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Long-term sensitivity of a High Arctic wetland to Holocene climate change

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Summary

1 The response of peat-rich permafrost soils to human-induced climate change may be especially important in modifying the global C-flux. We examined the Holocene developmental record of a High Arctic peat-forming wetland to investigate its sensitivity to past climate change and aid understanding of the likely effects of future climate warming on high-latitude ecosystems.
2 The microhabitat of mosses was quantified in the present-day polygon-complex at Bylot Island (73° N, 80° W) and used to interpret the radiocarbon-dated macrofossil record of three cores, comprising *c.* 3500 years of wetland development. Recurrent wet and dry phases in the reconstructed palaeohydrological record indicated pronounced temporal variability. Wet and dry phases were compared between cores and with palaeoclimatic proxy values, measured as percentage melt and $\delta^{18}O$ in nearby ice cores.
3 Periodic wet and dry phases appear unrelated to past climate over *c.* 50% of the combined stratigraphic records, and are attributable instead to geomorphological mechanisms. At other times, association of wet and dry phases with significantly lower and higher values of percentage melt and $\delta^{18}O$ indicate a possible effect of past climate change on polygon hydrology and vegetation, although inconsistencies between cores suggest that local geomorphological processes continued to modify a regional climatic effect. However, during a period incorporating the Little Ice Age (*c.* 305–530 cal. years BP), reconstructed moisture and vegetation change is pronounced and consistent among all three cores.
4 The results provide strong evidence for the sensitivity of a High Arctic terrestrial ecosystem to past climate change during the Holocene. The estimated magnitude of changes in soil moisture between wet and dry phases is sufficient to imply recurrent shifts in wetland function, periodically impacted upon by pronounced climatic variability, although controlled principally by autogenic processes. The structure and function of such wetlands may therefore be susceptible to predicted, human-induced climate warming.

Keywords: Arctic, climate change, Holocene, macrofossils, mosses, palaeohydrology, peat formation, tundra polygons, wetlands

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Introduction

Human-induced climate change is expected to cause severe warming at high latitudes (Mitchell *et al*. 1990; Maxwell 1992), prompting concerns that the role of Arctic ecosystems might consequently shift from a store (or sink) to a source of greenhouse gases (CO_2 and CH_4) (Shaver *et al*. 1992; Chapin *et al*. 1997). The structure and function of extensive Arctic and Subarctic wetlands (Tarnocai & Zoltai 1988; Bliss 1997) are expected to be particularly important in regulating the flux of carbon between land and atmosphere. Peat-rich soils associated with such wetlands have contributed a net sink for carbon during the Holocene and are estimated to store > 97% of the tundra carbon reserve, comprising *c.* 180–190 × 10^{15} g of soil-C (Post *et al*. 1982; Oechel & Vourtilis 1994). Climate change

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and subsequent soil drying may cause a shift in wetland function from net C-input (or storage) to C-output (Oechel *et al*. 1993, 1995), resulting in a significant positive feedback on the global warming effects of greenhouse gases.

Recent studies in Arctic ecology have examined the response of vegetation and soils to experimental changes in factors such as temperature, water availability and nutrient status (Chapin *et al*. 1995; Arft *et al*. 1999) to demonstrate the direct and indirect effects of proxy climate change on structure and function of tundra vegetation. These short-term experiments (typically < 10 years) suggest that the climatic sensitivity of Arctic ecosystems is balanced by factors conferring both responsiveness and resilience (Wookey & Robinson 1997), but the results lack a long-term ecological context. Palaeoecological research is therefore essential to establishing whether climate sensitivity described by short-term studies may also control tundra development over the long term (i.e. during the Holocene), providing a perspective for interpreting and predicting future climatically controlled change in ecosystem structure and function, and a template for the 'scaling-up' of experimental data (Davis 1994).

This paper compares the long-term sensitivity of a polygon-patterned High Arctic wetland (cf. Tarnocai & Zoltai 1988; Bliss 1997) to known insolation- and volcanically forced decade- to century-scale variability in the Arctic climate (Overpeck *et al*. 1997; Mann *et al*. 1998). Existing macrofossil evidence for century-scale shifts in tundra development lack consensus, and high-resolution palaeoecological data are especially scarce for the High Arctic. Studies in the Low to Mid Arctic support the sensitivity of tundra to past climate change (Ovenden 1982; Bennike 1992; Vardy *et al*. 1997), consistent with evidence for the effect of human-induced global warming at similar latitudes (Jorgenson *et al*. 2001; Nelson *et al*. 2001). However, some studies in the High Arctic have invoked slope processes and local geomorphology rather than climate as controlling factors in vegetation–soil development (LaFarge-England *et al*. 1991; but see Garneau 1992), and a lack of data prevents an adequate assessment of the relative importance of climate and autogenic processes (Ellis & Rochefort 2004).

We investigate whether there is evidence that the climatic sensitivity of tundra vegetation and soils described by short-term experiments might also have occurred over longer time scales (≥ 100 years) and in response to natural climatic variability. If so, then to what degree might climatically mediated shifts in the vegetation–soil complex have affected long-term wetland function?

Study area

The study site occurs at *c*. 10 m a.s.l. to the south of Qunguliqtut Valley in western Bylot Island, within the Simirlik National Park (73.08° N; 80.00° W), part of the Canadian Arctic Archipelago (cf. Ellis & Rochefort 2004). Mean annual precipitation measured at Pond Inlet (1951–1980), adjacent to Baffin Island, was 159 mm, with maximum (August) and minimum (February) mean temperatures of 4.9 °C and −32.7 °C, respectively (Zoltai *et al*. 1983). The study area comprises low-lying terraces, which developed with the accretion of aeolian sands and silts and the concurrent deposition of peat. Terrace formation was initiated sometime after a marine transgression following glacial retreat (dated using shell fragments to *c.* 6020 ± 80 years BP), but before active peat deposition, which commenced at or before *c.* 2900 ± 90 years BP (Allard 1996). The upward growth of ice-wedges in the aggrading sediments has resulted in extensive polygon-patterned ground, and the terraces include a range of associated landforms: low-centre and high-centre polygons, polygon-ponds and thaw-lakes (cf. Billings & Peterson 1980). The polygon complex is fed by meltwater from hills to the south, and the vegetation is dominated by sedges (e.g. *Carex aquatilis* var. *stans*, *Eriophorum scheuchzeri*), grasses (e.g. *Arctagrostis latifolium*, *Dupontia fischeri*, *Pleuropogon sabinei*) and fen mosses (e.g. *Drepanocladus* spp., *Aulocomnium* spp.).

PROCESS IN THE FORMATION OF THE POLYGON-PATTERNED WETLAND

The development of tundra polygons is described in detail by French (1996). Low-centre polygons (ridges raised by the growth of ice-wedges, surrounding lower and wetter polygon centres) persist due to the upward growth of syngenetic ice-wedges, at a rate that is limited by the accumulation of sediment and the development of permafrost. Polygon-ponds, which form during the inundation of low-centre polygons, may coalesce to form thaw-lakes. High-centre polygons occur where ice-wedges surrounding low-centre polygons are denuded, with the consequent collapse of ridges and formation of troughs around the now higher polygon centres and the cessation of upward sediment and ice-wedge growth.

Methods

PERMAFROST CORES

Sediment cores were extracted from the centres of a low-centre polygon and high-centre polygon in June 1999 (BY-LowC and BY-HighC, respectively, 298 cm and 230 cm deep). Sediments from the active layer (to *c.* 30 cm depth) were sampled as 2-cm slices from an unfrozen peat monolith (*c.* 10 cm^2). Permafrost sediment cores were collected as contiguous 5-cm-diameter, 50-cm segments, using a machine-driven corer (built by M. Allard, Université Laval). Cored sections were examined in the field to ensure that sediments were horizontally bedded and undisturbed. The frozen 50-cm sections were cut where possible into 2-cm slices and stored in sealed polythene bags in the dark at < 4 °C.

VEGETATION–SOIL DESCRIPTION

In late July and early August 2000, present-day moss assemblages were quantified based on species presence–absence in 25 5 × 5 cm subunits within 25-cm quadrats (identification and nomenclature follows Nyholm 1954–1969). Ninety-nine quadrats were analysed including representative samples from all recognized habitats: low-centre polygon ridges, flanks and centres, high-centre polygon centres and eroding flanks, polygon-pond flanks and standing water, water courses and areas of active aeolian deposition.

Sampling for the analysis of soil properties was during a single rain-free period in early August, the warmest and wettest period of the year (Zoltai *et al.* 1983). A turf (5 cm^2 × 5 cm deep) was cut from the centre of each quadrat and divided into two equal halves. The green 'living' moss layer (*c.* 1 cm in thickness) was removed from one half and the remaining peat–sediment sample was weighed before and after drying for 24 h at *c.* 60 °C.

Soil samples were sealed in polythene bags and stored on ice in the dark, before transfer to the laboratory. The partially dried samples were then re-weighed and dried at 105 °C for 18 h. Percentage dry weight per unit volume for each quadrat was calculated from the final laboratory dry weight. The same samples were incinerated at 550 °C for 5 h: loss on ignition (LOI) was used to calculate organic content and percentage mineral material (ash weight as a fraction of the pre-LOI dry weight). Within 5 days of arrival in the laboratory, the freshly stored samples were analysed for pH, using a Fisher Scientific accumet model-10 pH meter, and for conductivity (µS cm^{-1}), using an Orion model-122 conductivity meter (Brady 1990). Conductivity was corrected for temperature and pH according to Sjörs (1950).

STRATIGRAPHIC MACROFOSSILS AND LOI

A 1-cm^3 sediment sample was removed from each contiguous horizon. Macrofossils were extracted by treatment in 20 mL of 7% KOH and quantified as percentage frequency of occurrence according to Tallis (1985). Attempts to quantify the volume of permafrost sediment are complicated by variations in ice content and mineral content, and this method quantifies moss remains, including those from permafrost sediments (Ellis & Rochefort 2004), independently of volume (Tallis 1985), whereas standard measures of bryophyte concentration are based on peat volume (Janssens 1983, 1988). Macrofossil specimens (typically bryophyte stems and leaves) were identified using a modern reference collection at the Université Laval Herbarium (QFA) and Nyholm (1954–1969).

A second sample from each horizon was oven dried at 105 °C for 18 h, weighed and the mineral content quantified after incineration at 550 °C for 5 h. Values are expressed as the three-point weighted average, calculated to minimize high-frequency noise, and emphasizing low-frequency cycles (Green 1995).

RADIOCARBON DATING

Before being submitted for radiocarbon analysis, samples were pretreated to prevent contamination by carbon-rich Tertiary deposits (Gajewski *et al.* 1995), which occur on Bylot Island adjacent to and within the catchment area of the sampling site (Klassen 1993). A sediment sample of *c.* 2 cm^3 was washed in distilled water and filtered through a 0.3-mm mesh sieve. In the absence of woody remains, bryophyte stems and leaves were collected from the organic residue and rinsed in distilled water. They were dried at 60 °C and samples of ≥ 0.1 g submitted to Beta Analytic Ltd (Miami, FL, USA), for analysis by accelerator mass spectrometry (AMS).

Material was radiocarbon-dated at horizons delimiting a significant change in the stratigraphic record. Conventional radiocarbon ages (years BP) are shown in Table 1 but are generally presented as calibrated years before present (cal. years BP, according to INTCAL 98, Stuiver *et al.* 1998).

MOSS DISTRIBUTION AND ENVIRONMENTAL GRADIENTS

Quadrat data describing the distribution of mosses in the present-day polygon wetland were summarized using detrended correspondence analysis (DCA, with rare species down-weighted), computed using the program MVSP 3.1 (Kovach 1986–1999). The first four orthogonal axes of the DCA were compared, using a general linear model, with values of soil moisture, pH, corrected conductivity of a bulk soil–water sample and soil organic/mineral matter. Stepwise selection was used to derive the most effective multiple regression, calculated using the program Genstat 7.1 (Genstat 7.1 2003). The power of the individual environmental variables in explaining the position of moss taxa along each of the four axes was examined by comparing the adjusted R^2 value for a multiple regression including the variable with the model with the variable selectively removed.

PALAEOENVIRONMENTAL RECONSTRUCTION

The records of cores BY-LowC and BY-HighC were supplemented by re-analysis of a third core (BY-a), from a high-centre polygon in the same complex, which has previously been shown to indicate climatic sensitivity (Ellis & Rochefort 2004).

Macrofossil records were initially tested for evidence of allochthonous deposition, which would confound palaeoenvironmental reconstruction based on the assumption that sediments are autochthonous (see Appendix S1, available as supplementary material online). The first orthogonal axis of the DCA for present-day moss assemblages was assumed to summarize the autochthonous record of macrofossil mosses in each core. Axis one values for individual species were used

Table 1 Radiocarbon dates for cores BY-LowC and BY-HighC, Qunguliqtut Valley, Bylot Island (73.08° N; 80.00° W); with calibrated ages calculated using the computer program CALIB 4.3 (Stuiver *et al*. 1998). Results for the additional core BY-a (formerly presented by Ellis & Rochefort 2004) are also shown

Core; depth	Laboratory code	Conventional radiocarbon age (yr BP ± 1 SE)	Calibrated age (cal. yr BP) Mid-point of 1δ-range
BY-LowC; 6–10 cm	Beta-143329	105 (modern)	–
BY-LowC; 29–35 cm	Beta-143330	2420 ± 50	2700 – **2370** – 2355
BY-LowC; 37–39 cm	Beta-195789	3230 ± 40	3470 – **3460** – 3390
BY-LowC; 81–83 cm	Beta-143331	910 ± 50	915 – **795 –** 755
BY-LowC; 127–129 cm	Beta-143332	2430 ± 50	2705 – **2415** – 2355
BY-LowC; 161–163	Beta-195790	2530 ± 40	2740 – **2730** – 2510
BY-LowC; 192–194	Beta-195791	2800 ± 40	2940 – **2880** – 2850
BY-LowC; 296–298 cm	Beta-143333	3100 ± 50	3370 – **3345** – 3255
BY-HighC; 2–6 cm	Beta-143334	280 ± 40	425 – **305 –** 295
BY-HighC; 50–52 cm	Beta-195792	670 ± 40	660 – **650 –** 570
BY-HighC; 100–102 cm	Beta-143335	1170 ± 50	1165 – **1070** – 995
BY-HighC; 118–120 cm	Beta-143336	1920 ± 40	1895 – **1870** – 1830
BY-HighC; 188–190 cm	Beta-195793	2260 ± 40	2340 – **2320** – 2180
BY-HighC; 228–230 cm	Beta-143337	2590 ± 50	2760 – **2745** – 2730
BY-a; 2–6 cm	Beta-143338	120 ± 40	271 – **140** – 0
BY-a; 18 cm	Beta-152427	270 ± 40	420 – **300** – 290
BY-a; 40 cm	Beta-152428	390 ± 40	500 – **480** – 330
BY-a; 52–54 cm	Beta-152429	520 ± 40	540 – **530** – 520
BY-a; 62 cm	Beta-152430	710 ± 40	680 – **660** – 650
BY-a; 74 cm	Beta-152431	620 ± 40	650 – **590** – 550
BY-a; 114 cm	Beta-152432	1040 ± 40	970 – **950** – 930
BY-a; 140–142 cm	Beta-152433	1590 ± 40	1530 – **1510** – 1420
BY-a; 162 cm	Beta-152434	1520 ± 40	1420 – **1400** – 1350
BY-a; 208–210 cm	Beta-143339	1660 ± 40	1600 – **1545** – 1520

to calculate a weighted average (WA) score (Curtis & McIntosh 1950, 1951) for each stratigraphic horizon. The stratigraphic profiles of WA scores were smoothed using a three-point weighted average to minimize high-frequency noise (Green 1995) and linear regression was used to derive lines of best fit for continuous periods (between hiatuses) in BY-LowC, BY-HighC and BY-a. The data were then replotted for each core as the residuals. Discrete periods with residual WA values above or below the long-term mean (i.e. the regression line) were interpreted as contiguous wet and dry phases. Two different age models were used to infer sedimentation rates (Appendix S2): linear interpretation for BY-LowC and BY-HighC and linear regression for core BY-a.

A semi-quantitative estimate of past soil moisture conditions was derived by classifying present-day values as the average for each unit interval along the first axis of the DCA, and using analysis of variance and least-squared difference at the 5% level to identify discrete moisture classes (Genstat 7.1 2003). These were then used to interpret the stratigraphic record of WA ordination scores.

PALAEOCLIMATIC COMPARISON

The radiocarbon-dated records of residual WA values were compared with proxy-climate records available for the same High Arctic region as our study site. Five-year average values of percentage melt in the stratigraphy of the Agassiz-84 ice core, Ellesmere Island (Koerner & Fisher 1990), from AD 1961 to 9 BC and 5-year average values of $\delta^{18}O$ for the combined stratigraphies of two adjacent cores from the Devon Island ice cap (Paterson *et al*. 1977) from AD 1973 to 727 BC were provided by the US National Oceanic and Atmospheric Administration through the World Data Center for Paleoclimatology at Boulder, Colorado, USA. Despite noted complexities in interpreting palaeoclimatic trends (Koerner 1977; Fisher *et al*. 1983; Bradley 1990), it is reasonable to assume that these records provide an approximation of past climate change during the mid to late Holocene (Bradley 1985, 1990; Fisher & Koerner 1994). Percentage melt measures the changing concentration of textural melt layers with depth and is a proxy for summer temperature (Koerner 1977; Koerner & Fisher 1990), reflecting long-term variations in net radiation (R_n), which will directly control spring snow-melt [i.e. precipitation (P)] (Young & Lewkowicz 1990; Young *et al*. 1997), and evapotranspiration (ET) (Vourtilis & Oechel 1997). The ratio of oxygen isotopes $^{18}O/^{16}O$, $\delta^{18}O$, provides a proxy-record of mean annual palaeotemperature (Paterson *et al*. 1977; Bradley 1985). The palaeoecological record was compared since 1800 cal. year BP with 5-year values of both percentage melt and $\delta^{18}O$, and with values of $\delta^{18}O$ only for the previous 700 years.

Values of percentage melt and $\delta^{18}O$ were compared between contiguous wet and dry phases using analysis of variance and least-squares differences at the 5% level to determine significance (Genstat 7.1 2003). A combined record of palaeohydrology, based on the contemporaneous occurrence in different cores of wet or dry phases that corresponded to significantly different values of percentage melt and $\delta^{18}O$, was constructed. This was then compared with palaeoclimatic proxy values using a two-tailed unpaired *t*-test (Genstat 7.1 2003) on values of percentage melt and $\delta^{18}O$ between wet or dry phases that occurred (i) only in one core or contemporaneously in either (ii) two or (iii) three cores.

Results

MOSSES – PRESENT-DAY HABITATS

The DCA identifies soil moisture as the single most important variable in the present-day distribution and abundance of mosses (Table 2) and analysis of variance demonstrates that first axis sample scores can be divided into two classes corresponding to significantly wetter and drier soil moisture around a DCA score of 3 (Fig. 1).

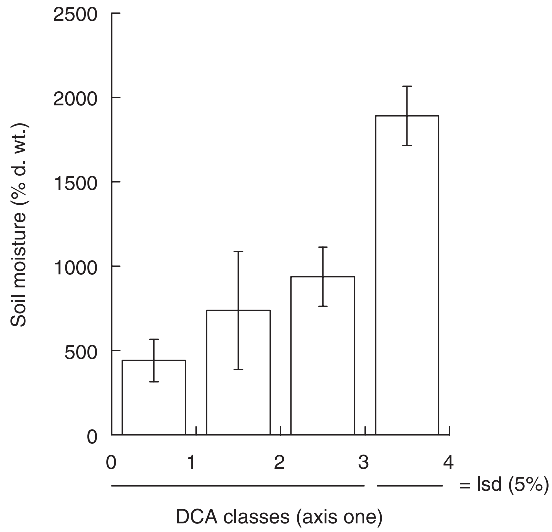

Fig. 1 Comparison of average soil moisture (% d. wt.) for present-day moss samples grouped according to their score along the first axis derived using DCA (Table 2). Bars show the standard error difference after analysis of variance ($F \leq 0.001$ with 3 and 91 d.f.). The least square difference (5% probability) recognises two separate groups: DCA axis one values 0–3 (drier) and values 3–4 (wetter).

MACROFOSSIL MOSSES

Macrofossil mosses in cores BY-LowC and BY-HighC exhibit striking variability during polygon development (Figs 2 & 3, respectively). However, there are sections in the macrofossil records of each core where moss remains are few or absent, with lenses of mineral sediment suspended in segregation ice at 127–81 cm and 116–102 cm depth in BY-LowC and BY-HighC, respectively (Figs 2 & 3), and a second, lesser hiatus at 27–14 cm in BY-LowC accompanying a peak in mineral content (Fig. 2). The stratigraphic records of each core nevertheless provide clear evidence for vegetation change during polygon development.

RADIOCARBON DATES

Radiocarbon dates for two horizons in the stratigraphy of BY-LowC were thought to be erroneous and cautiously rejected from the timeframe (Appendix S4).

Based on linear interpolation between radiocarbon-dated horizons in BY-LowC and BY-HighC, the sedimentation rate of peat-rich deposits varies between *c.* 0.22 cm yr^{-1} and 0.057 cm yr^{-1}, with a combined average rate of *c.* 0.11 cm yr^{-1} (Table 1, Fig. 4). This is consistent with data from comparable High Arctic habitats (LaFarge-England *et al.* 1991; Bennike 1992; Vardy *et al.* 1997). However, sedimentation appears to have been slower (*c.* 0.022 cm yr^{-1}) at 128–82 cm depth in BY-LowC and 119–101 cm depth in BY-HighC (Table 1, Fig. 4), matching the shared hiatus in the macrofossil records (Figs 2 & 3). There was no segregation ice in the stratigraphy of BY-a (Ellis & Rochefort 2004) and a linear regression between the scatter of radiocarbon-dated horizons suggests a sedimentation rate of 0.13 cm yr^{-1} (Fig. 4), similar to the average estimated for BY-LowC and BY-HighC, and within the 95% confidence interval for the range of growth rates in these two cores (i.e. 0.14–0.08 cm yr^{-1}). Linear interpolation, rather than regression, estimates sedimentation rates of up to 2 cm yr^{-1} for BY-a, inconsistent with data from this and other studies (LaFarge-England *et al.* 1991; Bennike 1992; Vardy *et al.* 1997). The balance of evidence suggests that two different but consistent age models – linear interpolation in BY-LowC and BY-HighC and linear regression in BY-a – provides the most realistic

Table 2 Comparison of environmental variables with sample scores (DCA) for the distribution of mosses in the present-day polygon wetland. Eigenvalues (λ) and the percentage variation explained are shown for the first four orthogonal axes. Values for each environmental variable show the effect on adjusted R^2 of removing it from a general linear model, generated as a stepwise multiple regression to explain sample scores (DCA) using the four measured variables

DCA	λ	% variation explained (cumulative)	Environmental variable: Soil moisture	pH	LOI	Conductivity	Adjusted R^2 and F-value (improvement if variables dropped)
Axis 1	0.608	34.1 (34.1)	−22.8***	−11.4***	−3.6***	−0.01***	0.624, $F \leq 0.001$
Axis 2	0.181	10.15 (44.25)	−0.01***	Dropped	Dropped	Excess residual *v*	0.29, $F \leq 0.001$ (+0.06)
Axis 3	0.103	5.8 (50.05)	−21.3	−13.5**	−5***	Dropped	0.235, $F \leq 0.001$ (+0.05)
Axis 4	0.086	4.81 (54.85)	−22.7	−14.4**	−3.4***	+0.2***	0.235, $F \leq 0.001$

$F \leq 0.001$***, < 0.01**, < 0.05*.

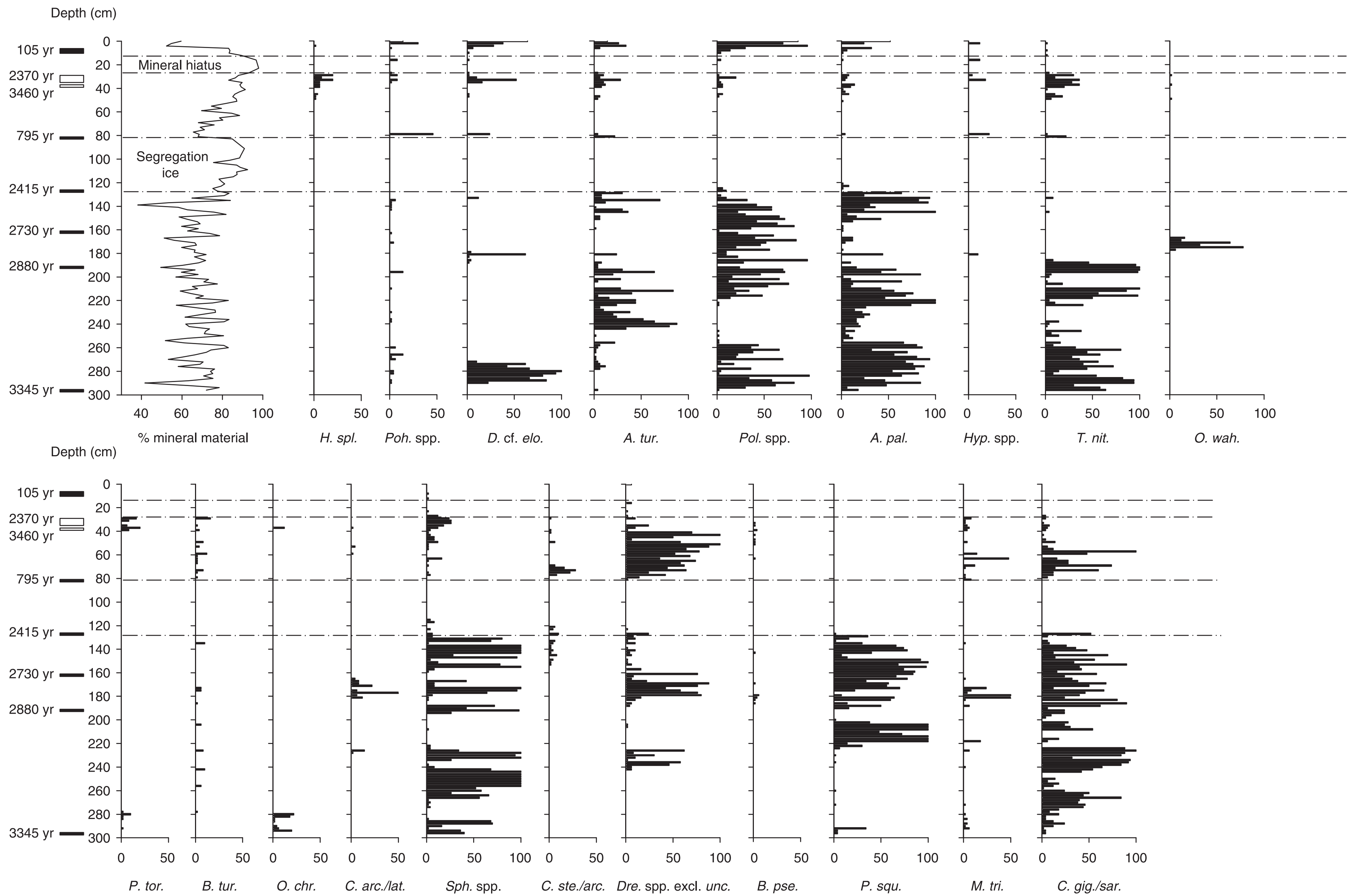

Fig. 2 Low-centre polygon core BY-LowC: radiocarbon-dated stratigraphic record of macrofossil mosses (% frequency of occurrence) and sediment lithology (% mineral material, LOI). Bars to the left of the *y*-axes show the 1 – δ mid-point of calibrated radiocarbon dates (cf. Table 1) with anomalous dates shown in white (see Appendix S4). Abbreviations of macrofossil taxa refer to Appendix S3.

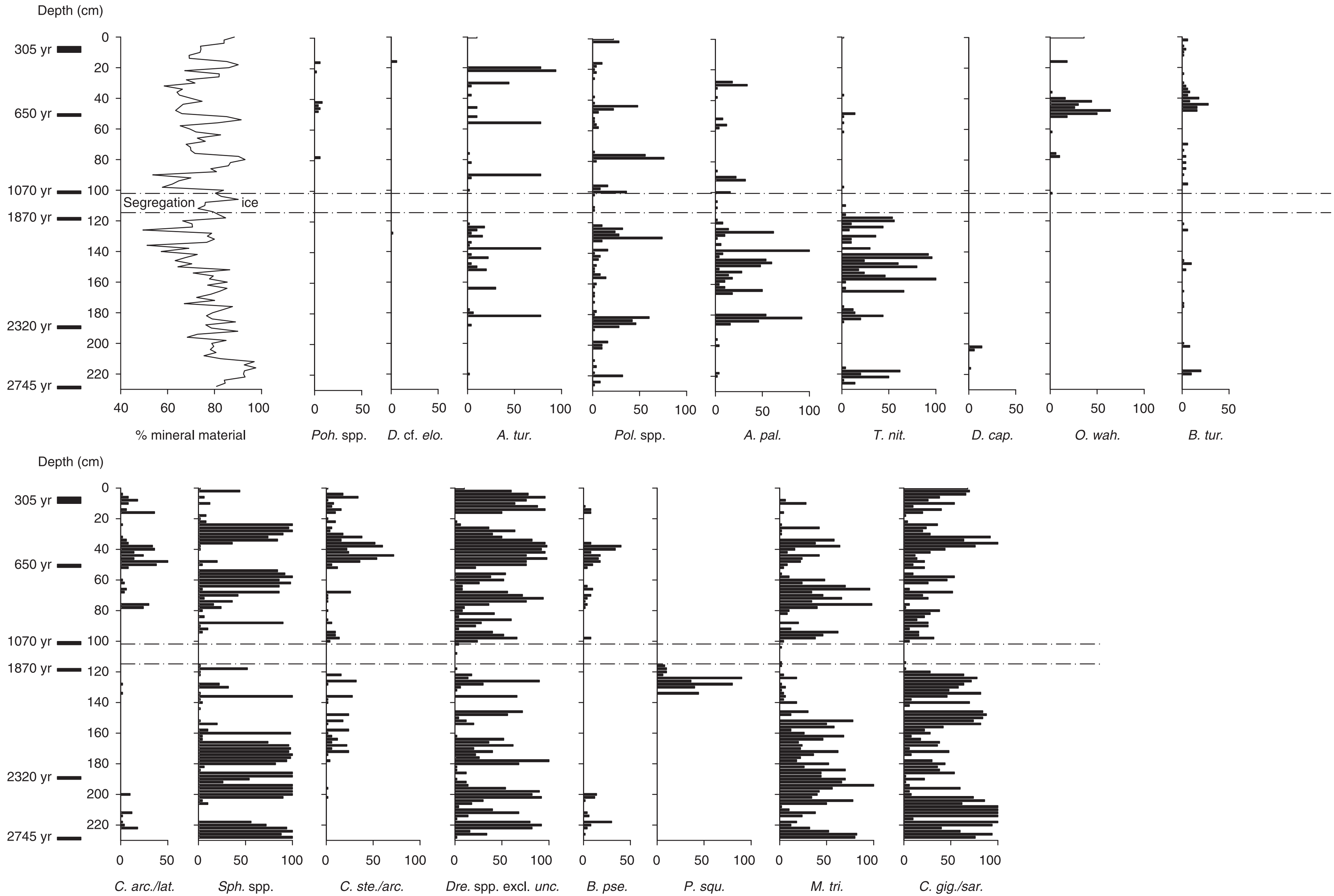

Fig. 3 High-centre polygon core BY-HighC: radiocarbon-dated stratigraphic record of macrofossil mosses and sediment lithology (% mineral material, LOI). Bars to the left of the y-axes show the 1 − δ mid-point of calibrated radiocarbon dates (cf. Table 1). Abbreviations of macrofossil taxa refer to Appendix S3.

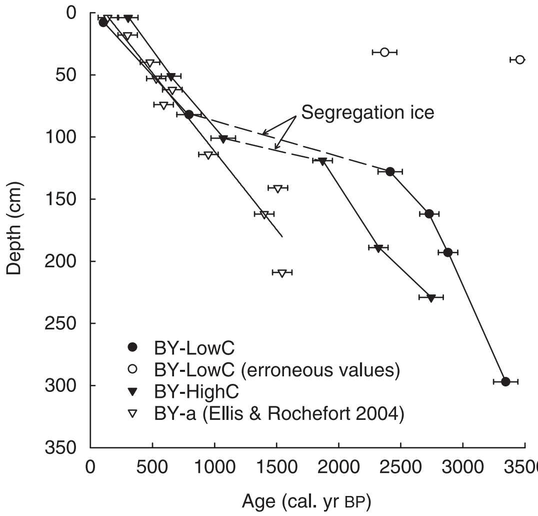

Fig. 4 Radiocarbon-dates (with 95% confidence intervals) compared to sediment depth in BY-LowC, BY-HighC and BY-a (Table 1). Lines show dating frameworks based on two different models though generating consistent sediment growth rates between cores in this and other comparable studies: (i) linear interpolation between dated horizons in BY-LowC and BY-HighC, and (ii) linear regression for a scatter of dates in BY-a ($R^2 = 0.939$, $P \leq 0.001$, with 9 d.f.).

scenario for the comparison of cores across a common timeframe.

Palaeocological interpretation

The application of DCA scores in the WA interpretation of macrofossil mosses is assumed to provide a reasonable proxy for past relative wetness, in which positive deviations in WA macrofossil horizon scores above the long-term mean indicate periods of increased soil moisture and vice versa. Comparing these scores for stratigraphic horizons with DCA sample scores for moss assemblages in the present-day wetland (Fig. 1) produces a semi-quantitative paleohydrological proxy, in which DCA or WA values above 3 are considered significant (Figs 1 & 5).

Proxy-climate comparison

The lower stratigraphy of BY-LowC (below the hiatus with segregation ice) pre-dates the palaeoclimatic records. However, averages for 5-year values in percentage melt and/or $\delta^{18}O$ were consistently significantly different between contiguous wet and dry phases during the period common to all cores (wetter phases have lower percentage melt in all three cores, but values of $\delta^{18}O$ did not change significantly in BY-LowC; Fig. 6). A combined palaeohydrological record demonstrates periods during which phases associated with significantly different palaeoclimatic proxy values occur in one core alone or contemporaneously in two or three cores. Values of percentage melt were significantly different between wet and dry phases when these were registered simultaneously in two or three cores (but not when registered in one core alone), whereas values of $\delta^{18}O$ were significantly different between wet and dry phases both when registered simultaneously in two cores and when registered in one core alone (Fig. 7).

Discussion

Phases in polygon hydrology: geomorphological and climatic controls

The long-term development of the three cores examined here is characterized by recurrent, contrasting phases in soil moisture and vegetation composition (Figs 2, 3 & 5), supporting a growing body of evidence for the dynamic nature of High Arctic wetland development (LaFarge-England *et al*. 1991; Ellis & Rochefort 2004) rather than the previously generally perceived view of Arctic vegetation as resistant. The development of three low-centre wetland polygons (cf. Tarnocai & Zoltai 1988; French 1996) was reconstructed up to the present-day (BY-LowC) or until the cessation of sediment growth with the shift to high-centre polygon conditions at *c.* 305 cal. years BP in BY-HighC and *c.* 140 cal. years BP in BY-a. Individual low-centre polygons are hydrologically discrete, comprising water-shedding polygonal ridges, raised by the growth of ice-wedges, around water-accumulating, lower and wetter polygon centres. Reconstructed changes in past soil moisture can be considered specific to individual polygons. The water balance (ΔS) of a plot within a given polygon can be approximated as:

$$\Delta S = P + Q_g + Q_s - ET \qquad \text{eqn 1}$$

influenced by climate, i.e. precipitation (P) and evapotranspiration (ET), and/or geomorphology, i.e. topography, which controls groundwater and surface-water input and output (Q_g and Q_s, respectively) and modifies inputs from precipitation (P) (Rovansek *et al*. 1996; Young *et al*. 1997). Climatic control may also be indirect, through the effect on topography of ice-wedge growth (Kasper & Allard 2001), which will in turn affect soil moisture (P, Q_g and Q_s) (Rovansek *et al*. 1996; Young *et al*. 1997). Garneau (1992) and Vardy *et al*. (1997) suggested that the long-term development of Arctic wetlands had been sensitive to past climatic variation, and Ellis & Rochefort (2004) observed a possible effect of the Little Ice Age (*c.* 300–465 cal. years BP) in the development of a High Arctic wetland polygon. However, they reported a generally low correspondence between proxy climate records and reconstructed soil moisture, and LaFarge-England *et al*. (1991) also suggested that local geomorphology was the principal factor controlling soil moisture during the development of High Arctic peat deposits. These palaeoecological studies (LaFarge-England *et al*. 1991; Ellis & Rochefort 2004) raise uncertainty about the extent to which a direct climatic effect on tundra vegetation described by short-term studies (Chapin *et al*. 1995; Arft *et al*. 1999)

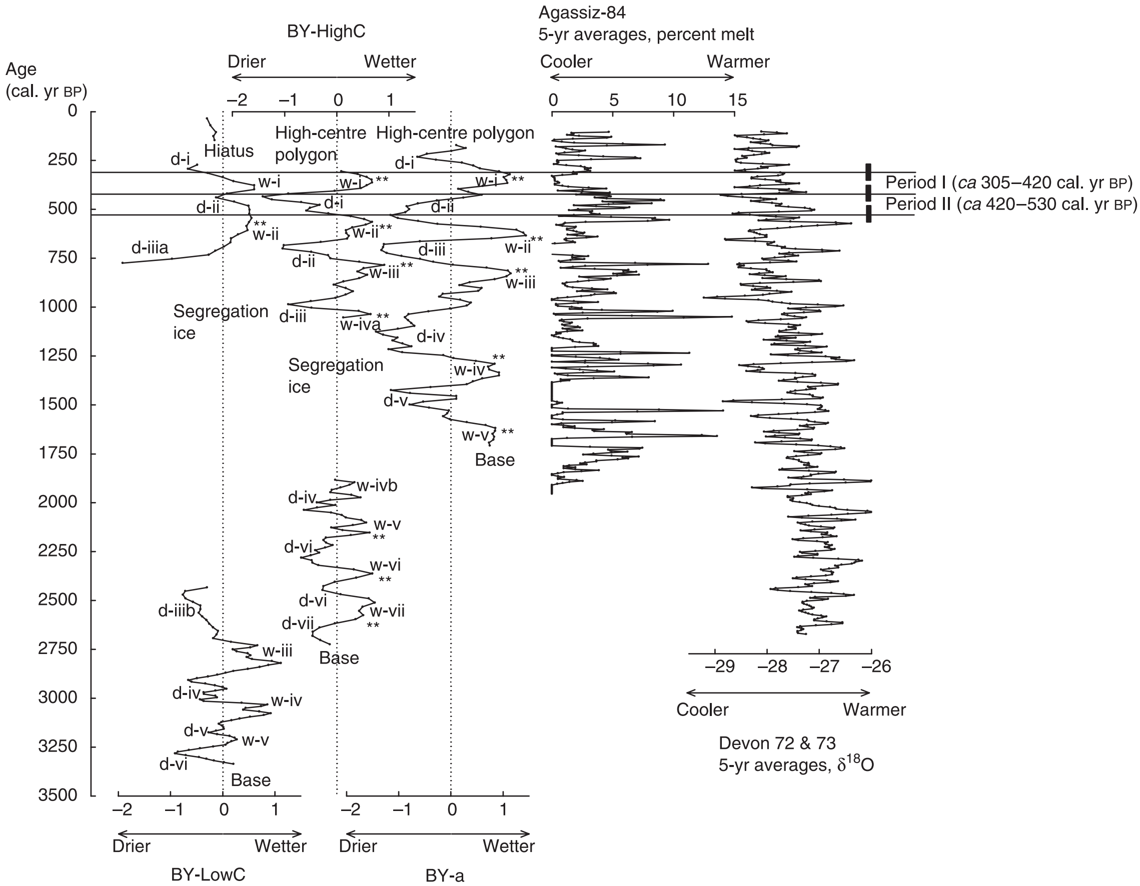

Fig. 5 Variations in WA scores for the macrofossil records of BY-Low-C (Fig. 2), BY-HighC (Fig. 3) and BY-a (cf. Ellis & Rochefort 2004), above and below the long-term mean. Wet phases identified as residuals above the long-term mean are labelled sequentially by the prefix 'w-', dry phases identified as residuals below the long-term mean by the prefix 'd-'. Wet phases during which the original WA scores exceed a value of three (cf. Fig. 1) are marked (**). The timeframe for macrofossil records is based on radiocarbon-dates (Fig. 4, Table 1) and provides the basis for a comparison with palaeoclimatic records: 5-year average values of percent melt in the Aggassiz-84 ice core (Koerner & Fisher 1990) and 5-year average values of $\delta^{18}O$ as the combined records of ice cores from the Devon Island ice cap, cores 72 and 73 (Paterson *et al.* 1977). Two periods are delimited, during which wet and dry phases in all three cores match significantly lower and higher values of percent melt and $\delta^{18}O$, respectively: Periods I and II, vertical black bars indicate 95% confidence intervals.

might also contribute to inherent, long-term vegetation change, including the direct effects of future climate warming. It is possible that soil moisture conditions and vegetation during development of tundra polygons are controlled principally by autogenic processes, i.e. the balance between sediment accumulation and upward development of syngenetic ice-wedges, which will control the topographic amplitude between polygon ridges and centres, and therefore values of Q_g, Q_s and P (Ellis & Rochefort 2004).

EVIDENCE FOR CLIMATIC CONTROL DURING POLYGON DEVELOPMENT

Evidence for the climatic control of soil moisture and vegetation during long-term development is circumscribed by a lack of replication and possible errors in both the radiocarbon dating scheme (Table 1, Fig. 4) and the dating of ice cores used as a paleoclimatic proxy (Fujii 1995). However, dating of ice cores over the past *c.* 5000 years is expected to be relatively precise (Paterson *et al.* 1977), and comparisons between ice cores suggest that a general interpretation of palaeotemperature is reasonable for the Holocene (Bradley 1985, 1990). Rates of sedimentation for the three cores appear consistent (Fig. 4), and the 95% confidence intervals for individual radiocarbon dates (75–100 years) are, on average, *c.* 45 years less than the mean duration of wet and dry phases (130 ± 15 years), suggesting that a circumspect comparison of phases may be justified. Based on the comparison between palaeoecological records and palaeoclimatic values of both percentage melt and $\delta^{18}O$, our evidence suggests that soil moisture of the wetland polygons investigated may have become drier during periods of climatic warming (dry phases associated with higher values of percentage melt and $\delta^{18}O$) and wetter during periods of climatic cooling (wet phases associated with lower values of percentage melt and $\delta^{18}O$). However, the relative importance of climate in controlling soil moisture is unlikely to have been consistent during polygon development and a climatic effect is therefore more strongly supported when similar

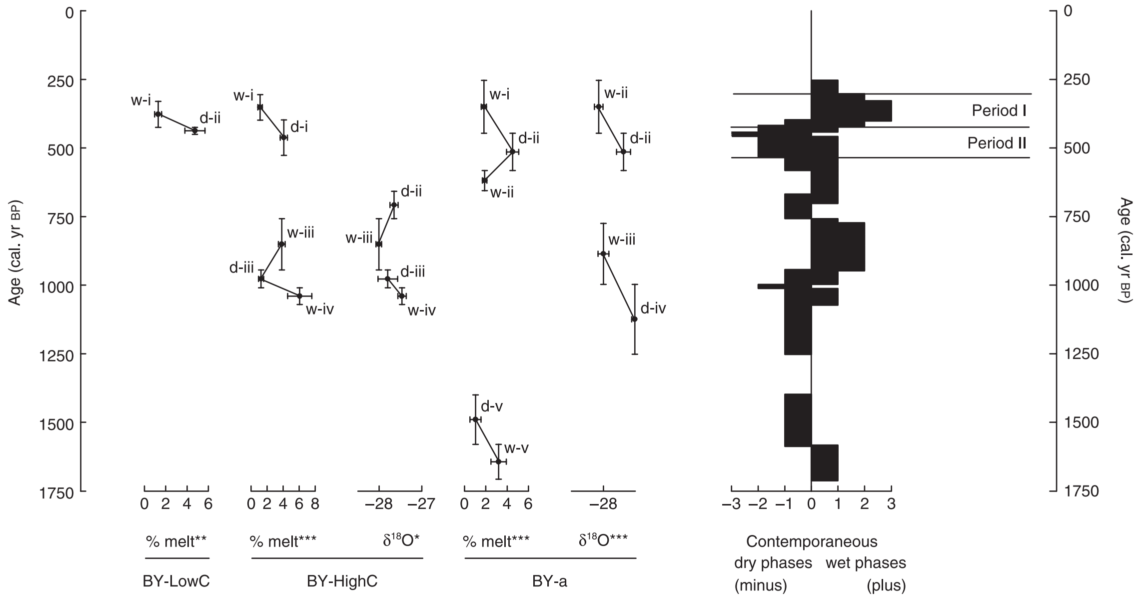

Fig. 6 Average values of percent melt and $\delta^{18}O$ compared between contiguous wet and dry phases in cores BY-LowC, -HighC and BY-a (cf. Fig. 5). Vertical bars (*y*-axis) indicate the time period of the phase, horizontal bars (*x*-axis) the standard error (±1 SE) for average palaeoclimatic proxy values. Lines between points indicate contiguous phases between which palaeoeclimatic proxy values are significantly different (based on the least square difference at the 5% level, $***P < 0.001$, $**P < 0.01$, $*P < 0.05$). The combined record of palaeohydrologic change shows the occurrence of contemporaneous wet and dry phases in BY-LowC, BY-HighC and BY-a (black bars, indicating wet or dry phases occurring in one core, or contemporaneously in two or three cores). Two periods are delimited, during which wet and dry phases in all three cores match significantly lower and higher values of percentage melt and/or $\delta^{18}O$, respectively: Periods I and II.

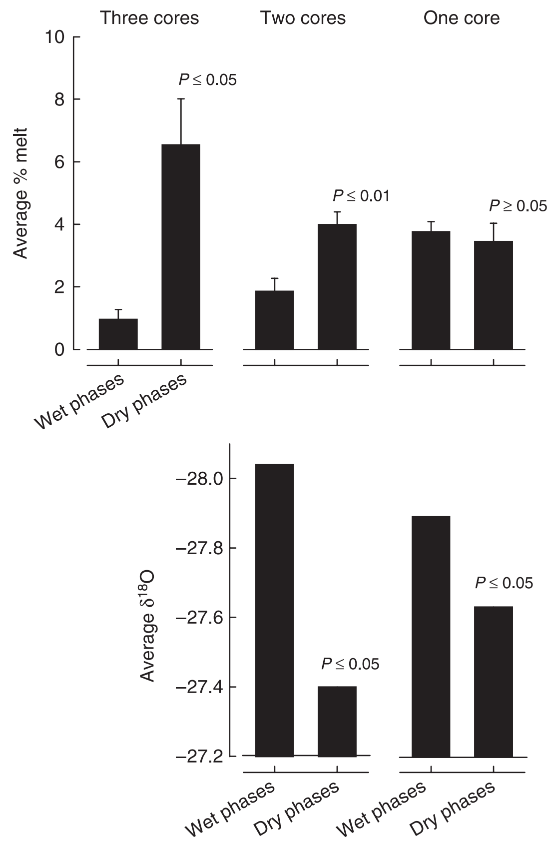

Fig. 7 Proxy palaeoclimatic values compared between wet and dry phases occurring in one core or contemporaneously in two or three cores (cf. Fig. 6).

phases are registered contemporaneously in the three cores (Fig. 7).

Given a combined palaeoecological record of *c.* 3885 years (i.e. the combined time span of BY-LowC, BY-HighC and BY-a over the period for which a comparison with palaeoclimatic records is possible), 50% of the period shows no evidence for a correspondence between wet and dry phases and palaeoclimatic proxy values in any core. There is evidence for a correspondence in only one core, or else contrasting evidence for a correspondence between phases and palaeoclimatic proxy values in several cores (i.e. significantly higher or lower values of percentage melt or $\delta^{18}O$ related to contrasting coeval wet and dry phases) over *c.* 44% of the palaeoecological record (i.e. *c.* 1710 years). Over only *c.* 6% of the palaeoecological record (i.e. *c.* 225 years) is there evidence for a correspondence between wet and dry phases and consistent change in the records of percentage melt (two to three cores) and $\delta^{18}O$ (two cores or one core).

The balance of evidence therefore supports an important role for autogenic geomorphological–vegetation change during the long-term development of the three wetland polygons examined (LaFarge-England *et al.* 1991; Ellis & Rochefort 2004). Periodic changes in vegetation and soil moisture during the development of Arctic wetland polygons, where unrelated to palaeoclimatic proxy records, might instead reflect local periglacial processes (Ellis & Rochefort 2004) resulting in amplitude changes between polygon ridges and centres. Deeper polygons will accumulate more snow in winter (resulting in higher values of *P*, Young *et al.*

1997) and will have greater rates of surface (Q_s) and groundwater (Q_g) input (Rovansek *et al*. 1996; Young *et al*. 1997), causing them to be wetter than polygons with a shallower topology. Wet and dry phases can then be explained by a feedback between sediment accumulation, controlled by the input of organic and mineral material, and the upward growth of ice-wedges, which is limited by the rate of sediment accumulation (Harry & Gozdzik 1988; Mackay 2000). Wet phases may correspond to periods when the amplitude between a polygon's ridges and centre is relatively large (higher values for Q_g, Q_s and P) although upward growth of ice-wedges, and the continued development of ridges, will gradually slow or cease, to be resumed only when sufficient sediments have accumulated in the polygon centre. This intervening period will lower the amplitude between polygon ridges and centre, and therefore lower values of Q_g, Q_s and P, causing the shift to drier soil moisture conditions evident in the palaeoecological record (Ellis & Rochefort 2004). A process of staggered ice-wedge formation resulting in a chevron pattern of growth (Dostovalov & Popov 1966; Mackay 1974; Lewkowicz 1994) might therefore explain recurrent shifts between wet and dry phases during the long-term development of low-centre polygons (Ellis & Rochefort 2004).

Where evidence for a climatic effect is based on a correspondence between palaeoecological and palaeoclimatic records in one core alone, or points to a contrasting response across several cores, it must be considered equivocal. However, a polygon in a dry state (with lower ridges relative to and surrounding the polygon centre and low values of Q_g, Q_s and P) may register a shift to a wetter and cooler climate, whereas one in a wet state (with higher ridges and values of Q_g, Q_s and P) may not. Thus, wet and dry phases in the combined record of palaeohydrological change matching significantly higher and lower palaeoclimatic proxy values (Fig. 7) may point to an underlying long-term climatic influence, which is modified by local geomorphological conditions so that it is only registered in individual cores.

There are, however, two distinct periods (Figs 5 & 6) during which a climatic effect on polygon development is well supported (*c*. 305–420 and 420–530 cal. years BP). Period I, characterized by contemporaneous wet phases in all three cores, and associated with significantly lower values of percentage melt (BY-LowC, BY-HighC and BY-a) and $\delta^{18}O$ (BY-a), is broadly coeval with a period of climatic cooling well documented from sites in the North Atlantic region (Lamb 1965; Williams & Wigley 1983; Millar & Woolfenden 1999) including the Arctic (Williams & Wigley 1983; Gajewski & Atkinson 2003): i.e. the Little Ice Age (LIA). The change from inferred drier soil moisture conditions during Period II to wetter conditions during Period I is also supported by evidence for a pronounced climatic effect at other High Arctic sites. Period I is coeval with geomorphological evidence for the effects of the LIA in the Qunguliqtut Valley (Klassen 1993; Allard 1996) and paleolimnological evidence for LIA cooling from Baffin Island (Hughen *et al*. 2000) and Ellesmere Island (Lamoureux & Bradley 1996). The direction of change is also consistent with evidence for colder though wetter LIA climatic conditions from Cornwall Island in the Canadian Arctic Archipelago (Lamoureux 2000; Lamoureux *et al*. 2001) and from central west Greenland (Bennike 1992).

THE FUNCTIONAL SIGNIFICANCE OF PALAEOENVIRONMENTAL VARIATION

The estimated values of past soil moisture, based on macrofossil mosses, suggest significant variation in hydrology during the development of low-centre polygons (Figs 1 & 5). Soil moisture exerts a control on tundra ecophysiology through production, decomposition and nutrient cycling (Miller *et al*. 1984), and a lowered water-table and increased thaw might be expected to accelerate the rate of soil decomposition (CO_2 source) over photosynthesis (CO_2 sink), so that the balance in tundra soils shifts from one of C-input, or storage, to C-output (Billings *et al*. 1982, 1983; Johnson *et al*. 1996). If the effect of decomposition were to increase nutrient availability, there may be an additional uptake of CO_2 owing to higher rates of photosynthesis (Shaver & Chapin 1986; Shaver *et al*. 1998; Johnson *et al*. 2000), although as sink strength in vascular plants decreases, productivity may be offset by substrate-controlled or nutrient-limited CO_2 loss from soil respiration by microorganisms (Nadelhoffer *et al*. 1991; Hobbie 1996; Jonasson *et al*. 1999). Larger sinks of CO_2 are accordingly associated with lower respiration rates in wetter habitats (Vourtilis *et al*. 2000), while short-term experiments designed to explain the net effect of climate warming on soil moisture and the C-balance of tundra plots (Johnson *et al*. 1996) support observational data demonstrating that a shift from net C-input to C-output accompanies the recent drying of tundra habitats (Oechel *et al*. 1993, 1995; Weller *et al*. 1995).

Inferred values for past changes in soil moisture are of a sufficient magnitude to affect CO_2 flux in wetland ecophysiology, varying periodically between values ranging from *c*. 705 ± 126.5% d. wt. (the average and SE for DCA axis 1 scores in the range 0–3) to *c*. 1891 ± 175% d. wt. (range 3–4) (Figs 1 & 5). A corollary is that the observed and predicted effects on tundra soil moisture of human-induced climate warming are, in High Arctic polygon-patterned wetlands, recent additions to previous, long-term fluctuations in ecosystem function. If the inferences of this study are confirmed for Arctic wetlands in general, an inherent variation in ecosystem function controlled by climate change will have to be taken into account when interpreting the results of short-term environmental manipulations (e.g. Arft *et al*. 1999), and of studies attempting to scale-up results from short-term experiments to longer-term processes (McKane *et al*. 1997; Epstein *et al*. 2001).

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References

Allard, M. (1996) Geomorphological changes and permafrost dynamics: key factors in changing arctic ecosystems. An example from Bylot Island, Nunavut, Canada. *Geoscience Canada*, **23**, 205–212.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jónsdóttir, I.S., Laine, K., Lévesque, E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenström, A., Totland, Ø., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M. & Wookey, P.A. (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.

Bennike, O. (1992) Paleoecology and paleoclimatology of a late Holocene peat deposit from Brœndevinsskœr, central west Greenland. *Arctic and Alpine Research*, **24**, 249–252.

Billings, W.D., Luken, J.O., Mortensen, D.A. & Peterson, K.M. (1982) Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia*, **53**, 7–11.

Billings, W.D., Luken, J.O., Mortensen, D.A. & Peterson, K.M. (1983) Increasing carbon dioxide: possible effects on arctic tundra. *Oecologia*, **58**, 286–289.

Billings, W.D. & Peterson, K.M. (1980) Vegetational change and ice-wedge polygons through the thaw-lake cycle in Arctic Alaska. *Arctic and Alpine Research*, **12**, 413–432.

Bliss, L.C. (1997) Arctic ecosystems of North America. *Ecosystems of the World, Vol. 3. Polar and Alpine Tundra* (ed. F.E. Wielgolaski), pp. 551–683. Elsevier, Amsterdam.

Bradley, R.S. (1985) *Quaternary Paleoclimatology*. Unwin-Hyman, Boston.

Bradley, R.S. (1990) Holocene paleoclimatology of the Queen Elizabeth Islands, Canadian High Arctic. *Quaternary Science Reviews*, **9**, 365–384.

Brady (1990) *The Nature and Properties of Soils*. MacMillan, New York.

Chapin, F.S., McFadden, J.P. & Hobbie, S.E. (1997) The role of arctic vegetation in ecosystem and global processes. *Ecology of Arctic Environments*. *British Ecological Society Special Publication no. 13* (eds S.J. Woodin & M. Marquiss), pp. 97–112. Blackwell Science, Oxford.

Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Curtis, J.T. & McIntosh, R.P. (1950) The inter-relations of certain analytic and synthetic phytosociological characters. *Ecology*, **31**, 434–455.

Curtis, J.T. & McIntosh, R.P. (1951) An upland forest continuum in the prairievforest border region of Wisconsin. *Ecology*, **32**, 476–496.

Davis, M.B. (1994) Ecology and paleoecology begin to merge. *Trends in Ecology and Evolution*, **9**, 357–358.

Dostovalov, B.N. & Popov, A.I. (1966) Polygonal systems of ice-wedges and conditions of their development. *Proceedings, First International Permafrost Conference*, pp. 102–105. Publ. 1287: National Academy of Sciences, Washington, DC and National Research Council of Canada, Ottawa.

Ellis, C.J. & Rochefort, L. (2004) Century-scale development of polygon-patterned tundra wetland, Bylot Island (73° N, 80° W). *Ecology*, **85**, 963–978.

Epstein, H.E., Chapin, F.S., Walker, M.D. & Starfield., A.M. (2001) Analyzing the functional type concept in arctic plants using a dynamic vegetation model. *Oikos*, **95**, 239–252.

Fisher, D.A. & Koerner, R.M. (1994) Signal and noise in four ice-core records from the Agassiz ice cap, Ellesmere Island, Canada: details of the last millennium for stable isotopes, melt and solid conductivity. *Holocene*, **4**, 113–120.

Fisher, D.A., Koerner, R.M., Paterson, W.S.B., Dansgaard, W., Gundestrup, N. & Reeh, N. (1983) Effect of wind scouring on climatic records from ice-core oxygen-isotope profiles. *Nature*, **301**, 205–209.

French, H.M. (1996) *The Periglacial Environment*. Longman, Harlow, UK.

Fujii, Y. (1995) Dating of glacier and ice sheet cores. *Quaternary Research*, **34**, 151–156.

Gajewski, K. & Atkinson., D.A. (2003) Climatic change in northern Canada. *Environmental Reviews*, **11**, 69–102.

Gajewski, K., Garneau, M. & Bourgeois, J.C. (1995) Paleoenvironments of the Canadian high arctic derived from pollen and plant macrofossils: problems and potentials. *Quaternary Science Reviews*, **14**, 609–629.

Garneau, M. (1992) Analyses macrofossiles d'un dépôt de tourbe dans la région de Hot Weather Creek, Péninsule de Fosheim, île d'Ellesmere, Territoires du Nord-ouest. *Géographie Physique et Quaternaire*, **46**, 285–294.

Genstat v.7.1. (2003) VSN International Ltd, Rothamsted, UK.

Green, D.G. (1995) Time and spatial analysis. *Statistical Modelling of Quaternary Science Data* (eds D. Maddy & J.S. Brew), pp. 65–105. Technical Guide no. 5, Quaternary Research Association, Cambridge.

Harry, D.G. & Gozdzik, J.S. (1988) Ice wedges: growth, thaw transformation, and palaeoenvironmental significance. *Journal of Quaternary Science*, **3**, 39–55.

Hobbie, S.E. (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, **66**, 503–522.

Hughen, K.A., Overpeck, J.T. & Anderson, R.F. (2000) Recent warming in a 500-year palaeotemperature record from varved sediments, Upper Soper Lake, Baffin Island, Canada. *The Holocene*, **10**, 9–19.

Janssens, J.A. (1983) A quantitative method for stratigraphic analysis of bryophytes in Holocene peat. *Journal of Ecology*, **71**, 189–196.

Janssens, J.A. (1988) Fossil bryophytes and paleoenvironmental reconstruction of peatlands. *Methods in Bryology*. *Proceedings of the Bryological Methods Workshop, Mainz* (ed. J.M. Glime), pp. 299–306. Hattori Botanical Laboratory, Nichinan.

Johnson, L.C., Shaver, G.R., Cades, D.H., Rastetter, E., Nadelhoffer, K., Giblin, A., Laundre, J. & Stanley, A. (2000) Plant carbon–nutrient interactions control CO_2 exchange in Alaskan wet sedge tundra ecosystems. *Ecology*, **81**, 453–469.

Johnson, L.C., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Rastetter, E.R., Laundre, J.A. & Murray, G.L. (1996) Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia*, **108**, 737–748.

Jonasson, S., Michelsen, A., Schmidt, I.K. & Nielsen, E.V. (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology*, **80**, 1828–1843.

Jorgenson, M.T., Racine, C.H., Walters, J.C. & Osterkamp, T.E. (2001) Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, **48**, 551–579.

Kasper, J.N. & Allard, M. (2001) Late-Holocene climatic changes as detected by the growth and decay of ice wedges on the southern shore of Hudson Strait, northern Québec, Canada. *The Holocene*, **11**, 563–577.

Klassen, R.A. (1993) *Quaternary Geology and Glacial History of Bylot Island, Northwest Territories*. Memoir 429. Geological Survey of Canada, Ottawa.

Koerner, R.M. (1977) Devon Island ice cap: core stratigraphy and paleoclimate. *Science*, **196**, 15–18.

Koerner, R.M. & Fisher, D.A. (1990) A record of Holocene summer climate from a Canadian high-arctic ice core. *Nature*, **343**, 630–631.

Kovach, W.L. (1986–1999) *MVSP – a multivariate statistical package for windows v. 3.1*. Kovach Computing Services, Pentraeth, Wales, UK.

LaFarge-England, C., Vitt, D.H. & England., J. (1991) Holocene soligenous fens on a high arctic fault block, northern Ellesmere Island (82° N), N.W.T., Canada. *Arctic and Alpine Research*, **23**, 80–98.

Lamb, H.H. (1965) The early Medieval warm epoch and its sequel. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **1**, 13–37.

Lamoureux, S. (2000) Five centuries of interannual sediment yield and rainfall-induced erosion in the Canadian high arctic recorded in lacustrine varves. *Water Resources Research*, **36**, 309–318.

Lamoureux, S.F. & Bradley, R.S. (1996) A Holocene varved sediment record of environmental change from northern Ellesmere Island, Canada. *Journal of Paleolimnology*, **16**, 239–255.

Lamoureux, S.F., England, J.H., Sharp, M.J. & Bush, A.B.G. (2001) A varve record of increased Little Ice Age rainfall associated with volcanic activity, Arctic Archipelago, Canada. *The Holocene*, **11**, 243–249.

Lewkowicz, A.G. (1994) Ice wedge rejuvenation, Fosheim Peninsula, Ellesmere Island, Canada. *Permafrost and Periglacial Processes*, **5**, 251–268.

Mackay, J.R. (1974) Ice-wedge cracks, Garry Island, North-west Territories. *Canadian Journal of Earth Sciences*, **11**, 1336–1383.

Mackay, J.R. (2000) Thermally induced movements in ice-wedge polygons, western Arctic coast: a long-term study. *Géographie Physique et Quaternaire*, **54**, 41–68.

Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392**, 779–787.

Maxwell, B. (1992) Arctic climate: potential for change under global warming. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective* (eds F.S. Chapin, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda), pp. 11–34. Academic Press, San Diego.

McKane, R.B., Rastetter, E.B., Shaver, G.R., Nadelhoffer, K.J., Giblin, A.E., Laundre, J.A. & Chapin, F.S. (1997) Reconstruction and analysis of historical changes in carbon storage in arctic tundra. *Ecology*, **78**, 1188–1198.

Millar, C.I. & Woolfenden, W.B. (1999) The role of climate change in interpreting historical variability. *Ecological Applications*, **9**, 1207–1216.

Miller, P.C., Miller, P.M., Blake-Jacobson, M., Chapin, F.S., Everett, K.R., Hilbert, D.W., Kummerow, J., Linkins, A.E., Marion, G.M., Oechel, W.C., Roberts, S.W. & Stuart., L. (1984) Plant–soil processes in *Eriophorum vaginatum* tussock tundra in Alaska: a systems modeling approach. *Ecological Monographs*, **54**, 361–405.

Mitchell, F.F.B., Manabe, S., Tokioka, T. & Meleshoko, V. (1990) Equilibrium climate change. *Climate Change, the IPCC Scientific Assessment* (eds J.T. Houghton, G.J. Jenkins & J.J. Ephraums), pp. 131–172. Cambridge University Press, Cambridge.

Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. & Laundre, J.A. (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. *Ecology*, **72**, 242–253.

Nelson, F.E., Anisimov, O.A. & Shiklomanov, N.I. (2001) Subsidence risk from thawing permafrost. *Nature*, **410**, 889–890.

Nyholm, E. (1954–1969) *The Illustrated Moss Flora of Fennoscandia. II. Musci Fascile 1–6*. Swedish Natural Science Research Council, Stockholm.

Oechel, W.C., Hastings, S.J., Vourtilis, G., Jenkins, M., Riechers, G. & Grulke, N. (1993) Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, **361**, 520–523.

Oechel, W.C. & Vourtilis, G.L. (1994) The effects of climate change on land–atmosphere feedbacks in arctic tundra regions. *Trends in Ecology and Evolution*, **9**, 324–329.

Oechel, W.C., Vourtilis, G.L., Hastings, S.J. & Bochkarev, S.A. (1995) Change in arctic CO_2 flux over two decades: effects of climate change at Barrow, Alaska. *Ecological Applications*, **5**, 846–855.

Ovenden, L. (1982) Vegetation history of a polygonal peatland, northern Yukon. *Boreas*, **11**, 209–224.

Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A. & Zielinski, G. (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.

Paterson, W.S.B., Koerner, R.M., Fisher, D., Johnson, S.J., Clausen, H.B., Dansgaard, W., Bucher, P. & Oeschger, H. (1977) An oxygen-isotope climatic record from the Devon Island ice cap, arctic Canada. *Nature*, **266**, 508–511.

Post, W.M., Emanuel, W.R., Zinke, P.J. & Stangenberger, A.G. (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156–159.

Rovansek, R.J., Hinzman, L.D. & Kane, D.L. (1996) Hydrology of a tundra wetland complex on the Alaskan arctic coastal plain, U.S.A. *Arctic and Alpine Research*, **28**, 311–317.

Shaver, G.R., Billings, W.D., Chapin, F.S., III, Giblin, A.E., Nadelhoffer, K.J., Oechel, W.C. & Rastetter, E.B. (1992) Global Change and the carbon balance of Arctic ecosystems. *BioScience*, **42**, 433–441.

Shaver, G.R. & Chapin, F.S. (1986) Effect of fertilizer on production and biomass of tussock tundra, Alaska, USA. *Arctic and Alpine Research*, **18**, 261–268.

Shaver, G.R., Johnson, L.C., Cades, D.H., Murray, G., Laundre, J.A., Rastetter, E.B., Nadelhoffer, K.J. & Giblin, A.E. (1998) Biomass and CO_2 flux in wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs*, **68**, 75–97.

Sjörs, H. (1950) On the relation between vegetation and electrolytes in north Swedish mire waters. *Oikos*, **2**, 241–257.

Stuiver, M., Burr, G., Hughen, K.A., Kromer, B., McCormac, G., Van, der, Plicht, J., Spurk, M., Reimer, P.J., Bard, E. & Beck, J.W. (1998) INTCAL98 radiocarbon age calibration, 24 000-0 cal. yr BP. *Radiocarbon*, **40**, 1041–1083.

Tallis, J.H. (1985) Mass movement and erosion of a southern Pennine blanket peat. *Journal of Ecology*, **73**, 283–315.

Tarnocai, C. & Zoltai., S.C. (1988) Wetlands of arctic Canada. *Wetlands of Canada* (National Wetlands Working Group, Canada Committee on Ecological Land Classification), pp. 30–53. Canadian Wildlife Service, Ottawa, Canada.

Vardy, S.R., Warner, B.G. & Aravena, R. (1997) Holocene climate effects on the development of a peatland on the

Tuktoyaktut Peninsula, Northwest Territories. *Quarternary Research*, **47**, 90–104.

Vourtilis, G.L., Harazono, Y., Oechel, W.C. & Yoshimoto, M. (2000) Spatial and temporal variations in hectare-scale net CO_2 flux, respiration and gross primary production of arctic tundra ecosystems. *Functional Ecology*, **14**, 203–214.

Vourtilis, G.L. & Oechel, W.C. (1997) Landscape-scale CO_2, H_2O vapour and energy flux of moist-wet coastal tundra ecosystems over two growing seasons. *Journal of Ecology*, **85**, 575–590.

Weller, G., Chapin, F.S., Everett, K.R., Hobbie, J.E., Kane, D., Oechel, W.C., Ping, C.L., Reeburgh, W.S., Walker, D. & Walsh, J. (1995) The arctic flux study: a regional view of trace gas release. *Journal of Biogeography*, **22**, 365–374.

Williams, L.D. & Wigley, T.M.L. (1983) A comparison of evidence for late Holocene summer temperature variations in the northern hemisphere. *Quaternary Research*, **20**, 286–307.

Wookey, P.A. & Robinson., C.H. (1997) Responsiveness and resilience of high arctic ecosystems to environmental change. *Opera Botanica*, **132**, 215–231.

Young, K.L. & Lewkowicz, A.G. (1990) Surface energy balance of a perennial snow bank, Melville Island, Northwest Territories, Canada. *Arctic and Alpine Research*, **22**, 290–301.

Young, K.L., Woo, M.-K. & Edlund, S.A. (1997) Influence of local topography, soils, and vegetation on microclimate and hydrology at a high arctic site, Ellesmere Island, Canada. *Arctic and Alpine Research*, **29**, 270–284.

Zoltai, S.C., McCormick, K.J. & Scotter, G.W. (1983) *A Natural Resource Survey of Bylot Island and Adjacent Baffin Island, Northwest Territories*. Parks Canada, Ottawa.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com:

Appendix S1 Evidence of allochthonous deposition

Appendix S2 Development of a radiocarbon time-frame

Appendix S3 Subfossil moss taxa abbreviated in Figs 2 & 3.

Appendix S4 Anomalous radiocarbon dates