platform from the Tyrrell Sea, the post-glacial precursor to modern day Hudson Bay. Since that time, a complex mosaic of patterned peatlands has resulted, extending over an area exceeding 325,000 km^2 (Riley, 2003).

The significance of HBL ecosystems lies in both ecology and biogeochemistry. Ecologically, the HBL represents an important repository of wetland plant species and associated food webs. The HBL extends from boreal-like conditions in the vicinity of James Bay to tundra conditions with continuous permafrost on the very northernmost coast of Ontario, yielding a diversity of landforms, vegetation communities, and associated wildlife habitats (Riley, 2011). In addition to the ecological importance of this region, it has significance in terms of the long-term storage of carbon derived from Holocene peatland development and in terms of its capacity as an ongoing carbon sink (Gorham, 1991; Martini, 2006). In light of these factors, and the vulnerability of the HBL to predicted rapid warming in the region (Tarnocai, 2006), it is critical to further develop our understanding of the functioning of these wetlands.

The paleoecological record provides an important opportunity to identify pathways of ecosystem development and drivers of change in HBL wetlands. Previous pollen or macrofossil studies of Ontario HBL peat cores from bog settings reveal a series of vegetation changes through the Holocene, generally consisting of a shift from a tidal marsh to a treed swamp, fen, or bog containing some fen indicators, and then to a non-forested *Sphagnum* bog, although with numerous local variations (Terasmae and Hughes, 1960; Klinger and Short, 1996; Kettles et al., 2000; Glaser et al., 2004). Although there are few studies, and they all focus on bog sites, available data suggest that drivers of long-term change in peatland vegetation in the HBL can be divided broadly into three factors: isostatic uplift, climate change, and autogenic succession.

Isostatic uplift has resulted in a series of new substrates for peatland initiation since the time of deglaciation, ~ 8000 yrs BP. The rate of isostatic uplift is spatially variable, with fastest rates in the southeast of the James Bay Lowland (Dredge and Cowan, 1989). These differential rates of uplift across the region drove changes in drainage networks in existing peatlands, resulting in spatial variability in vegetation history and peat accumulation (Glaser et al., 2004). The rate of uplift has also changed over time; the isobase maps of Andrews and Peltier (1989) suggest that the study site has been uplifted ~210 m since 7000 yrs BP. The rate was initially more rapid (>3 m century^{-1}), but as the post-glacial period continued, the rate slowed to its current value of ~1 m century^{-1}.

Paleoclimatic change is an important driver of vegetation change in wetlands (Singer et al., 1996). Since the initiation of the oldest peatlands in the HBL more than 7500 yrs BP, climate has changed on decadal to supra-millennial timescales. The middle Holocene is characterized by warmer temperatures and possibly drier conditions in many regions of northern Canada (e.g., Ritchie et al., 1983; Liu, 1990). Pollen-based temperature reconstructions and the presence of a thermophilous macrofossil at R Lake on the Sutton Ridges in the northern HBL suggest that there were warmer temperatures in the HBL in the mid-Holocene (McAndrews et al.,

1982; McAndrews and Campbell, 1993). Warmer temperatures at that time are also suggested by range extensions of *Pinus strobus* into northern Ontario (Terasmae and Anderson, 1970). Following this warming, pollen and macrofossil assemblages at R Lake suggest that temperatures cooled and conditions may have become wetter through the Neoglacial (McAndrews et al., 1982).

More recently, the shorter-term climatic changes surrounding the Medieval Warm Period (MWP) and Little Ice Age (LIA) also drove changes that affected HBL peatlands, including for example increased carbon accumulation during the MWP (Bunbury et al., 2012). Warmer temperatures promote biological productivity and potential for carbon accumulation, while drier conditions with lower water tables enhance decomposition and thereby reduce potential carbon accumulation. Thus, Holocene climate changes are important, and complex, factors affecting carbon accumulation in peatlands.

In addition to the allogenic drivers of isostatic rebound and paleoclimate change, autogenic change (successional processes internal to the peatlands), are also likely important drivers of change. These autogenic changes are related to the gradual accumulation of peat and vertical separation of living vegetation from the water table, resulting in decreased nutrient availability. They often are manifested in shifts from fen-like to bog-like conditions as nutrients become increasingly scarce as poorly decayed organic material builds up (Rydin and Jeglum, 2006). While these changes are continually taking place, they may be slowed or reversed any time by local allogenic factors or disturbance such as fire.

The available peat core stratigraphic records showing the vegetation history of Ontario's HBL peatlands as determined by pollen or macrofossils are limited to a small number of bog cores. These include a profile from an exposure along the Attawapiskat River (Terasmae and Hughes, 1960; Sjörs, 1963), a suite of cores in the vicinity of Kinosheo Lake (Klinger and Short, 1996; Kettles et al., 2000), and the Albany River, Oldman and Belec bog sites studied by Glaser et al. (2004) in the southern HBL (all sites shown in Fig. 1). Our
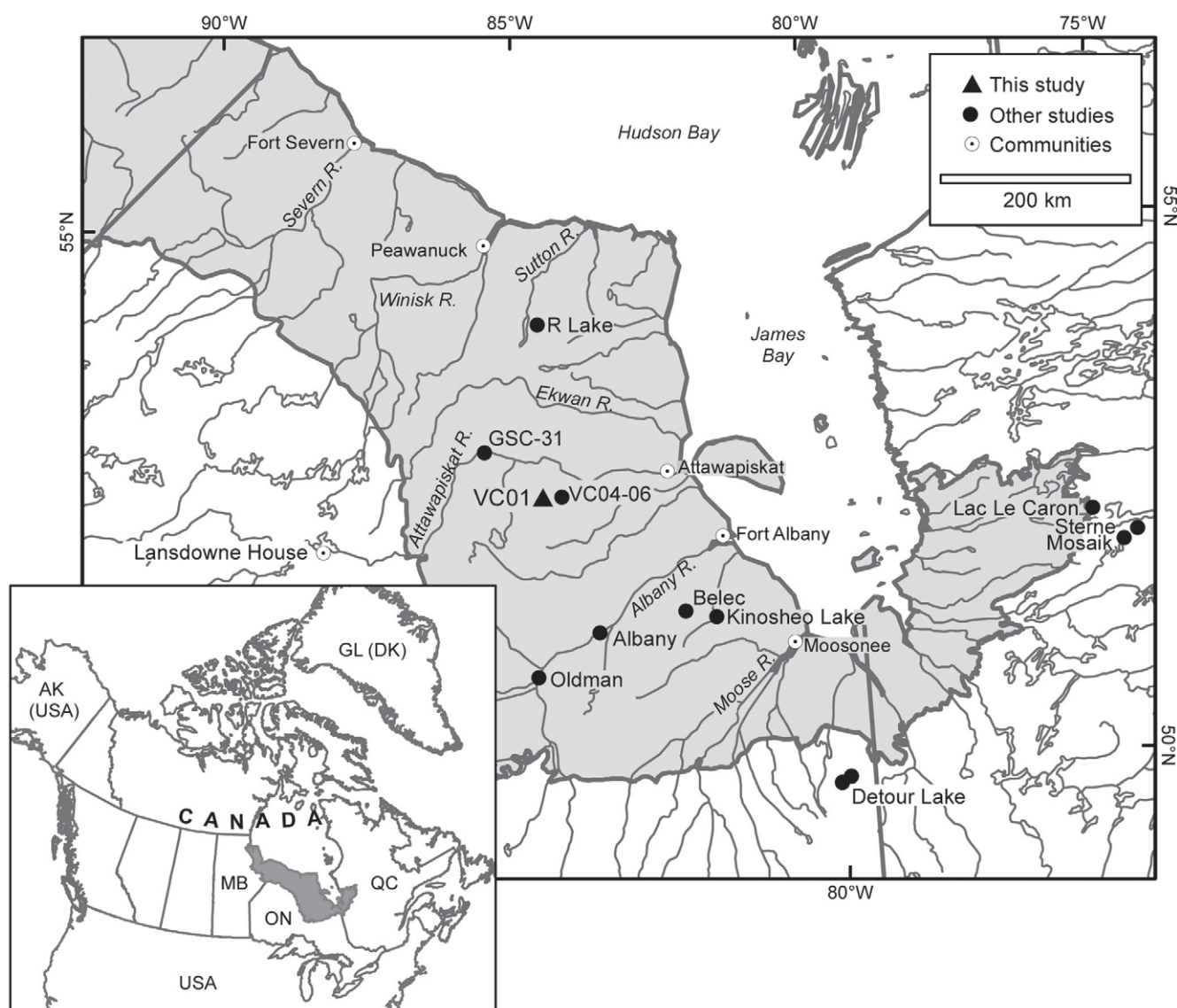
FIGURE 1. Canada's Hudson Bay Lowlands. The Victor Fen (VM-3-3) study site (labeled "VC01") is shown, along with other sites discussed in the text, including the Victor Bog (VC04-06/VM-4-3; Bunbury et al., 2012); R Lake (McAndrews et al., 1982); Oldman, Albany, and Belec bogs (Glaser et al., 2004); the Kinosheo bogs (Klinger and Short, 1996; Kettles et al., 2000); and the Eastmain region peatlands on the east side of James Bay (Loisel and Garneau, 2010; van Bellen et al., 2011a; van Bellen et al., 2011b).

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study presents a pollen record from a site in the central HBL classified as a fen with the goal of comparing the trajectory of fen development with general trends in paleovegetation and biogeochemistry of HBL bogs. The paleovegetation record derived from pollen assemblages is supplemented by analysis of carbon and nitrogen content, as well as peat humification. From those data, along with bulk density measurements and an age model based on radiocarbon dates, Holocene rates of carbon accumulation are presented for the fen core. The simultaneous presentation of both pollen and geochemical data from the same core permits analysis of the relationship between pollen assemblages and carbon accumulation. These results can then be compared to rates of isostatic uplift, paleoclimate data, and conceptual models of autogenic succession to elucidate the relationship through time between these drivers of change, peatland ecology, and carbon accumulation.

The calculations of the long-term rate of carbon accumulation (LORCA) are of particular importance as carbon-climate feedbacks are increasingly becoming integrated into Earth System models (e.g., Wania et al., 2009). The available pollen studies for Ontario's HBL do not provide calculations of LORCA, but calculated values for Holocene LORCA at bog sites in other northern peatlands in North America are generally in the range of 18–25 g C m^{-2} yr^{-1}, with considerable variability through time (Yu et al., 2010; van Bellen et al., 2011a). Turunen et al. (2002) reported that Finnish bogs had higher mean values for LORCA than fens, while the study of Botch et al. (1995) of Siberian peatlands reported higher values for fens. This study presents calculated LORCA for a fen site for comparison with that of an adjacent bog site (Bunbury et al., 2012) and with other northern peatlands. Unless otherwise indicated, all ages presented in the text refer to calibrated, calendar years before A.D. 1950.

Study Area

The Victor fen site is located in the Attawapiskat River watershed in the central HBL. Underlying bedrock consists of the Attawapiskat Formation, which is predominantly sedimentary carbonate rock (dolostone and limestone), with some sandstone, shale, and siltstone, and is of Middle to Lower Silurian age (Ontario Geological Survey, 1991). Deglaciation patterns, reconstructed using a radiocarbon database, indicate that the study site was deglaciated between 8600 and 8450 yrs BP (Dyke, 2004). The site then became covered by Lake Agassiz-Ojibway until the final abrupt drainage of this proglacial lake ~8200 yrs BP (Roy et al., 2011). Subsequently, this isostatically depressed region was flooded by the Tyrrell Sea marine incursion (Peltier and Andrews, 1983; Dredge and Cowan, 1989). The Tyrrell Sea reached its maximum extent between 7000 and 8000 yrs BP and then regressed with isostatic rebound (Lee, 1960; Dredge and Cowan, 1989). The sea laid down a silty clay, which was deposited as quiet water sediments at the study area (Fulton, 1995), and underlies the peat profile presented here from the Victor Fen site. The site lies adjacent to raised beaches or bars of glaciolacustrine, glaciomarine, or marine origin. These features are present northeast of the site (<10 km distant) and immediately southwest (<5 km distant), with many oriented north-northwest to south-southeast (Pala et al., 1991).

The Attawapiskat River watershed is located within the peatland and woodland floristic zone defined by Riley (2003). The peat coring site is a fen environment, in the context of a patterned peatland with nearby fens and bogs. The dominant vegetation in the immediate vicinity of the core site was categorized according to the Canadian Forest Ecosystem Classification. There was no coverage of trees taller than 10 m. The trees or shrubs between 2 and 10 m high were represented by *Larix laricina* and *Betula pumila*. There was herbaceous cover dominated by Cyperaceae, with *Menyanthes trifoliata* and bryophytes. Based on the classification of Riley (2011), the core site is considered a "Treed low-shrub fen".

Hudson Bay exerts a cooling effect on the surrounding Lowlands up to 500 km from the coast (Rouse, 1991). The climate is continental subarctic, characterized by long, cold and snowy winters, and short, warm summers. The closest representative climate station is located 260 km to the southwest of the study site at Lansdowne House, Ontario; it reports mean annual, January, and July temperatures of –1.3, –22.3, and 17.2 °C (Environment Canada, 2003). The study site is located ~90 km upriver from the closest coastline in the vicinity of Attawapiskat, Ontario. The study site falls within the zone of discontinuous permafrost in the scattered or sporadic subzone where permafrost occurs as islands in mostly unfrozen terrain (Hydrological Atlas of Canada, 1978). The study site is adjacent (separated by ~700 m) to the Victor bog site that was subject to a depth-to-water-table reconstruction based on testate amoebae, and calculations of LORCA (Bunbury et al., 2012). Further details on the study site can be found in O'Reilly (2011).

Materials and Methods

Complete cores through the peat sequence and into the Tyrrell Sea marine sediment were collected from the Victor Fen site (52.7123°N, 84.1714°W; 100 m a.s.l.; core code VM-3-3) in July 2009. The location was recorded with a handheld GPS. Permafrost was not encountered during the coring of the peatland, and the structure of the surface of the fen was uniform. The peat sequence extends to a depth of 245 cm, at which point the core grades into fine marine sediment. Peat cores were retrieved using a Jeglum box-type corer for the upper 35 cm and a Russian chamber corer of 5-cm diameter for the lower sections. Two Russian cores (the primary and replicate cores) were collected immediately adjacent to each other; the core breaks in the secondary core were offset to provide continuous sections over the core breaks in the primary core. The peat samples were wrapped in aluminum foil and drain pipe and stored in a cooler under refrigeration until analysis.

Samples of known volume from the top 20 cm of the box core were dried, weighed, and ground for measurement of ^{210}Pb activity by Flett Research (Winnipeg, Canada). Six peat samples from the primary Russian core were prepared for AMS radiocarbon dating by soaking in warm 5% KOH for 10 minutes, followed by sieving through a 90-µm nylon mesh and rinsing. Using a stereomicroscope, wood or conifer needles were then selected from each sample for dating at Beta Analytic (Miami, U.S.A.). Radiocarbon dates were calibrated using the program CALIB (v 6.0.1) and the INTCAL09 calibration curve (Reimer et al., 2009) for presentation in Table 1. The age-depth model was developed using a smooth spline model with spar = 0.3 in the *clam* package (Blaauw, 2010) implemented in R (R Development Core Team, 2011).

Contiguous subsamples spanning 3 cm in the core (dimensions: 3 cm × 1 cm × 1 cm) from the replicate core were prepared for bulk density measurements by extracting samples of known volume using a block and blade tool, and drying them to constant mass at 60 °C. Subsamples for elemental carbon (C) and nitrogen (N) content were taken from the main core; these were dried to constant mass and then ground to a fine powder and analyzed on an ESC 4010 Elemental Combustion System for CHNS-O (configured only for C and N) (Costech Analytical Technologies, Valencia, California,

U.S.A.). LORCA values were obtained by multiplying % C data by bulk density to retrieve carbon density (in g cm^{-3}) and then multiplying by the accumulation rate in cm yr^{-1}, as defined by the age-depth model, resulting in a value in g C cm^{-2} yr^{-1}, which was then converted to g C m^{-2} yr^{-1}.

Wet samples were taken from the primary core for peat humification analysis, which followed a protocol modified from Blackford and Chambers (1993). Samples were dried to constant weight at 60 °C and then ground. Samples of 0.2 g were then digested in 8% NaOH on a hotplate for 45 minutes and then centrifuged. The supernatant was filtered through a Whatman No. 1 filter paper, and then absorbance at 540 nm was measured on a spectrophotometer.

Standard methods for pollen processing were used (Fægri and Iversen, 1989), involving digestion in 10% HCl, 10% KOH, and acetolysis. Three samples at the base of the core necessitated treatment with concentrated HF because they were clay-rich. The remaining organic samples did not require treatment with HF for adequate concentration of grains. All samples were sieved through coarse (150-μm) and fine (10-μm) nylon sieves, stained with safranine, dehydrated with tert-butyl alcohol, and mounted in silicone oil. A known number of exotic *Lycopodium* marker spores were added to estimate pollen concentration (grains cm^{-3}) and influx (grains cm^{-2} yr^{-1}). Pollen grains were identified and enumerated using a combination of bright-field and differential interference contrast (DIC) microscopy at 400× magnification. Identification keys of McAndrews et al. (1973) and Kapp et al. (2000) were used, in addition to reference collections housed at University of Toronto and at the Royal Ontario Museum. For *Picea*-type pollen grains, grains with maximum diameter >110 μm were assigned to *P. glauca*, whereas smaller grains were assigned to *P. mariana* (Klinger and Short, 1996; Lindbladh et al., 2002).

Pollen percentages were calculated based on a main sum consisting of tree, shrub, and herb pollen, and excluding aquatics and spores. The average main sum was 268 grains (range = 221–329). Percentages for the, at times, very abundant local aquatic taxa (Cyperaceae, *Sphagnum*, *Typha* spp.) were based on the total number of pollen grains counted, i.e. [main sum] + [all other taxa]. Pollen zones were established using stratigraphically constrained hierarchical cluster analysis of percentage data (Grimm, 1987), and the significance of the zones was assessed using the broken stick technique (Bennett, 1996), and implemented using the *chclust* algorithm in *Rioja* (Juggins, 2009).

Paleoclimate reconstructions derived from the fossil pollen assemblages were produced using the Modern Analog Technique (Overpeck et al., 1985), implemented in the program C2 (Juggins, 2010). Mean annual air paleo-temperature (MAT) and total annual paleo-precipitation (TAP) were calculated by combining 17 fossil pollen taxa from 41 levels with two sets of data extracted from the North American Modern Pollen Database (Whitmore et al., 2005). The first subset included all sites in the modern database with pollen sums of 100 or more grains (3680 sites), whereas the second set included only those sites with pollen sums of 100 or more from wetland environments (303 sites). Taxa present in <0.5% abundance in the fossil data set were considered rare and removed from the analysis, as were aquatic pollen taxa and types that were not present in the modern data set; this resulted in the removal of *Drosera*, *Polypodium*, *Potamegeton, Tsuga*, *Typha* spp., and Tubuliflorae. Dissimilarity between the fossil and modern assemblages was measured using the squared chord distance (SCD; Overpeck et al., 1985). Climate estimates presented are the average of the top three analogs; multiple analog matches per sample reduce stochasticity and improve the precision of reconstructions (Williams and Shuman, 2008). Model performance was assessed via bootstrap cross-validation (500 iterations). *Picea glauca* and *P. mariana* were amalgamated for the reconstructions as they were not differentiated at most sites in the modern database.

Results

CORE CHRONOLOGY

Samples from the surface to a depth of 20 cm were submitted for measurement of activity of ^{210}Pb for dating purposes. The activity of the radioisotope remained nearly constant through the profile (data not shown), suggesting an ongoing groundwater-supplied input of unsupported ^{210}Pb to the upper section of the peat core. Therefore, a ^{210}Pb-based chronology could not be obtained. Inability to date recent fen peats with ^{210}Pb has been noted elsewhere (Urban et al., 1990). Thus, the age-depth relations for the core were developed based on six AMS radiocarbon dates (Table 1; Fig. 2). Initiation of peat accumulation at the site had taken place before 6420 yrs BP, as indicated by a radiocarbon date on conifer needles at a depth of 242.5 cm, close to the base of the peat deposit at depth 245 cm. The age-depth model shows significant changes in the rate of peat accumulation at the site during the Holocene, with a slower rate of accumulation from initiation until 1500 yrs BP, followed by more rapid accumulation up to present day. The age model suggests, in addition to a general increase in accumulation since 1500 yrs BP, a peak in accumulation around 1200 yrs BP

TABLE 1

AMS radiocarbon dates obtained from the VM-3-3 Victor Fen core. Radiocarbon dates were calibrated using the program CALIB (v 6.0.1) and the INTCAL09 calibration curve (Reimer et al., 2009).

| Laboratory number	Sample depth (cm)	Dated material	Conventional ^{14}C age (^{14}C yrs BP)	2-σ calibrated age (yrs BP)	Median calibrated age (yrs BP)	^{13}C/^{12}C Ratio (‰)
Beta-286595	37–38.5	Conifer needles	580 ± 40	577–653	600	–28.7
Beta-281774	60–61	Imbedded twig	1250 ± 40	1076–1276	1200	–26.2
Beta-281775	120–121	Wood	1660 ± 40	1507–1633	1560	–26.8
Beta-286596	157–158.5	Conifer needles	2730 ± 40	2756–2890	2820	–28.5
Beta-281776	194–195	Wood	5050 ± 40	5710–5908	5810	–26.9
Beta-281777	241.5–243.5	Conifer needles	5640 ± 40	6315–6494	6420	–28.6
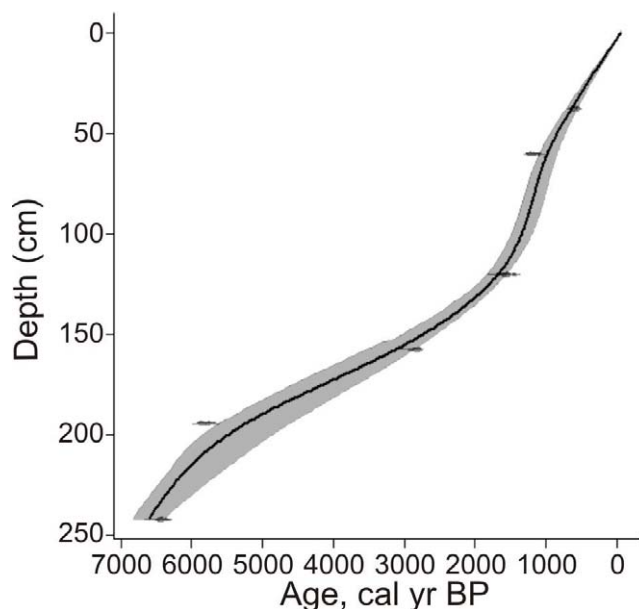
FIGURE 2. Age-depth model for the VM-3-3 Victor Fen core. The model is based on six AMS radiocarbon dates (Table 1) and was developed using a smooth spline model with spar = 0.3 in the clam package (Blaauw, 2010) implemented in R (R Development Core Team, 2011).

(Fig. 3). This peak corresponds to the inflection point in the age-depth model (Fig. 2).

PEAT STRATIGRAPHY

Mean bulk density for the VM-3-3 fen core is 0.09 g cm^{-3}, with some variability through the record and a notable decrease in the upper portion of the core that corresponds to the acrotelm-catotelm boundary (Fig. 3). Surface values for the carbon to nitrogen (C:N) quotient are about 25, close to average for sedge peat (Rydin and Jeglum, 2006), and are considerably lower than the mean value of 58 recorded for a bog adjacent to this site (Bunbury et al., 2012). The C:N quotient in the uppermost section of the core shows a decrease from surface values of 33 to minimum values of ~15 between depths 20 and 40 cm. This drop in C:N quotient is commonly observed in peat cores and results from the concentration of N as C is lost through decomposition in this relatively more aerated uppermost section of the profile (Malmer and Holm, 1984; Belyea and Warner, 1996). The % N profile shows a concomitant increase from the uppermost sample to depths 20–40 cm. The C:N quotient curve shows a small rise below 40 cm depth, indicating that the probable average position of the acrotelm-catotelm boundary lies above that point (Malmer and Holm, 1984), at around 25 cm depth in this core. The location of this boundary around the core depth of 25 cm is also suggested by the decrease in bulk density and in peat humification at that horizon (Fig. 3).

The average C content in the core is 45.9% ± 1.97. The lowest values (37.7%) are found in the uppermost samples; % C then increases down-core and stabilizes at about 47% at the acrotelm-catotelm boundary. The carbon content shows a gradual decline to the base of the core (Fig. 3). The average N content is

2.39% (±0.44), and is stable through much of the record. There is a notable excursion in C, N, and C:N quotient between ~5000 and 5800 yrs BP, with a peak in C:N and drop in N (Fig. 3). This excursion corresponds closely to a peak in relative and absolute abundance of *Sphagnum* spores (see below).

Peat humification as estimated by spectrophotometric absorbance increases with depth through the acrotelm as decomposition proceeds through the more aerated portion of the core (Fig. 3). Humification values below the acrotelm-catotelm boundary at ~25 cm in the core are variable through the Holocene, with highest values in the lowermost sections of the core. Humification values are correlated both to % C ($r = 0.76$) and to % N ($r = 0.52$), but these correlations are driven mainly by the strong relationship in the acrotelm (Fig. 3).

The age-depth model, inferred accumulation rates, bulk density, and carbon content were used to calculate LORCA (Fig. 3). The average LORCA for the whole record is 22.8 g C m^{-2} yr^{-1}. The rate is initially high (>25 g C m^{-2} yr^{-1}) for the first few centuries of the record (6300–6600 yrs BP), then slows to <15 g C m^{-2} yr^{-1} until about 1500 yrs BP. Concomitant with the increase in rate of peat accumulation (Fig. 2), LORCA then increases considerably, peaking at about 70 g C m^{-2} yr^{-1} at 1150 yrs BP. LORCA then slows, averaging about 15 g C m^{-2} yr^{-1} for the top 25 cm of the core, corresponding to the acrotelm (Fig. 3).

POLLEN BIOSTRATIGRAPHY

A total of 44 levels was analyzed for pollen assemblages (Fig. 4). The core section from 224 to 226 cm depth contained an overabundance of *Betula* pollen grains (>90% of the pollen sum, compared to average percentages of 13% in the rest of the core), suggesting the possibility of the deposition of a full polleniferous *Betula* catkin into the peat (Fægri and Iversen, 1989). Therefore, two samples in that section of the core were omitted from the analysis and diagram, leaving 42 samples. Pollen preservation was good throughout the core, with an average pollen concentration of 57,260 grains mL^{-1} (range = 9580–339,790 grains mL^{-1}). The age-depth model and concentration data were used to calculate and then plot pollen influxes (Fig. 5). Stratigraphically constrained clustering coupled with broken stick analysis produced three significant pollen zones (Zones 1, 2, and 3). We also designate subzones within Zones 1 and 2. Although the subzones were not significant in the broken stick analysis of the clusters, they correspond to the divisions in the dendrogram immediately following the significant zones.

Zone 1 (237–256 cm; 6600–6500 yrs BP)

The basal Zone 1 is divided into two subzones. Subzone 1a is represented by two samples in the uppermost marine sediment, and it contains an assemblage indicative of a fen or tidal marsh, as shown by the importance of pollen of Chenopodiaceae, Cyperaceae, and *Equisetum,* and the presence of *Potamogeton* and *Sparganium*-type pollen. Subzone 1b includes the two lowermost samples in the peat sequence. The pollen assemblages of Subzone 1b suggest the initial peat-forming vegetation was characteristic of a fen or tidal marsh environment dominated by Cyperaceae and *Typha*. Percentages of *Sphagnum* spores remain low throughout this zone. Conifer needles recovered from the basal peat section (Table 1) suggest local presence of trees; the pollen record suggests the local tree community contained *Betula, Larix,* and *Picea* (Fig. 4). *Pinus banksiana* may have been
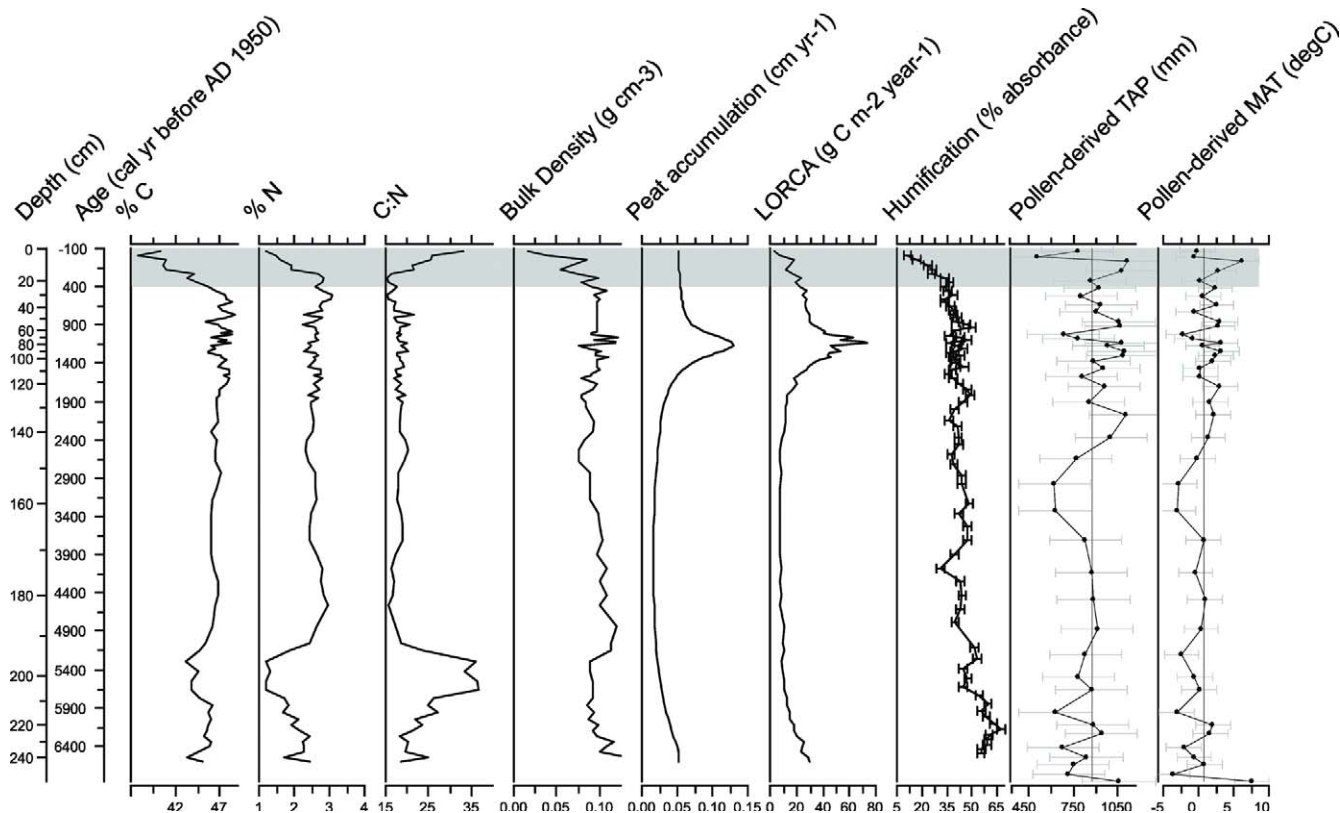
FIGURE 3. Peat and carbon stratigraphy for the VM-3-3 Victor Fen core. Values for peat accumulation were derived from the age-depth model (Fig. 2), and are used with bulk density and carbon content to calculate LORCA. Also shown is peat humification, as determined by spectrophotometric absorbance, and pollen-based paleoclimate reconstructions. The reference line on the total annual precipitation (TAP) curve corresponds to the modern value for TAP (700 mm); the reference line on the mean annual temperature (MAT) curve corresponds to the modern value (1.3 °C). Gray error bars on the pollen-derived TAP and MAT reconstructions correspond to the RMSEPs of the reconstructions (Table 2).

present locally in small numbers similar to at present, although modern pollen rain studies show that its pollen is strongly over-represented (Farley-Gill, 1980).

The pollen influx diagram aids in distinguishing between changes in relative abundances of different groups and absolute changes in the amount of pollen supplied to the peat. The influx diagram (Fig. 5) suggests that absolute amounts of local tree pollen were low throughout Zone 1, and pollen influx was mainly derived from salt marsh or fen taxa, principally Chenopodiaceae, Cyperaceae, *Salix*, and *Typha*. The larger percentages of *Pinus banksiana*–type pollen relative to other trees in Zone 1, and relative to *P. banksiana* percentages in overlying sections in the core, are likely mainly a regional signal as *P. banksiana* is not abundant locally and influx values remain low through Zone 1 (Fig. 5).

Zone 2 (17–237 cm; 6500–263 yrs BP)

Zone 2 is the pollen zone spanning the longest time period of the three zones (Fig. 4). The long persistence of the Zone 2 assemblages is indicative of stable Holocene vegetation at this site. Despite broadly similar pollen assemblages throughout the zone, a subzone boundary was established to discuss the only minor change in assemblages in the zone. Zone 2 is characterized by the disappearance of *Typha*, which dominated Zone 1, and a decline in Cyperaceae. In Subzone 2a, there is an increase in

pollen of the bog indicators *Sphagnum* and Ericaceae. Subzone 2b is delineated on the basis of an increase in percentages of Cyperaceae and *Larix* pollen, the reappearance of *Equisetum*, and a decrease in *Sphagnum* spores. Arboreal pollen throughout Zone 2 is dominated by *Picea* with lower representation of *Pinus, Alnus, Betula,* and *Salix*, all in relatively stable proportions (Fig. 4).

Zone 3 (0–17 cm; 263 yrs BP–A.D. 2009)

The uppermost zone is characterized by further increases in Cyperaceae and decreases in *Sphagnum* and *Picea* (Fig. 4). Small rises in *Alnus* and *Betula* pollen are also recorded. An "*Ambrosia* rise" is also apparent in Zone 3 and is accompanied by small increases in pollen of Chenopodiaceae. *Ambrosia* is not found locally (Riley, 2011) but a long-distance transport signal has been noted in other HBL pollen diagrams (Terasmae and Hughes, 1960; Klinger and Short, 1996; Kettles et al., 2000; Glaser et al., 2004). Pollen of temperate trees is present through the record, indicating long-distance transport of regional pollen types such as *Acer, Juglans,* and *Quercus* (Fig. 4).

PALEOCLIMATE RECONSTRUCTIONS

Two modern pollen subsets extracted from the data set of Whitmore et al. (2005) were combined with the fossil pollen
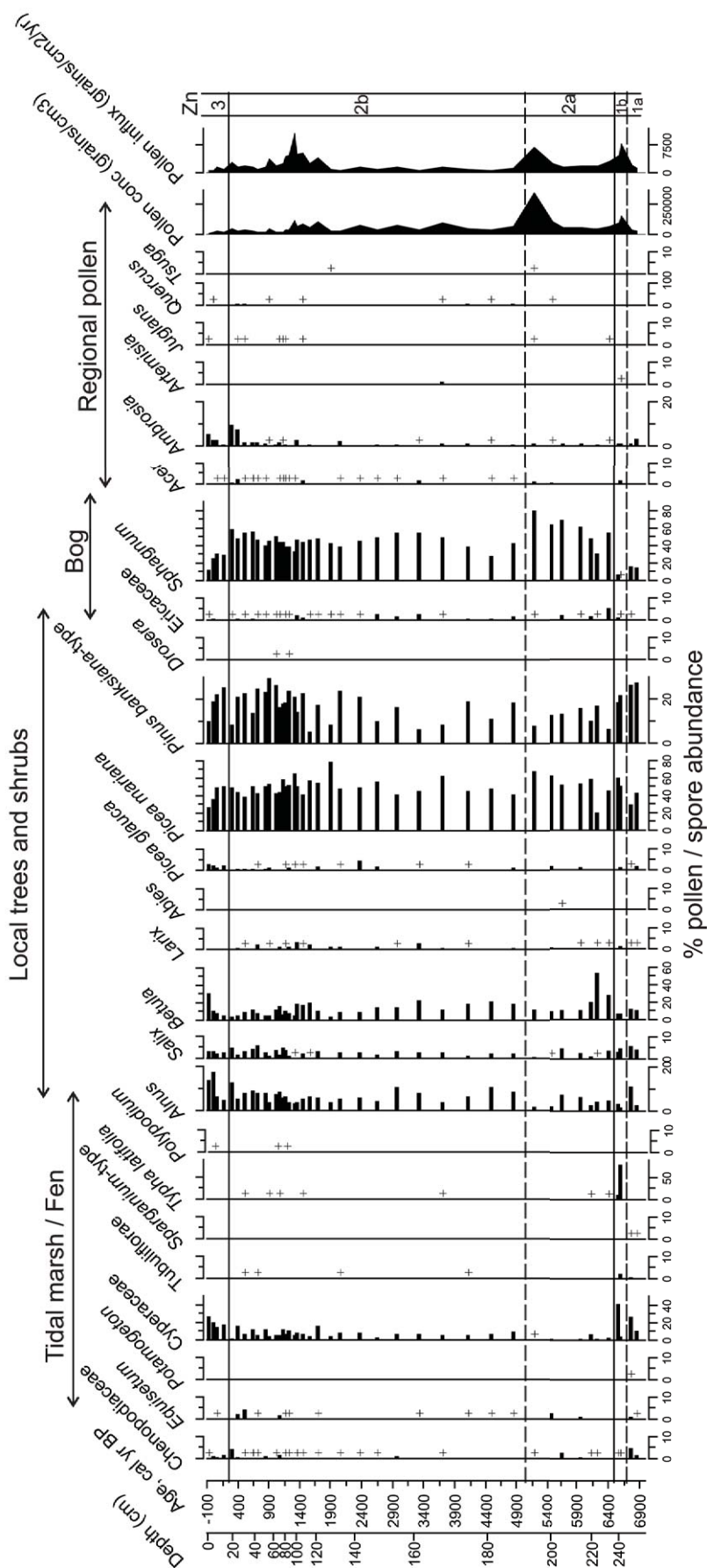
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FIGURE 4. Percent pollen diagram for VM-3-3 Victor Fen core. Note that scaling varies. The column labeled "Zn" indicates pollen zonation, as defined by stratigraphically constrained cluster analysis. The main divisions between zones 1, 2, and 3 were significant based on the broken stick method. The "Local trees and shrubs" category refers to taxa that are known to occur in the region today (Riley, 2003, 2011); it is possible, however, that the percentages of those taxa contain grains that were deposited via long-distance transport. Analyst: B. O'Reilly.

data from Victor Fen core VM-3-3 to derive pollen-based estimates for MAT and TAP. The $r^2_{(boot)}$ generated by the models indicates that the predictive ability is better for temperature estimates than precipitation, and that the 3680-site data set outperforms the 303-site data set (Table 2). The $r^2_{(boot)}$ statistic represents the strength of the relationship between the observed and predicted values and can be used to compare models that reconstruct different environmental variables (Birks, 1998). The maximum biases [max bias$_{(boot)}$] are high for both models due to the wide range of temperature and particularly precipitation values. Low dissimilarity values (SCD) between the modern and fossil samples from the 3680-site data set suggest that the reconstructions generated using this modern calibration set are the most reliable.

The reconstructed total annual precipitation (Fig. 3) shows generally lower values from the base of the core until ~2400 yrs BP, after which time precipitation increased. The reconstructed temperature curve shows little systematic change through the record, other than a drop in temperature between 2700 and 3400 yrs BP, coinciding with relatively drier conditions in the precipitation reconstruction. The data point at the base of the reconstruction indicates warm and dry conditions, but is likely mostly a result of the presence of pollen taxa deposited through long-distance transport. This idea is supported by the very low influxes of the taxa used in the reconstruction in this sample (Fig. 5). The same difficulty was reported by McAndrews and Campbell (1993) in a reconstruction from R Lake in the northern HBL, in which anomalously high temperatures were reconstructed due to high abundances of non-local pollen.

Discussion

CARBON ACCUMULATION

The peat and carbon stratigraphy in the Victor Fen core are similar in many respects to other northern peatlands. The mean bulk density of 0.09 g cm^{-3} is the same as the mean value recorded in a bog core situated ~700 m away (Bunbury et al., 2012) and is similar to that recorded at other northern peatlands (Gorham, 1991). The mean peat carbon content of 45.9% in the

TABLE 2

Performance statistics for Modern Analog Technique paleoclimate reconstructions based on pollen assemblages in the VM-3-3 Victor Fen core, using two possible modern pollen training sets from the North American Modern Pollen Database (Whitmore et al., 2005) (N = 3680 sites; N = 303 sites). RMSEP: root mean squared error of prediction. MAT: mean annual air paleo-temperature; TAP: total annual paleo-precipitation. Note the high values for max bias$_{(boot)}$ for TAP; these are due to very high values in the training set (up to 4100 mm).

Variable	$r^2_{(boot)}$	Max bias$_{(boot)}$	RMSEP
3680 sites			
MAT (°C)	0.93	5.29	2.47
TAP (mm)	0.75	2447	243
303 sites			
MAT (°C)	0.92	5.18	3.09
TAP (mm)	0.55	2502	281

Victor Fen core is somewhat lower than that reported for other boreal or subarctic peatlands (51.7%, Gorham, 1991; 51.8%, Vitt et al., 2000; 52.7%, Turunen et al., 2001; 52%, Beilman et al., 2009) but is also the same as that recorded in the nearby bog core (46%, Bunbury et al., 2012). The average N content (2.39%) is close to the average for intermediate fens (2.52%) studied by Bridgham et al. (1998) and close to the mean given for sedge peats (2.2% and 2.1%) from northwestern and northeastern Ontario by Riley and Michaud (1989) and Riley (1994). The core from the nearby bog site (Bunbury et al., 2012) and the bogs reported on by Bridgham et al. (1998) had a significantly lower N content (on average 1%), a finding which serves to emphasize the large difference between the two nearby sites in terms of peatland type.

The calculated Holocene mean value for LORCA (mean; range: 22.8; 3.48 – 73.2 g C m^{-2} yr^{-1}) is broadly similar to that recorded for other northern peatlands (e.g., Yu et al., 2010; van Bellen et al., 2011a) and is somewhat higher than the Holocene mean recorded for the nearby bog site (mean ± SD, 18.9 ± 7.32 g C m^{-2} yr^{-1}; Bunbury et al., 2012). The fen site reported on here and the bog site of Bunbury et al. (2012) have similar basal peat dates (6600 yrs BP at the fen site compared to 6670 yrs BP at the bog site), but there has been less vertical peat accumulation at the fen site compared to the bog site (245 cm vs. 319 cm). Despite LORCA values at the fen site that are on average higher than the bog site, the portion of the record spanning 6600 to 1500 yrs BP was characterized by lower LORCA at the fen site (~13 g C m^{-2} yr^{-1}), resulting in an overall lower peat accumulation up to present day, relative to the bog site. The differences between the two sites in terms of Holocene variability in LORCA and overall accumulation suggest an important role for highly local hydrological factors in determining the rate and absolute amount of carbon accumulated. The origins of fen and bog systems in close spatial proximity may lie in underlying topography or in the slow evolution of drainage patterns in this low-relief region which has been subject to major isostatic uplift (Riley, 2003; Rydin and Jeglum, 2006). Such small-scale variability in peat depth and carbon accumulation shows some of the complexity of modeling the total carbon accumulation in a region such as the HBL. Similar variability in peat accumulation rates at sites situated in the same region have also reported in a study of peatlands in James Bay Lowland of Quebec (Loisel and Garneau, 2010).

The values for LORCA for the Victor Fen site are also highly variable through the Holocene as a result of the large changes in rate of peat accumulation suggested by the age-depth model (Fig. 2). LORCA is relatively high at the beginning of the record, and this is also recorded in the nearby bog site (Fig. 6; Bunbury et al., 2012). In both records, biological proxies suggest fen-type systems during these early periods of higher LORCA; high rates of carbon accumulation for early-successional fens (Botch et al., 1995; Charman, 2002) and tidal marshes have been recorded elsewhere (Pendea and Chmura, 2012). Following the period of initially higher accumulation, the time period between 5500 and 2500 yrs BP is characterized by minimum values for LORCA. The late Holocene is associated with increases in LORCA, for both this record and that of the nearby bog site (Fig. 6). This finding can be compared with other studies showing maximum rates of peat accumulation in a synthesis of northern peatland records in the early Holocene (Yu et al., 2009; Yu, 2011), and in northern Quebec during the middle Holocene (van Bellen et al., 2011a, 2011b). It must be
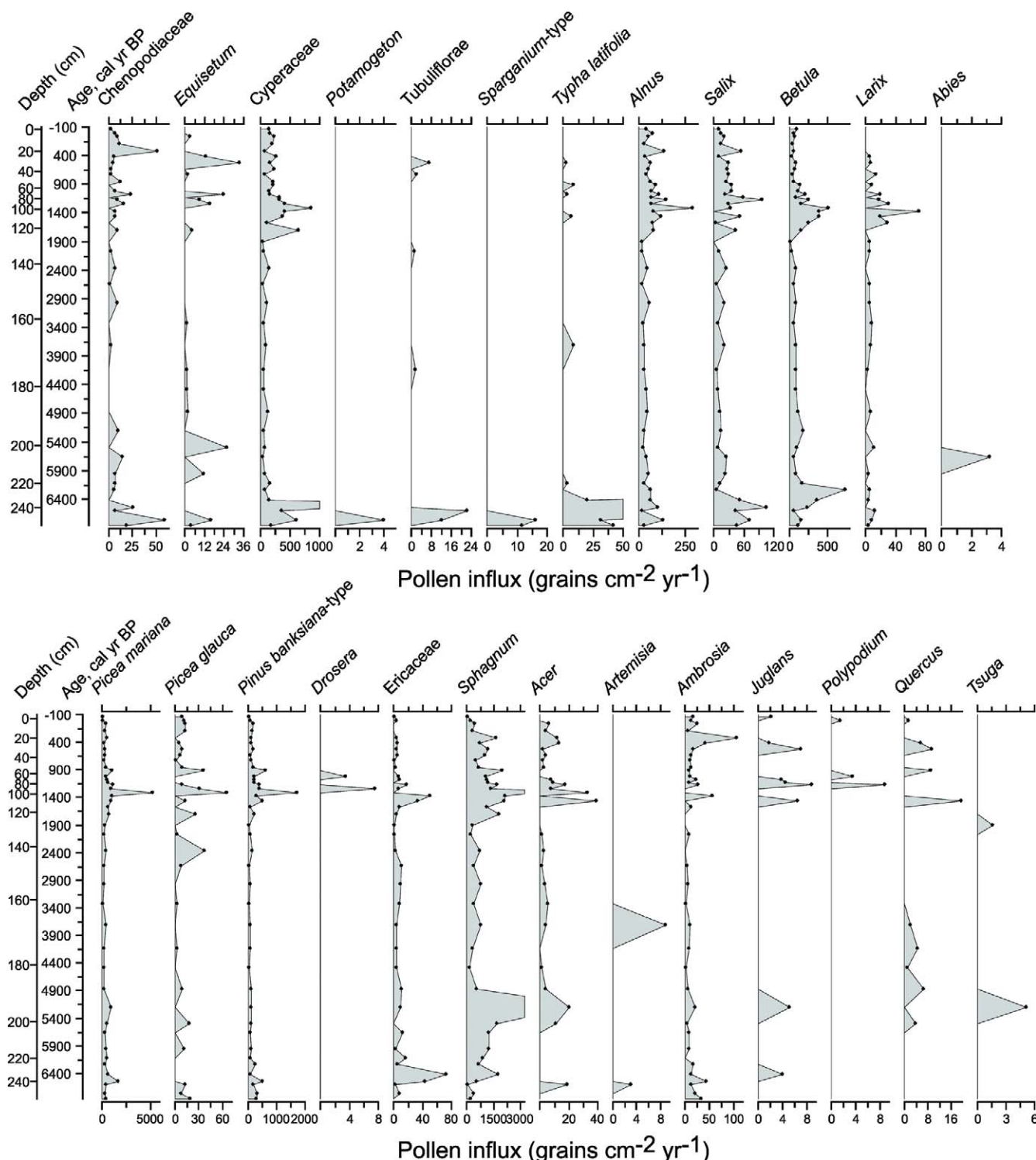
FIGURE 5. Pollen influx diagram for VM-3-3 Victor Fen core. Zero values are not plotted. Note that scaling varies. The x-axis axis for Typha is truncated at 50 grains cm⁻² yr⁻¹ (values for Typha influx in the two samples between 6560 and 6610 range from 1000 to 5300 grains cm⁻² yr⁻¹); the x-axis for Sphagnum is truncated at 3000 grains cm⁻² yr⁻¹ (values for Sphagnum influx exceed 3000 grains cm⁻² yr⁻¹ at two levels, at 1320 yrs BP [4570 grains cm⁻² yr⁻¹] and 5205 yrs BP [6200 grains cm⁻² yr⁻¹]); the x-axis for Cyperaceae is truncated at 1000 grains cm⁻² yr⁻¹ (one sample, at 6560 yrs BP, had an influx of 3270 grains cm⁻² yr⁻¹).

noted however, that Ontario's HBL peatlands differ from the majority of sites discussed by Yu (2011) and Yu et al. (2010) in terms of their relatively late initiation (after 7000 yrs BP). The pollen record of local vegetation change, and paleoclimate data, aid in the interpretation of this variability.

VEGETATION RECONSTRUCTION

The inorganic sediment underlying the peat deposit at this site contains a local pollen assemblage indicative of brackish conditions and a tidal marsh. Similar assemblages were reported in

basal peats at three HBL sites along the Albany River (Glaser et al., 2004) and along the Attawapiskat River (Terasmae and Hughes, 1960), and correspond to a coastal system immediately following uplift from the sea. These conditions abruptly shifted around 6700 yrs BP to a *Typha*-dominated marsh, which persisted for 1–2 centuries. The high abundance of *Typha* pollen in the basal peat suggests a role for the rapid isostatic uplift of the time (Andrews and Peltier, 1989) in isolating the site from brackish conditions. The high productivity associated with tidal and *Typha*-dominated marsh systems is reflected in the high value for LORCA in the early portion of the core (Fig. 3).

Pollen Zone 2 is characterized by the relatively abrupt development of a poor fen system, with *Sphagnum* spore abundance increasing from 7% to >50% in about a century (Fig. 4), and a marked decrease in % N in the peat (Fig. 3). These changes suggest the development of a more nutrient-limited peatland. Rapid isostatic rebound rates at this time (2.65–3 m century^{-1}; Andrews and Peltier, 1989) suggest a possible role for rebound in isolating the peatland to some extent from minerotrophic inputs around 6500 yrs BP. Differential rates of uplift across the HBL would likely affect local and regional hydrologic gradients, as suggested by Glaser et al. (2004) for a series of bog sites in the southern HBL, perhaps in a step-wise fashion as thresholds are reached which could reorganize drainage. While this site has had fen-like characteristics throughout its Holocene history, suggesting a persistently high water table, continued peat vertical growth may have reduced to some extent the influence of more nutrient-rich groundwater (Rydin and Jeglum 2006). These two processes,

differential isostatic uplift and vertical peat accumulation, may have both contributed to the shift towards a vegetation assemblage more characteristic of nutrient limitation.

The pollen assemblages of Zone 2 suggest the persistence of a poor fen community for several millennia. The record does not show the fen-to-bog transition recorded in the palynological records from present-day bog sites in the HBL (Terasmae and Hughes, 1960; Klinger and Short, 1996; Kettles et al., 2000; Glaser et al., 2004). While some bog indicators are present, they are at lower abundance. Ericaceae, for example, reach at most ~2% in this record, whereas in the bog records of Glaser et al. (2004), Ericaceae reach upwards of 40–50%. The pollen assemblages of Zone 2 are similar to contemporary surface pollen spectra at a series of fen sites in southwestern James Bay Lowland (Farley-Gill, 1980). After ~5000 yrs BP, % N increases (Fig. 3), along with pollen abundances of the minerotrophic indicators Cyperaceae and *Larix* (Fig. 4), suggesting enhanced minerotrophic inputs from that time. Thus, this first pollen record from an HBL fen site shows ongoing minerotrophic influences and associated long persistence for fen-type vegetation. The stable peat humification (Fig. 3) through Zone 2 further supports the idea of uniform peat type and little change in the degree of decomposition. After about 2500 yrs BP, the carbon stratigraphy (Fig. 3) indicates enhanced rates of peat and carbon accumulation. These increases are not matched by a concomitant vegetation change, suggesting other drivers for increased vegetation production, leading to increased LORCA.

The uppermost pollen Zone 3 is marked by a further increase in fen indicators and a marked decrease in the abundance of *Sphagnum*
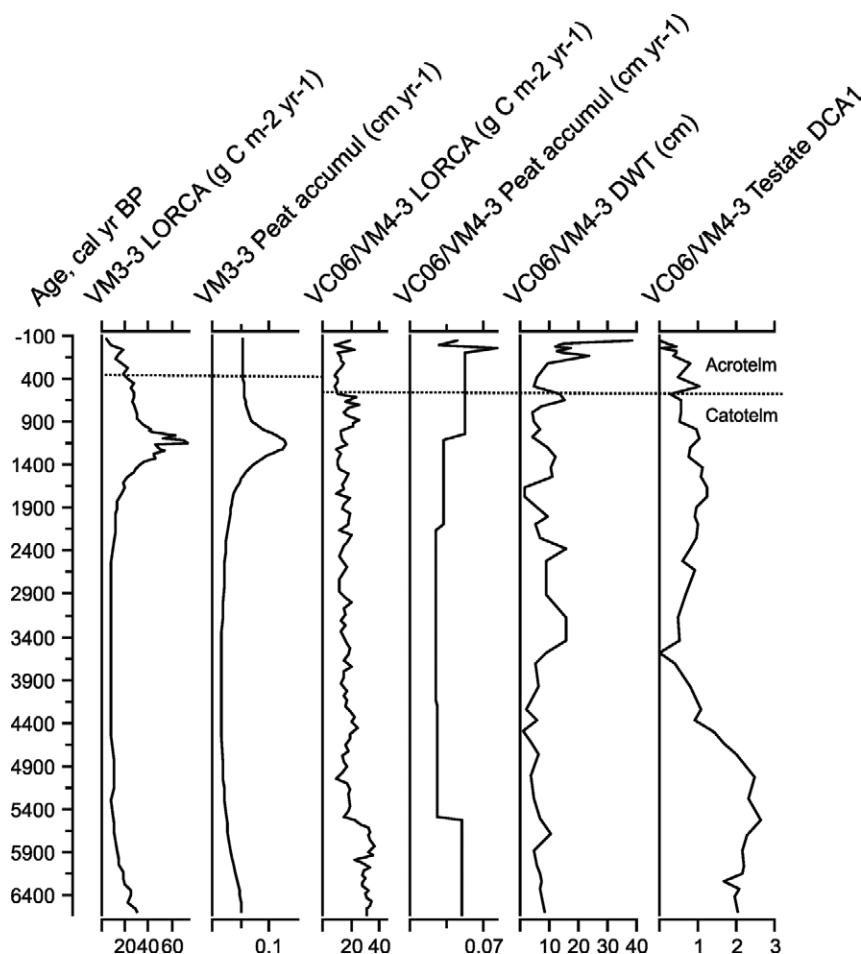

FIGURE 6. Comparison of LORCA and rates of peat accumulation for the VM-3-3 Victor Fen site (this study) and the VC06 (VM-4-3)Victor bog site located ~700 m away. Also shown are depth to water table reconstruction inferred from testate amoebae assemblages for the Victor bog and the ordination axis scores for those testate amoebae (DCA axis 1). Source for data from the Victor Bog: Bunbury et al. (2012).

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spores over the past two centuries. These changes are particularly evident over the past 100 years. Percent *Sphagnum* spores in the uppermost two samples approach the minima observed in the tidal marsh zone in pollen Zone 1 at the base of the record. Other recent changes in terms of local pollen taxa include increases in *Alnus* and *Betula*, also suggestive of increasingly minerotrophic conditions (Riley, 2011). Further work is required to identify the drivers of these recent shifts, but there is a clear signal in the pollen record of recent vegetation change following several millennia of stasis. Possible explanations for these recent changes include anthropogenic climate warming, and although supporting data for the HBL are not available, increased atmospheric loading of nitrogen has been recorded elsewhere in the northern hemisphere and this could affect vegetation composition. The interpretation of LORCA in pollen Zone 3 is complicated by the fact that this zone is located within the acrotelm. As decomposition rates are much higher in this portion of the core, the rates of peat or carbon accumulation are not directly comparable to those in the catotelm. Our interpretation of this zone is also complicated by the fact that *Alnus* and *Betula* are large pollen producers and part of the signal could reflect long-distance transport.

ROLE OF CLIMATE

The pollen record also provided data to run a quantitative paleoclimate reconstruction using the modern analog technique. The larger subset of the modern pollen database gave the more robust reconstruction, but among the 3680 modern sites included, there were few analogs actually used. Only 22 unique analogs were selected, out of 123 potential analogs (top 3 for each of the 41 fossil pollen samples). There are few modern samples that are similar to the fossil assemblages in the Victor Fen record. For example, only 26 sites in the modern database had >50% *Sphagnum* spores, yet *Sphagnum* is the most abundant taxon in the Victor Fen record. Furthermore, there are various differences between analysts in pollen sum used to compute *Sphagnum* percentages, making analog matching more difficult.

Despite these difficulties, the reconstructions provide curves broadly similar to the paleoclimate record derived from R Lake (McAndrews et al., 1982; McAndrews and Campbell, 1993; Bunbury et al., 2012). Notably, there is little change in temperature and there is an increase in precipitation after ~2400 yrs BP. Reconstructed depth to the water table also decreased at the nearby bog site around this time (Fig. 6; Bunbury et al., 2012), further supporting the establishment of locally wetter conditions in the Attawapiskat watershed in the late Holocene. Wetter conditions in the late Holocene have been reported in numerous other regional paleoclimate records, including those from sites in northern and central Quebec, east of Hudson Bay (Garalla and Gajewski, 1992; Ali et al., 2009). These wetter conditions coincide with the increase in peat accumulation and in LORCA at Victor Fen site and at the nearby Victor Bog site (Bunbury et al., 2012), suggesting an important role for moisture conditions in LORCA. Surprisingly, the peat humification curve (Fig. 3) does not decrease to reflect an increase in the water table position and resulting decline in degree of peat decomposition following 2400 yrs BP. This finding indicates that peat humification measured in this way is not always sensitive enough to track changes in degree of decomposition, perhaps more so in a fen-like setting where water tables are consistently high.

The comparison of available paleoclimate data with the paleoecological record also helps to elucidate the roles of autogenic vs. allogenic processes in peatland development. The increase in precipitation in the HBL noted in several records after

~2400 yrs BP is not associated at the Victor Fen site with changes in vegetation, insofar as it can determined given the taxonomic limitations of palynology. For example, it is possible that the species of Cyperaceae or Ericaceae present are changing without detection in the pollen record. Nevertheless, the relatively unchanging humification curve, the stable C:N ratios alongside the palynology, suggests limited vegetation change for several thousand years. While it might be expected that the allogenic drivers of climate and rapid rates of differential isostatic uplift would lead to vegetation change during the late Holocene, a fen-type system persists. Furthermore, the typical pattern of peatland development whereby autogenic processes (i.e. the vertical accumulation of peat) result in a transition from a fen to a bog as the peatland surface becomes further removed from the influence of groundwater with vertical growth has also apparently not taken place either at this site. Thus, the long persistence of fen-type vegetation is somewhat surprising given these known external drivers, and given autogenic processes inherent to peat growth which tend to promote transition to a bog.

The persistence of fen-type vegetation, and lack of succession to bog, suggest a continued source of run-on, and/or a persistently high water table, which supplies enough moisture to maintain the water table position as peat accumulates. The lack of apparent change in wetland vegetation for the latter portion of the Victor Fen record also suggests a lack of sensitivity to the increased precipitation reconstructed for the late Holocene, which is perhaps not surprising given the high water tables associated with fens. This system is exhibiting very recent changes, namely increases in minerotrophic taxa and a decline in *Sphagnum* spores. Despite several millennia of stability, this system may not prove to be resilient to the projected rapid climate warming for the region, which may lower the water table and drive significant vegetation change.

Conclusions

The Victor fen contains a 6900-year record of wetland dynamics from the mid-Holocene to the present. Past paleoecological studies in the HBL have focused almost exclusively on bogs, highlighting the need for studies of fen systems, the other major peatland type in the HBL. Rapid post-glacial isostatic uplift provided a substrate for peatland initiation and continued to exert an influence on the ecosystem, contributing to the rapid succession from salt marsh to fen. Once the ecosystem became established as a fen, it did not undergo any major vegetation changes, despite known hydroclimatic changes, suggesting some resilience in the system.

LORCA at the Victor Fen site is high during the early successional salt marsh stage, and during the late Holocene (~2400 yrs BP to present). The late Holocene increase may be a response to the moister climate regime of the Neoglacial, suggested by the pollen-based paleoclimate reconstruction. Overall, LORCA was on average slightly higher at the Victor Fen site compared to the nearby Victor bog record (Bunbury et al., 2012), but due to lower rates between 6600 and 1500 yrs BP, less peat has accumulated at the fen. Thus, subtle differences in underlying topography and associated hydrological controls influence the rate of peat and carbon accumulation in the HBL, showing the complexity of modeling carbon accumulation across this expansive landscape. Efforts to quantify and explain changes in Holocene carbon accumulation in the HBL must account for isostatic uplift, paleoclimatic change, local drainage, and successional processes. These efforts are particularly important given the recent vegetation changes suggested by the pollen record from the Victor Fen site.

Acknowledgments

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