CENTURY-SCALE DEVELOPMENT OF POLYGON-PATTERNED TUNDRA WETLAND, BYLOT ISLAND (73° N, 80° W)

Christopher James Ellis[1] and Line Rochefort

Département de phytologie and Centre d'études nordiques, Pavillon Paul-Comtois, Université Laval, Québec, Québec, Canada G1K 7P4

Abstract. Previous studies in tundra ecology provide evidence for sensitivity of the vegetation–soil complex to climate. Short-term experiments (≤10 yr) suggest that climate change may have a decade-scale effect on soil moisture, decomposition and nutrient availability, plant phenology, and plant growth. In contrast, there exists little evidence to confirm or refute the role of climate in structuring tundra vegetation over longer time scales (10 to 1000 yr). This study accordingly examines ~1500 yr in the stratigraphy of two permafrost sediment cores from a High Arctic, polygon-patterned, graminoid–moss tundra. Present-day bryophyte–environment relationships are quantified, and the radiocarbon-dated macrofossil record of bryophytes is used to reconstruct past changes in soil moisture. The paleoecological record is characterized by pronounced variability during polygon development. As the hydrology of tundra polygons is controlled by known climatic and geomorphologic mechanisms, the recurrent development of polygon vegetation (cf. hydrologic change) is compared to an independent paleoclimatic proxy for net radiation (R_n). Based on this comparison, the vegetation provides support for a pronounced shift to colder and wetter conditions during the Little Ice Age (~300–465 yr BP), though the long-term response to past climate change is otherwise equivocal. We suggest accordingly that autogenic geomorphologic-vegetation processes may have been generally more important than climate in the long-term development of the polygon-patterned wetland examined. A framework for such processes is presented. We caution that previous research to simulate and describe the effects of climate warming might not have properly accounted for the dynamic role of geomorphology in regulating tundra microclimate.

Key words: bryophytes; climate change; High Arctic wetland; Little Ice Age; paleohydrology; tundra polygons.

Introduction

Recent research in tundra ecology has focused on the spatial structure and function of tundra vegetation (Shaver and Chapin 1991) and soils (Giblin et al. 1991, Nadelhoffer et al. 1991), and the effects on the vegetation–soil complex of simulated environmental change (Chapin et al. 1995, Robinson et al. 1995, 1998, Chapin and Shaver 1996). These short-term studies provide evidence for a pronounced sensitivity of the tundra to climate. Indirect and direct climatic effects may include, for example, an effect on soil moisture, decomposition and nutrient availability (Chapin et al. 1995, Jonasson et al. 1999, Johnson et al. 2000) and a species-specific temperature response in phenology and growth (Wookey et al. 1993, Molau 1997). However, the effect of climate on tundra ecology should also be examined by describing the sensitivity of tundra ecosystems to past climatic variability, using the paleoecological record.

Recent paleoenvironmental research points to an insolation- and volcanically forced decade- to century-scale variability in the Arctic climate (Overpeck et al. 1997, Mann et al. 1998). The sensitivity of High Arctic tundra vegetation in response to this intrinsic pattern of environmental change remains unknown. There is limited evidence from Holocene pollen records to demonstrate a millennium-scale response in Arctic vegetation to a Holocene thermal maximum that occurred in the Eastern Arctic Archipelago between ~7000 and 5000 yr BP (Mode 1996), though the response is weak in pollen records from High Arctic sites (Hyvärinen 1985, Bourgeois 1986). Studies that have examined decade- to century-scale processes in tundra vegetation are inconclusive (Ovenden 1982) or contradictory, some invoking local geomorphology and not climate (LaFarge-England et al. 1991) while others support climate (Garneau 1992, Vardy et al. 1997) as a controlling factor in vegetation–soil development. Thus, it remains impossible to determine the extent to which the climatic sensitivity of tundra vegetation described by short-term studies might contribute also to inherent, long-term, vegetation change. Understanding such long-term change is likely to be critical in confirming or refuting the "scaling-up" of previous small-scale experiments.
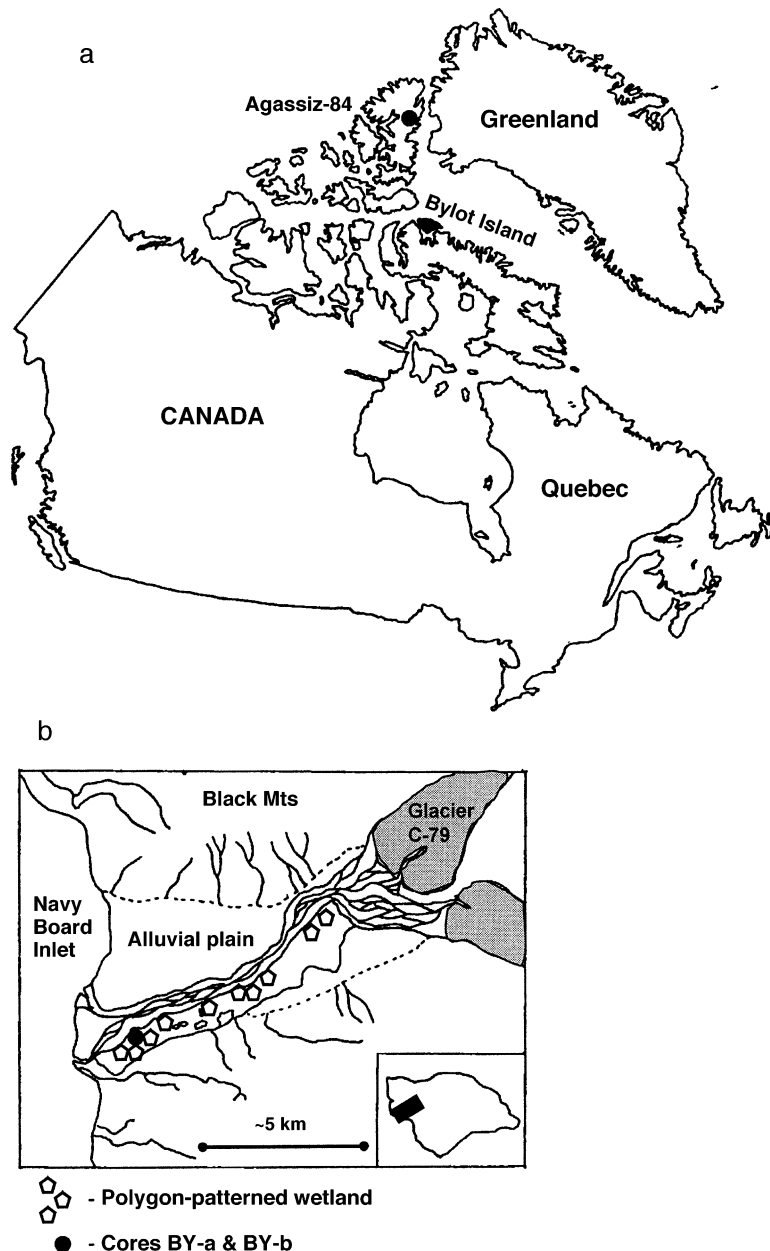
FIG. 1. Map showing (a) the location of Bylot Island and the Agassiz-84 ice core (Ellesmere Island) in the Canadian Arctic Archipelago, and (b) the approximate position in the Qunguliqtut Valley of sediment cores BY-a and BY-b.

This paper examines evidence for and against past century-scale change in the vegetation structure and function of a High Arctic tundra. It is significant in describing one of very few studies as yet undertaken to describe in detail the long-term development of a High Arctic terrestrial ecosystem. Modern bryophyte–environment relationships are quantified and combined with the radiocarbon-dated macrofossil record to describe ~1500 yr in the vegetation development and paleohydrology of a polygon-patterned tundra wetland on Bylot Island, in the Canadian Arctic Archipelago.

STUDY SITE

The study site is a wetland area of graminoid–moss tundra (sensu Bliss 1997) occurring on eolian terraces to the south of the Qunguliqtut Valley in western Bylot Island (73°08′ N, 80°00′ W; Fig. 1). Bylot Island forms part of the Canadian Arctic Archipelago between latitudes 72° and 74° N and longitudes 75° and 82° W. For the period 1951—1980, mean total annual precipitation at Pond Inlet (adjacent to Baffin Island) was 159 mm, while the warmest month (July) had a mean air temperature of 7.9°C (Zoltai et al. 1983).

Qunguliqtut Valley comprises a braided river which drains glaciers from the Island's central ice cap and enters Navy Board Inlet as a wide delta. It is bound to the north and the south by hills composed of Cretaceous and Tertiary age sedimentary rock. An aggradation of alluvial fan sediments on the plain to the north of the river is causing the fluvial erosion of low-lying terraces to the south (Allard 1996). The southern terraces have developed as the accretion of eolian sands and silts and the concurrent deposition of peat. Their formation is thought to have been initiated sometime after a marine transgression that followed glacial retreat, dated from shell fragments to ~6000 yr BP, but before active peat deposition, which commenced at or before ~2900 yr BP (Allard 1996). A network of ice wedges has developed concomitant with the aggradation of the terraces (for process descriptions, see French 1996). The syngenetic growth of ice wedges has resulted in the extensive development of polygon-patterned ground, and the southern bank of the river today includes a range of polygon-types and associated land forms: low-center and high-center polygons, polygon ponds, and thaw lakes (cf. Billings and Peterson 1980). The polygon complex is fed by melt water from the hills to the south, and the vegetation is typically 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.).

METHODS

Field methods

Two sediment cores were collected in June 1999, from the center of adjacent high-center polygons separated by a secondary ice wedge (BY-a and BY-b, 210 cm and 204 cm deep, respectively, and ~15 m apart). Sediments from the active layer (to ~30 cm depth) were sampled as 2-cm slices cut with a knife from an unfrozen peat monolith (~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). The low torque at the chamber, when coring below a depth of ~2 m, made it impossible to sample the entire sediment column, and neither of the cores encompass the total sediment depth. The cored sections were examined in the field to ensure that sediments were horizontally bedded. The frozen 50-cm segments were cut into 2-cm slices which were then sealed in labeled polythene bags. Samples were stored in a dark cool box packed with ice for the remainder of the field season (eight weeks) and thereafter in the dark at 4°C.

Vegetation description to quantify bryophyte–environment relationships was carried out in late July and early August 2000. Bryophyte distribution in the polygon wetland was compared to four generic environmental variables: (1) soil moisture (hydrological), (2)

pH, (3) corrected conductivity of a bulk soil–water sample (both chemical), and (4) soil organic/mineral matter as loss on ignition (LOI) (physical). Present-day bryophyte assemblages were quantified as presence–absence data in each of 25, 5 × 5 cm subunits comprising a single 25-cm quadrat, totaling an unsubdivided area of 625 cm^2. Percentage frequency of occurrence was thus estimated on a 25-point scale between 0 and 1. Species identification and nomenclature follows Nyholm (1954–1964). A total of 99 quadrats were systematically chosen and examined to include representative samples from recognized habitats: low-center polygon ridges, flanks and centers, high-center polygon centers and eroding flanks, polygon-pond flanks and standing water, water courses, and areas of active eolian 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 center of each quadrat and divided into two equal halves, which were sealed in separate polythene bags. One turf from each quadrat was preserved for laboratory analysis. It was sealed in a second outer bag and stored for between two and three weeks in a dark cool box packed with ice. The green ''living'' moss layer (~1 cm in thickness) was removed from the second turf. The remaining peat–sediment sample was weighed wet then dried for 24 h at ~60°C in a wooden drying box suspended above a diesel room heater. The dry mass was measured and samples were resealed.

Laboratory analyses

Macrofossils and LOI.—Plant macrofossil analysis was used to describe the vegetation history of the polygons. A 1-cm^3 sediment sample was extracted from each of the contiguous 2-cm slices. Samples were gently macerated in ~20 mL of 7% potassium hydroxide (KOH) and simmered at 90°C for 45 min. The sediment–KOH mixture was filtered through a 0.3-mm wire sieve and the residue washed into a clear Petri dish. Macrofossils were scored as presence/absence in 50, equidistant, 2-mm^2 quadrats, placed within the confines of the Petri dish (Tallis 1985). Taxa were quantified as the percentage frequency of occurrence for each stratigraphic level. Macrofossil specimens (typically bryophyte stems and leaves) were identified at 6–40×, 200×, and 400× magnification, according to a modern reference collection. Identification and nomenclature follows Nyholm (1954–1969). Specimens of macrofossil and present-day bryophyte taxa were collected, preserved, and placed in the Herbier Louis-Marie (QFA) at Université Laval, Quebec, Canada.

A second sample from each horizon was oven dried at 105°C for 18 h, weighed, and the percentage contribution of mineral material quantified as ash weight after incineration (LOI) at 550°C for 5 h. Stratigraphic values are expressed as the seven-point weighted av-

TABLE 1. Radiocarbon dates from Bylot Island (BY-a and BY-b); with calibrated ages calculated using INTCAL 98 (Stuiver et al. 1998).

Core	Depth (cm)	Lab code	Conventional radiocarbon age (yr BP ± 1 SE)	Calibrated radiocarbon age (calibrated yr BP and 1 sigma range)	Stratigraphic setting (i.e., macrofossil shift upward across the horizon)
BY-1a	2–6	Beta 143338	120 ± 40	140 (271–0)	Surface peat
	208–210	Beta 143339	1660 ± 40	1545 (1600–1520)	Base of core
BY-1a	18	Beta 152427	270 ± 40	300 (420–290)	Shift from wet to dry assemblage
	40	Beta 152428	390 ± 40	480 (500–330)	Shift from dry to wet assemblage
	52–54	Beta 152429	520 ± 40	530 (540–520)	Shift from wet to dry assemblage
	62	Beta 152430	710 ± 40	660 (680–650)	Shift from dry to wet assemblage
	74	Beta 152431	620 ± 40	590 (650–550)	Shift from wet to dry assemblage
	114	Beta 152432	1040 ± 40	950 (970–930)	Shift from dry to wet assemblage
	140–142	Beta 152433	1590 ± 40	1510 (1530–1420)	Shift from wet to dry assemblage
	162	Beta 152434	1520 ± 40	1400 (1420–1350)	Shift from dry to wet assemblage
By-1b	10	Beta 152435	210 ± 40	165 (298–4)	Shift from wet to dry assemblage
	170	Beta 152436	1370 ± 40	1290 (1300–1270)	Shift from wet to dry assemblage
	182	Beta 152437	1470 ± 40	1340 (1390–1310)	Shift from dry to wet assemblage

erage, calculated to emphasize low-frequency cycles and minimize noise (Green 1995).

Radiocarbon dating.—Samples were pretreated before being submitted for radiocarbon analysis, to mitigate against contamination by carbon-rich Tertiary deposits (Gajewski et al. 1995), which occur on Bylot Island adjacent to and within the catchment area of the study site (Klassen 1993). A sediment sample of ~2 cm^3 was washed in distilled water and sieved through a 0.3-mm sieve. In the absence of woody remains, bryophyte stems and leaves were collected from the residue and rinsed in distilled water. They were dried at 60°C and samples of ≥0.1 g were submitted for radiocarbon analysis by accelerator mass spectrometry (AMS).

Bryophyte remains from the surface and basal sediments of BY-a were radiocarbon dated at Beta Analytic, (Miami, Florida, USA). A further 11 samples were dated (eight from BY-a and three from BY-b) from horizons delimiting stratigraphically important levels in the macrofossil record: i.e., they were positioned at horizons that maximized variance in the macrofossil record intercalated between dated levels. Results of the radiocarbon-analysis are presented in Table 1. Conventional radiocarbon ages (years BP) were calibrated using INTCAL 98 (Stuiver et al. 1998) and are presented in the text as calibrated years before present (calibrated yr BP).

Soil physical and chemical properties.—The turfs collected from each of the quadrats were reweighed and oven dried at 105°C for 18 h. The laboratory dry mass was used to estimate a soil moisture value for each quadrat, as percentage dry mass per unit volume. The content of organic matter and mineral material was estimated as LOI for the same samples, after incineration at 550°C for 5 h. Within 5 d of their arrival at Université Laval, the turfs that had been previously stored as fresh material were analyzed for pH, using a Fisher Scientific Accumet model 10 pH meter (Fisher Scientific, Hampton, New Hampshire, USA), and for conductivity (μS/cm), using an Orion model 122 con-

ductivity meter (Orion, Milan, Spain). Conductivity was corrected for temperature and pH according to Sjörs (1950).

Statistical analyses

Quadrat data.—An ordination of the quadrat data was performed using a canonical correspondence analysis (with rare species downweighted) and computed using the program MVSP 3.1 (Kovach 1986–1999). Derivation of each component was constrained using the four environmental variables. Additionally, we estimated for 16 of the most common bryophyte taxa (1) the weighted average optima and (2) the tolerance range (Birks 1995) for soil moisture and pH. The results provide an approximation of parameters otherwise derived from unimodal Gaussian response curves (Ter Braak and Prentice 1988), examples of which have been described for bryophytes by Birks et al. (1997). The results are tested and consequently applied to the macrofossil record, providing an analogue for the reconstruction of soil moisture during the development of BY-a and BY-b.

Stratigraphic record.—Polygon hydrology is controlled by known climatic and geomorphologic mechanisms. Assuming each polygon acts as a watershed and basin (i.e., ridges and polygon centers), the water balance (ΔS) of a plot within a given polygon can be approximated as

$$\Delta S = P + Q_g + Q_s - ET \tag{1}$$

where P is precipitation, Q_g is groundwater flow through the active layer soil, Q_s is surface inflow or outflow, and ET is evapotranspiration (Rovansek et al. 1996). To estimate the role of climate during vegetation development, the paleohydrologic record of soil moisture is compared to an independent proxy-climatic record for the Eastern Arctic Archipelago: five-year average values of percentage melt, measured in the stratigraphy of the Agassiz-84 ice-core, Ellesmere Island (Koerner and Fisher 1990). Linear regression was used
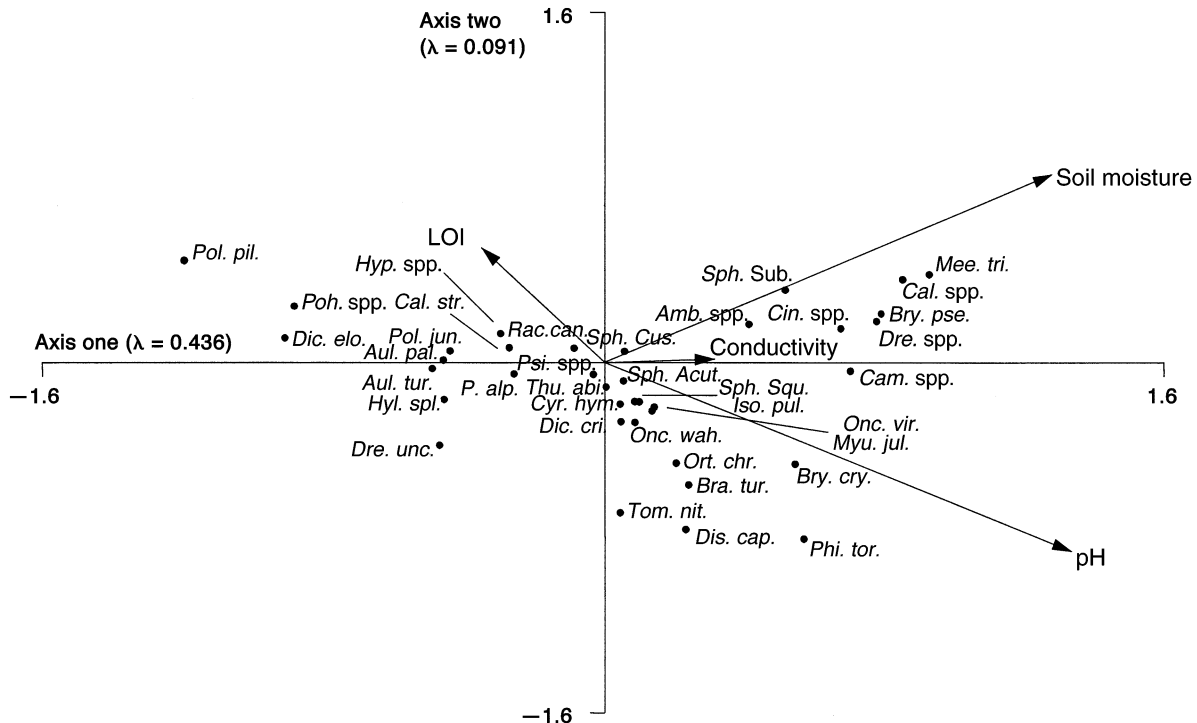
FIG. 2. Species ordination based on the canonical correspondence analysis to describe the present-day distribution of bryophytes. Bryophyte taxa, in alphabetical order: *Amblystegium riparium, Aulacomnium palustre, Aulacomnium turgidens, Brachythecium turgidum, Bryum cryophilum, Bryum pseudotriquetrum, Calliergon giganteum* and *sarmentosum, Calliergon straminuem, Campylium arcticum* and *stellatum, Cinclidium arcticum* and *latifolium, Cyrtomnium hymenophylloides, Dicranella crispa, Dicranum* cf. *elongatum, Distichium capillaceum, Drepanocladus* spp. excl. *uncinatus, Drepanocladus uncinatus, Hylocomnium splendens, Hypnum* spp., *Isopterygium pulchellum, Meesia triquetra, Myurella julacea, Oncophorus virens, Oncophorus wahlenbergii, Orthothecium chryseum, Philonotis tormentella, Pohlia* spp., *Polytrichastrum juniperum, Polytrichum alpinum, Polytrichum piliferum, Psilobium* spp., *Racomitrium canescens, Sphagnum* section Acutifolia, *Sphagnum* section Cuspidata, *Sphagnum* section Squarrosa, *Sphagnum* section Subsecunda, *Thuidium abietunum,* and *Tomenthypnum nitens.*

to compare the stratigraphic records for those periods intercalated between radiocarbon dates, by matching horizons of corresponding age. Reconstructed soil moisture based on macrofossil analysis (see *Statistical analysis: Quadrat data*) was regressed against the Agassiz-84 paleoclimatic record. Variance in the macrofossil record attributable to paleoclimatic change was therefore estimated as values of R^2. In addition, to account for a possible lag in the vegetation response, the reconstructed record of soil moisture (macrofossils) was compared to preceding paleoclimatic horizons (Agassiz-84), for contiguous intervals of between 5 and 40 yr, up to a maximum lag period of 130 yr. The resolution of the comparison and attendant lag period were therefore determined by the rate of sedimentation.

RESULTS

Bryophyte–environment relationships

In describing the relationship between bryophytes and environmental variables, the first axis of the canonical correspondence analysis explains 21.8% of variation in the data set, the second axis only 4.5% (26.3% cumulative). Accordingly, an ordination of species scores and environmental covariates is plotted for the first two axes only (Fig. 2). Soil moisture and pH correlate with the first axis and are apparently important factors explaining the distribution of the bryophyte taxa. Conductivity and loss on ignition are less significant. The occurrence of mesic species toward the left of the diagram (e.g., *Dicranum* cf. *elongatum, Drepanocladus uncinatus, Hylocomnium splendens, Polytrichum piliferum*) and hydric species toward the right (e.g., *Calliergon giganteum/sarmentosum, Drepanocladus* spp., *Meesia triquetra*) is consistent with covarying environmental gradients in soil moisture and pH. These patterns are manifest in the present-day polygon complex as a predictable change in the bryophyte community along a topographic gradient from well-drained polygon ridges (mesic) to the wet centers of low-center polygons (hydric).

The estimated optima and tolerance range of the sixteen most common taxa are plotted for soil moisture and pH as a bivariate environmental ordination (Fig. 3). There are three species clusters, two of which are contrasting: (1) a group whose estimated optima are located in a region of relatively dry soil moisture values and lower pH (mesic group, Fig. 3, lower left); (2) a cluster whose estimated optima occupy a range of rel-
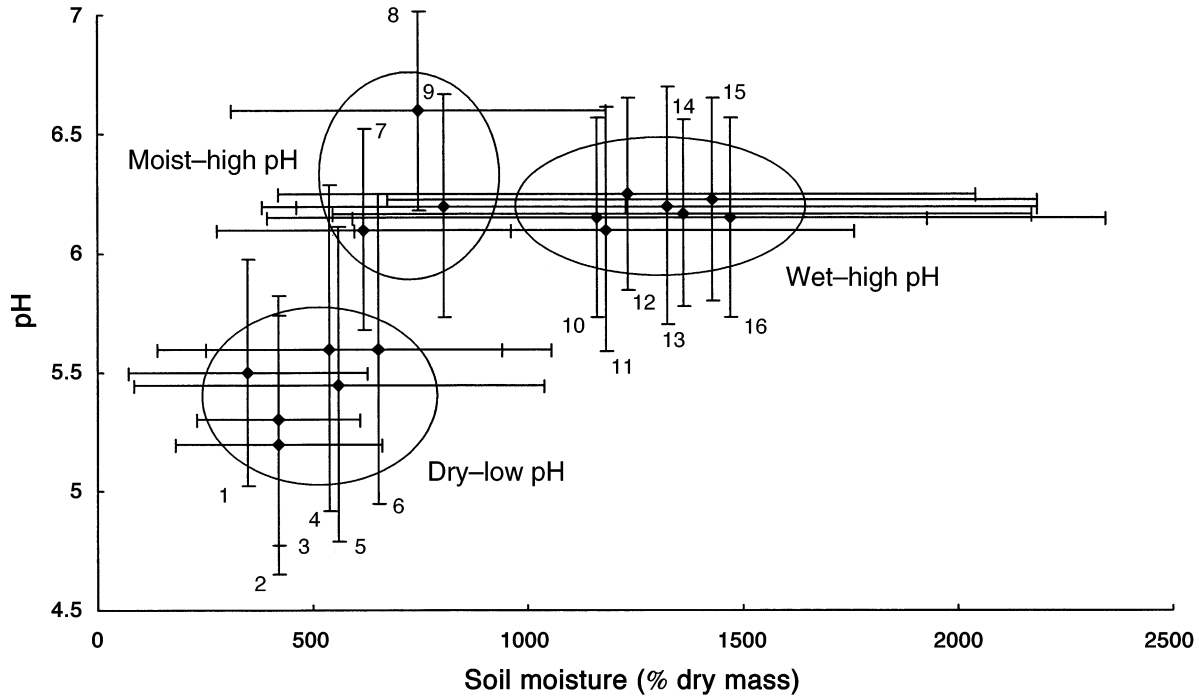
Fig. 3. Bivariate ordination for the 16 most common bryophyte taxa, calculated as the estimated optima (points) and range (bars) of values for soil moisture and pH. Distinct ecological groups are delimited as follows: 1, *Hylocomnium splendens*; 2, *Pohlia* spp.; 3, *Dicranum* cf. *elongatum*; 4, *Aulocomnium turgidum*; 5, *Polytrichum* spp.; 6, *Aulocomnium palustre*; 7, *Tomentypnum nitens*; 8, *Philonotis tormentella*; 9, *Brachythecium turgidum*; 10, *Cinclidium arcticum/latifolium*; 11, *Sphagnum* spp.; 12, *Campylium stellatum/arcticum*; 13, *Drepanocladus* spp.; 14, *Bryum pseudotriquetum*; 15, *Meesia triquetra*; 16, *Calliergon giganteum/sarmentosum*.

atively wet soil moisture values and higher pH (hydric group, Fig. 3, upper right); and (3) a third cluster (intermediate group), which is transitional between the mesic and hydric groups, and comprises species whose estimated optima occur within a region of low to medium soil-moisture values and relatively high pH.

The estimated optima are significantly different for two of the species groups, mesic and hydric. This was tested using a modified *t* test for small populations with unequal variances (Parker 1979); for soil moisture, $t = 12.74$ and $P < 0.001$; for pH, $t = 12.13$ and $P < 0.001$, both with df $= 11$.

Radiocarbon timescale

Linear interpolation between radiocarbon dates is used to estimate a continuous time scale, though two of the radiocarbon dates in BY-a are inverted (Fig. 4). There are therefore two regions in the stratigraphy of
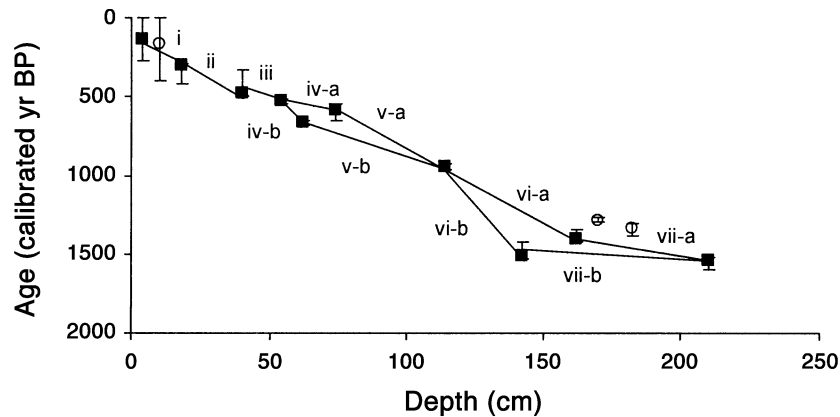

Fig. 4. Sediment age–depth profile, based on calibrated radiocarbon dates and one-sigma errors for BY-a (filled squares) and BY-b (empty circles). The interpolation between radiocarbon dates is shown for BY-a.

BY-a where the dating scheme bifurcates (incorporating sections IV and V and VI and VII). The limited number of radiocarbon dates in BY-b provides a discrete timescale only (Fig. 4).

The dating scheme for BY-a and BY-b demonstrates the accretion of permafrost sediments since at least ~1500 calibrated yr BP (Table 1). Recent dates for the near surface sediments in BY-a (~140 calibrated yr BP, 2–6 cm depth) and BY-b (~165 calibrated yr BP, 10 cm depth) identify the age at which the active accumulation of sediment ceased, presumably evidencing the degradation of the former low-center polygon complex and the initiation of the current high-center polygons.

Macrofossil record

The macrofossil records for BY-a and BY-b (Figs. 5 and 6, respectively) demonstrate significant vegetation change during the development of the polygons examined, while the correspondence between soil moisture and the occurrence of bryophyte taxa (Figs. 2 and 3) provides a clear analogue for the interpretation of the paleoecological record. The macrofossil records suggest that while BY-a has fluctuated between distinct periods of drier and wetter conditions (characterized in Fig. 5 by alternate peaks in the remains of *Drepanocladus* spp. and *Aulacomnium palustre*), BY-b has, over the developmental period examined, been consistently wetter. Above a layer of *Aulacomnium palustre* at the base of BY-b in Fig. 6, and except for several smaller layers characterized by *Aulacomnium* spp. at ~170–160 cm, 110 cm, and 10–0 cm depth, the stratigraphy is dominated by known hydric elements, especially *Drepanocladus* spp. with *Cinclidium* spp., *Bryum* cf. *pseudotriquetrum*, *Meesia triquetra*, and *Calliergon giganteum* and *sarmentosum*. In contrast to BY-a, the development of BY-b appears to have been buffered against climatic and geomorphologic effects on soil moisture (cf. Eq. 1), explaining the different macrofossil records in closely adjacent cores. However, where there is evidence for paleoecological change in either BY-a or BY-b, the moisture preferences of the macrofossil taxa suggest that the effect on soil moisture is likely to have been significant (cf. Fig. 3 with Figs. 5 and 6).

The environmental gradients estimated in Fig. 3 are too short (<2 SD in Fig. 2) to permit the application of Gaussian-type models to the macrofossil record (Birks 1995). However, the contribution of hydric and mesic macrofossil elements can be used to approximate relative values of soil moisture during polygon development. Changes in the contribution of macrofossils classified as mesic and hydric taxa in Fig. 3 are therefore plotted for BY-a and BY-b in Fig. 7, along with the percentage of mineral material. The input of mineral material in BY-a is apparently closely associated with the paleohydrologic record, increasing and decreasing during wetter and drier periods, respectively.

Core BY-b, which has a wetter, less variable hydrologic record, also has a sediment lithology with higher though less variable values of mineral material; the variance in the percentage of mineral material is significantly greater in the stratigraphy of BY-a ($s^2 = 99$) than BY-b ($s^2 = 49$), $F_{104, 102} = 2.02$, and $P < 0.05$.

Invoking an assumption that (i) the proxy data and (ii) the dating framework for the sediment stratigraphy of BY-a (Table 1, Fig. 4) and the Agassiz-84 ice-core (Fujii 1995) are accurate, mesic-hydric elements in the macrofossil record are tentatively compared to values of percentage melt for periods intercalated between radiocarbon dates (Fig. 8). Maximum values of R^2 therefore vary from 0.72 with a time lag of 15 yr during the period ~300–465 calibrated yr BP (section II) to 0.08 with a time lag of 5 yr during the period ~1400–1540 calibrated yr BP (section VIIa), though they are generally less than 0.5 and occur mostly between ~0.15 and 0.4 (Fig. 8).

DISCUSSION

The permafrost cores BY-a and BY-b demonstrate striking temporal and spatial variation in the vegetation development of a High Arctic tundra wetland during the past ~1500 yr. This variability contrasts importantly with the linear succession toward terrestrialization described for polygon-patterned, peat-forming wetlands in the western Canadian Arctic and sub-Arctic (Zoltai and Tarnocai 1975). Three points in the following discussion are critical to the explanation of this variation. First, temporal shifts in mesic and hydric bryophyte groups are consistent with the sensitivity of Arctic vegetation to local variation in soil moisture (Drury 1962, Peterson and Billings 1980, Sheard and Geale 1983, Miller and Alpert 1984). Second, the vegetation of the polygons was apparently affected by wetter and cooler climatic conditions during the Little Ice Age of ~300–465 calibrated yr BP. However, third, climate change has not predominantly controlled long-term fluctuations in vegetation composition (Fig. 8) and recurrent shifts in mesic and hydric elements are attributable instead to autogenic polygon development. The palaeoecology of cores BY-a and BY-b thus indicates that very local geomorphologic processes may play a significant role in determining moisture regime and microhabitat for particular vegetation types.

The paleoenvironmental record

The ordination of bryophyte species along a moisture gradient agrees with previous observations by Steere (1976, 1978), Vitt and Pakarinen (1977) and LaFarge-England (1989), who found that water availability was the single most important factor controlling the distribution of Arctic bryophytes. However, the corresponding influence of pH on bryophyte distribution, as well as moisture, accords well with studies in the plant ecology of north temperate and boreal fens. Such studies have described a nonrandom series of bryophytes along
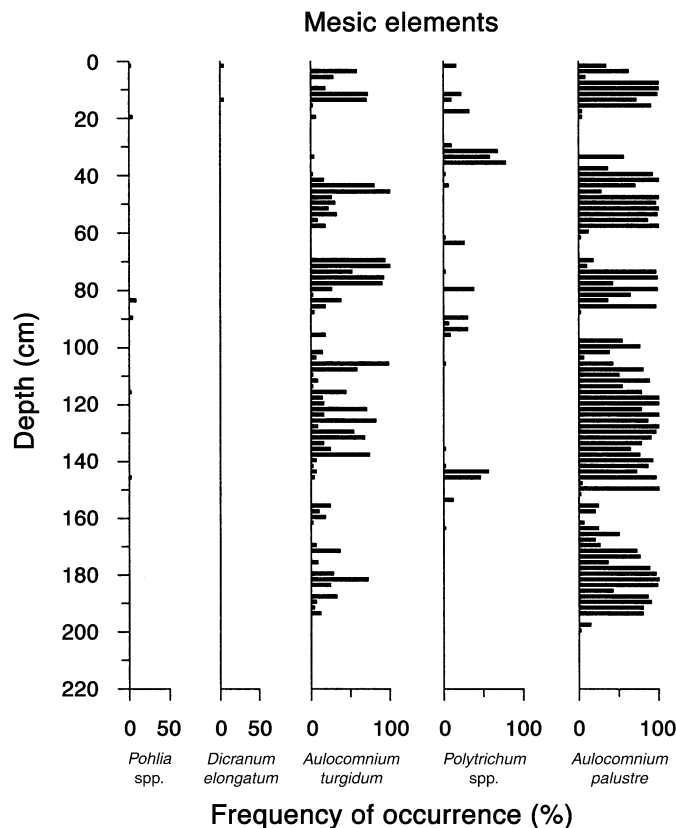
FIG. 5. Summary stratigraphic record: macrofossil bryophyte taxa in core BY-a. Dominant macrofossil bryophytes are arranged as a hydrological series, with mesic and hydric elements delimited (cf. Figs. 2 and 3).

environmental gradients controlled principally by microtopography, namely, from higher (hummocks) to lower (pools) and, accordingly, dry to wet (Vitt et al. 1975, Slack et al. 1980) and low to high pH (Chee and Vitt 1989, Vitt and Chee 1990). The specific pattern of bryophyte species may vary across climatic boundaries (Gignac et al. 1991) and an analogous ecological gradient is evidenced by the ordination of Arctic species (Fig. 2). The macrofossil record of bryophytes provides therefore a credible proxy for the reconstruction of past relative wetness or dryness (Fig. 7).

Climate change and polygon development

Evidence for the effect of regional climate on the development of ice-wedges is provided by their distribution (Péwé 1966), though the study site lies well within the climatic threshold for ice-wedge activity (Zoltai et al. 1983) and is likely to have been sufficiently cold for persistent ice-wedge growth during at least the past 3000 yr (Bradley 1990). To test for the role of climate in the development of the polygon complex, the paleohydrologic record of BY-a (the core with the most variable stratigraphy) was compared to 5-yr average values of percentage melt in the stratigraphy of the Agassiz-84 ice core, Ellesmere Island (Koerner and Fisher 1990). Measured as the changing concen-

tration with depth of textural melt layers, percentage melt is a proxy for past summer temperature during the period of snow deposition (Koerner 1977, Koerner and Fisher 1990). The record of percentage melt in Agassiz-84 is a significant paleoclimatic indicator for the Eastern Arctic Archipelago (Bradley 1990). It reflects long-term variations in net radiation (R_n), which controls spring snowmelt (Young and Lewkowicz 1990, Young et al. 1997) and evapotranspiration (ET) (Vourtilis and Oechel 1997). The additional climatic effect of precipitation (P) will be strongly modified by the local topography (Rovansek et al. 1996, Young et al. 1997).

Compared as a linear regression, values of R^2 are highest (>0.72) for the period comprising section II, ~300–465 calibrated yr BP (Fig. 8). This period is coeval with the Little Ice Age (Lamb 1977), the effects of which are evident in the geomorphology of Qunguliqtut Valley as the advance and subsequent retreat of a local glacier, C-79 (Klassen 1993, Allard 1996). The percentage contribution of hydric elements in BY-a increases (as increasing soil moisture) as the paleoclimatic record indicates cooling (as decreasing values of percentage melt). The direction of vegetation change thus is consistent with recent evidence to suggest colder though wetter climatic conditions in the Canadian Arctic Archipelago during this period (Lamoureux 2000,
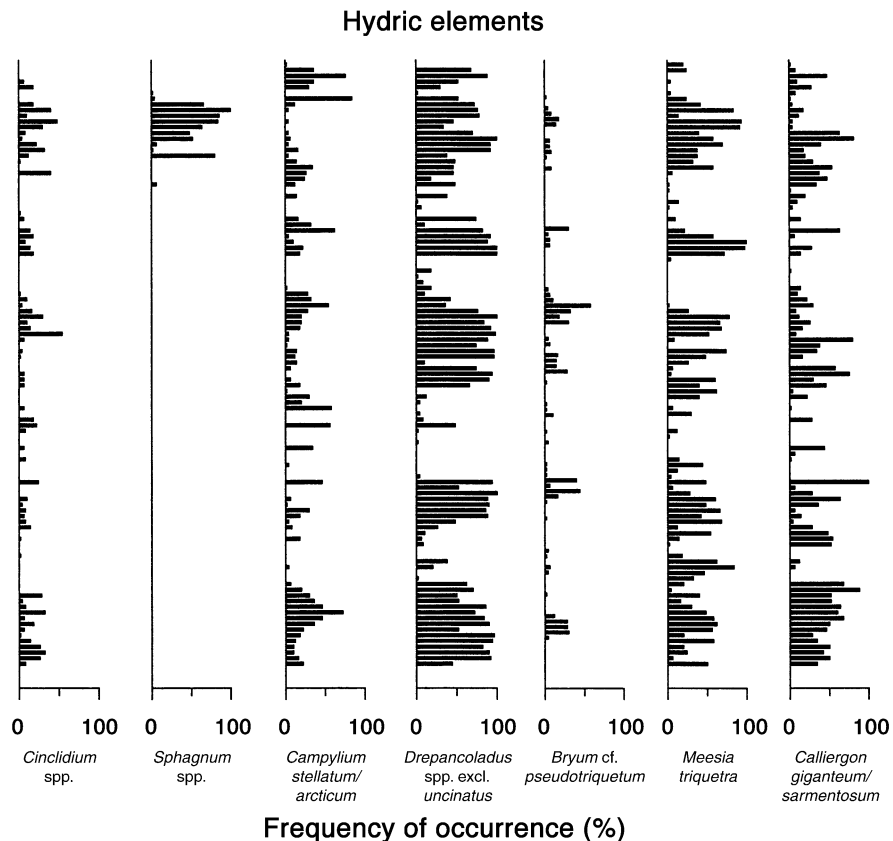
Hydric elements

Fig. 5. Continued.

Lamoureux et al. 2001). The data also agrees with evidence from central-west Greenland, documenting a shift in peat-forming vegetation toward wetter conditions between AD 950 and 1760 (Bennike 1992).

Establishing unequivocally the presence or absence of a climate signal during polygon development is negated by the lack of replication and consequent restricted geographic scope of this study. The composition of the sediments analyzed here, predominantly moss remains, and their rate of accumulation, also weaken a direct comparison between our results and those of previous studies, which have sought mostly to demonstrate a rapid, subdecade-scale effect of simulated climate change on vascular plants only. Confirmation or refutation of the climate signal observed during the period of the Little Ice Age would benefit from wider paleoecological analyses in the High Arctic, at higher resolution if possible, while its relevance to a fuller range of vegetation might be examined by including different taxonomic groups, such as diatoms and vascular plant remains. However, a circumspect comparison of the paleoecological and paleoclimatic records for periods preceding or succeeding the Little Ice Age (section II, ~300–465 calibrated yr BP) suggests only a modest link between climate and hydrologically controlled vegetation change (Fig. 8). Except

for the Little Ice Age, there is only equivocal evidence for the effect of past climate change on the long-term development of the examined polygons.

Geomorphology and hydrologic-vegetation change

In the absence of evidence for a strong climatic effect, geomorphology, expressed as the effect of polygon topography on Q_s and Q_g (Eq. 1) is invoked as the principal environmental factor controlling hydrology and vegetation change during polygon development. Differences in the paleoecological records of BY-a and BY-b are more likely attributable to the influence on hydrology of local topographic variation (Rovansek et al. 1996, Young et al. 1997). Polygon ridges will accumulate less snow and, consequently, receive less water from snowmelt than sheltered concavities (Young et al. 1997). By contrast, runoff is rapidly transported along hydraulic gradients (Q_s and Q_g), collecting in low-lying polygon centers (Rovansek et al. 1996, Young et al. 1997). Hydrologic change during polygon development will be affected by the position in a polygon center relative to the surrounding ridge, the slope of its flanks and the height and width of the polygon ridge. Local topographic variation can thus explain the contrasting development of closely adjacent cores, whereas regional climate change cannot.
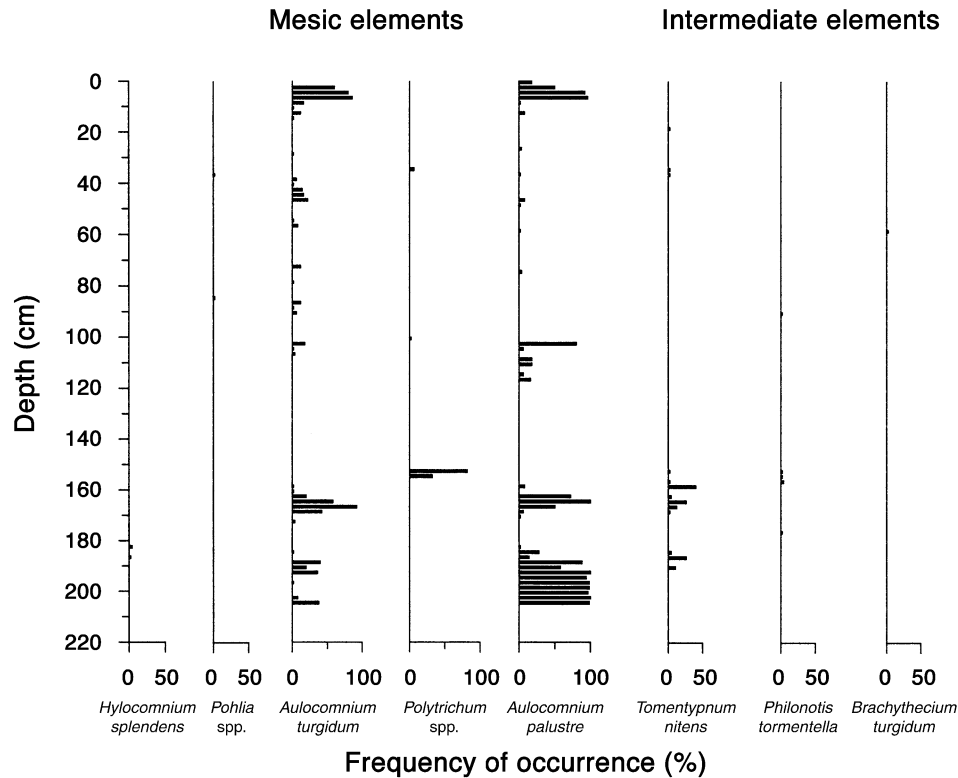
FIG. 6.   Summary stratigraphic record: macrofossil bryophyte taxa in core BY-b. Dominant macrofossil bryophytes are arranged as a hydrological series, with mesic, intermediate, and hydric elements delimited (cf. Figs. 2 and 3).

Autogenic vegetation-geomorphologic change

Developmental patterns common to BY-a and BY-b suggest a functional inter-relationship between vegetation processes (i.e., production–decomposition) and geomorphology during polygon development.

Accumulation of organic matter.—Soil moisture may be functionally related to the accumulation of organic matter, through an effect on net primary production and rates of decomposition. The productivity of bryophyte species decreases along a wet to dry habitat gradient, though their total nitrogen and phosphorus content increases (Vitt and Pakarinen 1977). The nutrient content of bryophytes may be important in controlling species-specific decomposition rates (Clymo and Hayward 1982, Aerts et al. 1999). In addition, the depth to the permafrost table, which is inversely related to soil moisture (Woo and Xia 1996), might control the amount of time during which plant necromass decays in the active layer, comparable to the diplotelmic model of peat growth (Clymo 1984, 1991).

Mineral sedimentation.—The pattern of mineral sediments suggests that the distribution of wind-blown material is modified locally by water flow (Fig. 7). The secondary deposition of eolian sands and silts would therefore follow water-transport gradients (Q_s and Q_g), accumulating in lower-lying, water-collecting, polygon centers.

The hypothetical application of these patterns is explained graphically in Fig. 9. Growth of syngenetic ice wedges occurs under the limiting conditions of slow, continuous sedimentation and repeated frost-cracking (Harry and Gozdzik 1988). We thus invoke a feedback between (i) the effect of mineral and organic sedimentation on the rate of ice-wedge growth and (ii) the rate of ice-wedge growth on polygon topography and, therefore, hydrology and vegetation. During periods of active ice-wedge growth (Fig. 9A), the increased amplitude between polygon ridges and centers will enhance the accumulation of snow during winter (*P*) and increase the hydraulic gradient (Q_s and Q_g). As a consequence, the deposition of mineral sediment and soil wetness will both increase, with attendant vegetation change and accompanying shifts in rates of productivity and decomposition. The effect of such local, small-scale factors on ice-wedge cracking has been demonstrated by Mackay (1991, 1993). The upward growth of polygon ridges should slow down or cease at a point where the continued growth of syngenetic ice wedges becomes impeded by decreased rates of vertical deposition (Harry and Gozdzik 1988, Mackay 2000). This may occur as the ridge becomes higher, rising above the surrounding sediments. However, continued sedimentation and peat accumulation in the polygon center (Fig. 9B) might subsequently lower the amplitude be-
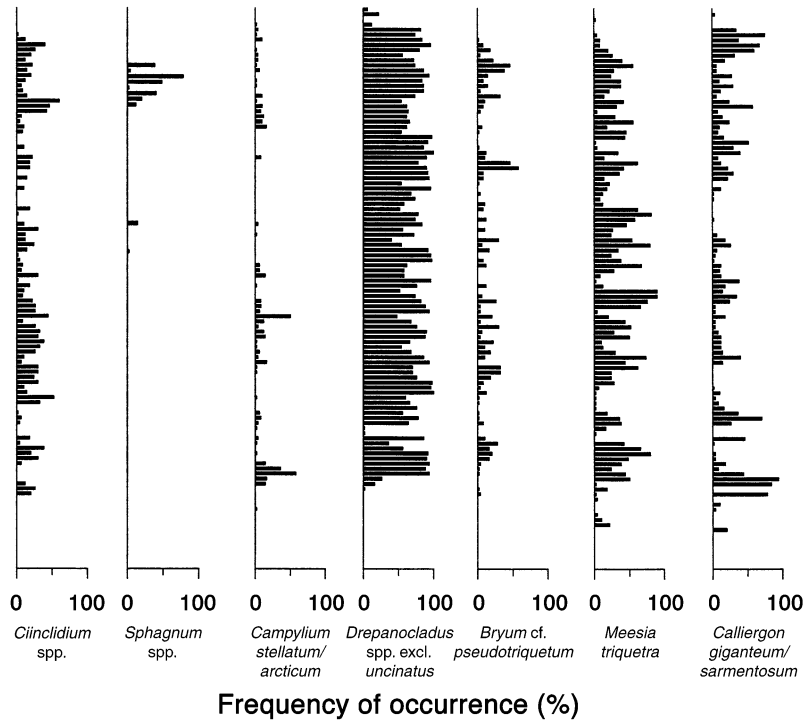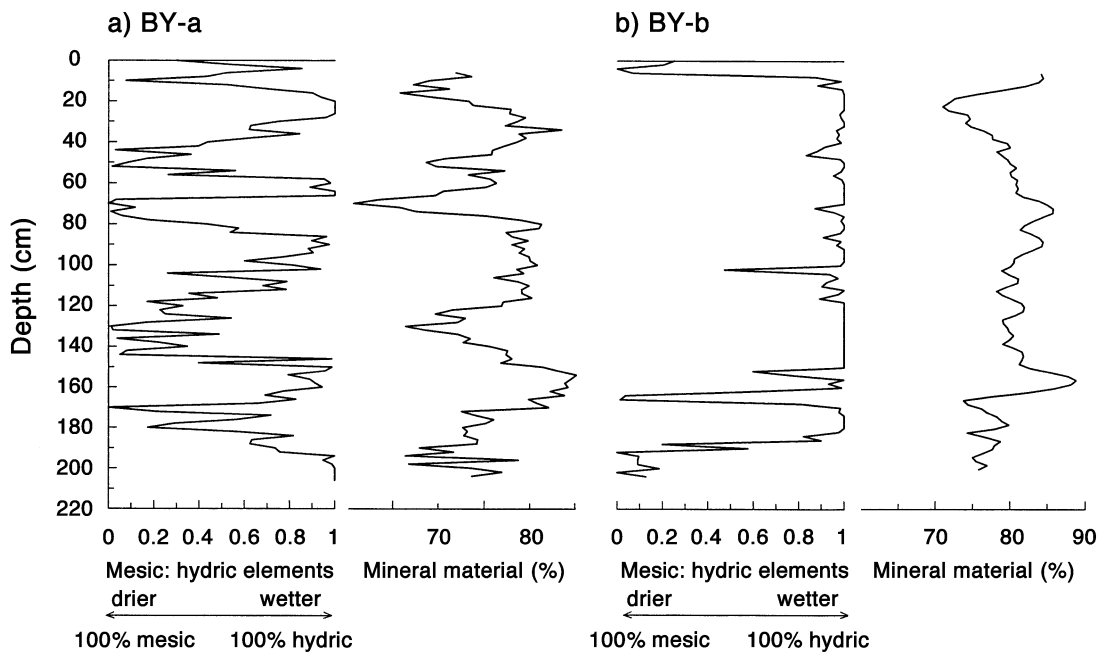
Hydric elements

FIG. 6. Continued.

FIG. 7. Bryophyte macrofossil record of BY-a and BY-b, recalculated as percentage contribution of hydric vs. mesic bryophyte elements, and the percentage mass contribution of mineral material (seven-point weighted average).
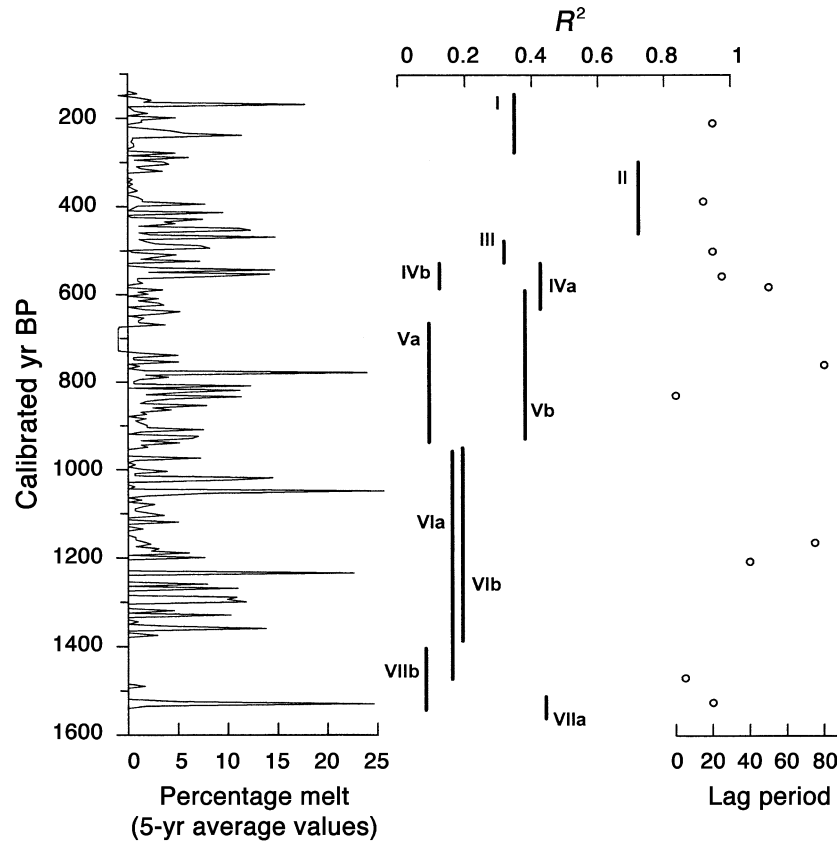
FIG. 8. The record of percentage melt in the Aggasiz-84 ice core (Ellesmere Island) and values of R^2 based on the linear regression with mesic : hydric elements in BY-a. The highest values of R^2 are shown separately for periods intercalated between radiocarbon dates (Fig. 4), based on the corresponding time lag. Paleoclimatic data provided by the U.S. National Oceanic and Atmospheric Administration through the World Data Center for Paleoclimatology at Boulder, Colorado, USA.

tween the polygon ridges and centers, reducing the topographic effect on soil moisture of Q_s and Q_g and P. Decreasing soil moisture will be accompanied by plant succession toward a drier facies. With continued sedimentation and the outward transfer of surface material to the periphery of the polygon (Mackay 2000), syngenetic ice-wedge growth may be rejuvenated (Fig. 9C), resulting in the recurrent growth of polygon-ridges and a staggered or vertically discontinuous chevron pattern of ice-wedge growth (Dostovalov and Popov 1963, Mackay 1974, 1990, Lewkowicz 1994).

Significance to Arctic plant ecology

The paleoecological record of the BY-a and BY-b cores suggests that climate has not been the most important factor governing long-term vegetation development. Instead, local geomorphologic processes are invoked as having controlled polygon hydrology and autogenic vegetation development. Macrofossil change during the Little Ice Age indicates the potential sensitivity of the vegetation to climate, ostensibly supporting the effect of simulated rapid and severe climate warming described by short-term studies (Chapin et al. 1995, Robinson et al. 1995, 1998, Chapin and Shaver

1996, Jonasson et al. 1999, Johnson et al. 2000). It remains possible though that the effect of the Little Ice Age on hydrology and vegetation was indirect, owing to a climatic influence on sedimentation rates and/or ice-wedge growth, resulting in effects on local topography (Kasper and Allard 2001). On the basis of the evidence presented here, we caution that previous studies to simulate and describe the effects of climate warming might not have properly accounted for the dynamic role of geomorphology in regulating tundra microclimate. The rate of vegetation change described by the paleoecological record is admittedly different from the rate of simulated climate change in short-term experiments, though there is a detectable effect of recent climate warming on permafrost (Lachenbruch and Marshall 1986, Osterkamp and Romanovsky 1999). This effect is manifested in certain areas as significant and rapid geomorphologic and ecological change (Jorgenson et al. 2001, Nelson et al. 2001). We suggest therefore that the principal effect of climate change on the vegetation of polygon-patterned tundra will be indirect, via the climatic control of periglacial geomorphologic processes.
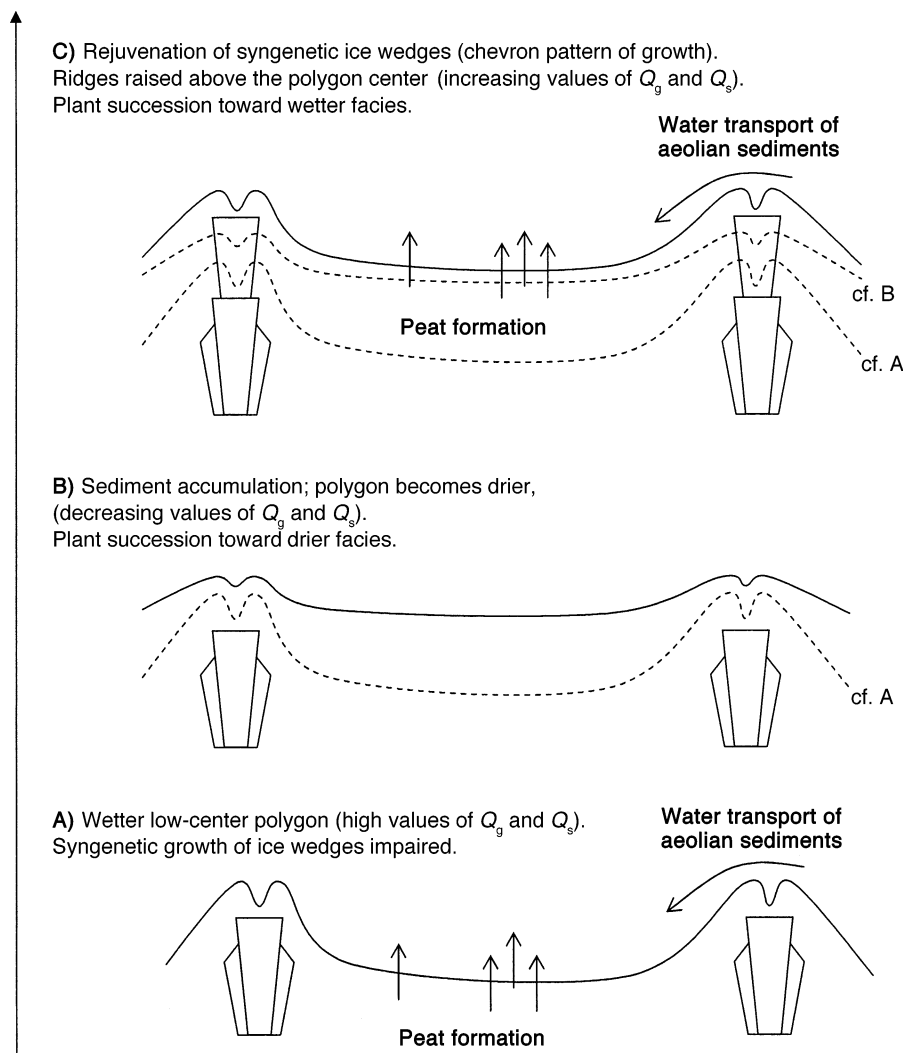
C) Rejuvenation of syngenetic ice wedges (chevron pattern of growth).
Ridges raised above the polygon center (increasing values of Q_g and Q_s).
Plant succession toward wetter facies.

Water transport of
aeolian sediments

Peat formation

cf. B

cf. A

B) Sediment accumulation; polygon becomes drier,
(decreasing values of Q_g and Q_s).
Plant succession toward drier facies.

cf. A

A) Wetter low-center polygon (high values of Q_g and Q_s).
Syngenetic growth of ice wedges impaired.

Water transport of
aeolian sediments

Peat formation

FIG. 9. Mechanisms explaining inferred topographic, hydrologic, and vegetation change during the development of the polygon-patterned wetland. Vertical arrows indicate the time course.

Conclusion

The topography of polygon-patterned ground influences strongly the spatial distribution of Arctic vegetation in wetlands (Drury 1962, Billings and Peterson 1980, Schaefer and Messier 1994). We suggest here that topographic variation during the development of tundra polygons may explain the temporal patterns evidenced in the BY-a and BY-b cores. These patterns might be modified by pronounced climate change, which may have occurred during the Little Ice Age, though climate has apparently been generally less important in polygon development than autogenic geomorphologic-vegetation processes. LaFarge-England et al. (1991) similarly suggested that slope processes and consequent changes in local hydrology have been more important than macroclimatic change during the development of a High Arctic wetland on Ellesmere Island. We conclude that long-term variability in the structure and function of polygon-patterned tundra wetland, implied by this study, may be controlled in part by climate, though additionally by local geomorphology and autogenic vegetation processes.

LITERATURE CITED

Aerts, R., J. T. A. Verhoeven, and D. F. Whigham. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80:2170–2181.

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.

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., and K. M. Peterson. 1980. Vegetational change and ice-wedge polygons through the thaw-lake cycle in Arctic Alaska. Arctic and Alpine Research 12:413–432.

Birks, J. H. B. 1995. Quantitative palaeoenvironmental reconstructions. Pages 161–254 in D. Maddy and J. S. Brew, editors. Statistical modelling of Quaternary science data. Quaternary Research Association Technical Guide No. 5. Quaternary Research Association, Cambridge, UK.

Birks, H. J. B., E. Heegard, H. H. Birks, and B. Jonsgard. 1997. Quantifying bryophyte–environment relationships. Pages 305–319 in J. W. Bates, N. W. Ashton, and J. G. Duckett, editors. Bryology for the twenty-first century. Centenary Symposium of the British Bryological Society. Maney Publishing, Leeds, UK.

Bliss, L. C. 1997. Arctic ecosystems of North America. Pages 551–683 in F. E. Wielgolaski, editor. Ecosystems of the world. Volume 3. Polar and Alpine Tundra. Elsevier, Amsterdam, The Netherlands.

Bourgeois, J. C. 1986. A pollen record from the Agassiz ice cap, northern Ellesmere Island, Canada. Boreas 15:345–354.

Bradley, R. S. 1990. Holocene palaeoclimatology of the Queen Elizabeth Islands, Canadian High Arctic. Quaternary Science Reviews 9:365–384.

Chapin, F. S., and G. R. Shaver. 1996. Physiological and growth responses of Arctic plants to a field experiment simulating climatic change. Ecology 77:822–840.

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

Chee, W-L., and D. H. Vitt. 1989. The vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada. Wetlands 9:227–261.

Clymo, R. S. 1984. The limits to peat bog growth. Philosophical Transactions of the Royal Society, Series B 303:605–654.

Clymo, R. S. 1991. Peat growth. Pages 76–112 in L. C. K. Shane and E. J. Cushing, editors. Quaternary landscapes. Belhaven Press, London, UK.

Clymo, R. S., and P. M. Hayward. 1982. The ecology of Sphagnum. Pages 229–291 in A. J. Smith, editor. Bryophyte ecology. David and Charles, Newton Abbot, UK.

Dostovalov, B. N., and A. I. Popov. 1966. Polygonal systems of ice wedges and conditions of their development. Pages 102–105 in Proceedings, First International Permafrost Conference. Publication 1287. National Academy of Science, Washington, D.C., USA, and National Research Council of Canada, Ottawa, Ontario, Canada.

Drury, W. H. 1962. Patterned ground and vegetation on southern Bylot Island, Northwest Territories, Canada. Contributions from the Gray Herbarium Press, No. CXC, Gray Herbarium of Harvard University, Cambridge, Massachusetts, USA.

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., M. Garneau, and J. C. Bourgeois. 1995. Palaeoenvironments 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.

Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre, and A. J. McKerrow. 1991. Biochemical diversity along a riverside toposequence in Arctic Alaska. Ecological Monographs 61:415–435.

Gignac, L. D., D. H. Vitt, S. C. Zoltai, and S. E. Bayley. 1991. Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. Nova Hedwigia 53:27–71.

Green, D. G. 1995. Time and Spatial Analysis. Pages 65–105 in D. Maddy and J. S. Brew, editors. Statistical modelling of Quaternary science data. Quaternary Research Association Technical Guide No. 5. Quaternary Research Association, Cambridge, UK.

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

Hyvärinen, H. 1985. Holocene pollen stratigraphy of Baird Inlet, east-central Ellesmere Island, Arctic Canada. Boreas 14:19–32.

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

Jonasson, S., A. Michelsen, I. K. Schmidt, and E. Nielsen. 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. Ecology 80:1828–1843.

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

Kasper, J. N., and M. Allard. 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. 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, Ontario, Canada.

Koerner, R. M. 1977. Devon Island ice cap: core stratigraphy and palaeoclimate. Science 196:15–18.

Koerner, R. M., and D. A. Fisher. 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 version 3.1. Kovach Computing Services, Pentraeth, Wales, UK.

Lachenbruch, A. H., and B. V. Marshall. 1986. Changing climate: geothermal evidence from permafrost in the Alaskan Arctic. Science 234:689–696.

LaFarge-England, C. 1989. The contemporary moss assemblages of a High Arctic upland, northern Ellesmere Island, N.W.T., Canada. Canadian Journal of Botany 67:491–504.

LaFarge-England, C., D. H. Vitt, and J. England. 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. 1977. Climate: past, present and future. Volume 2. Climatic history and the future. Methuen, London, UK.

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., J. H. England, M. J. Sharp, and A. B. G. Bush. 2001. A varve record of increased 'Little Ice Age' rainfall associated with volcanic activity, Arctic Archipelago, Canada. 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, Northwest Territories. Canadian Journal of Earth Sciences **11**: 1336–1383.

Mackay, J. R. 1990. Some observations on the growth and deformation of epigenetic, syngenetic and anti-syngenetic ice wedges. Permafrost and Periglacial Processes **1**:15–29.

Mackay, J. R. 1991. The frequency of ice-wedge cracking (1967–1987) at Garry Island, western Arctic coast, Canada. Canadian Journal of Earth Sciences **29**:236–248.

Mackay, J. R. 1993. Air temperature, snow cover, creep of frozen ground, and the time of ice-wedge cracking, western Arctic coast. Canadian Journal of Earth Sciences **30**:1720–1729.

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

Miller, N. G., and P. Alpert. 1984. Plant associations and edaphic features of a High Arctic mesotrophic setting. Arctic and Alpine Research **16**:11–24.

Mode, W. N. 1996. The terrestrial record of postglacial vegetation and climate from the Arctic/Sub-Arctic of Eastern Canada and Greenland. Geoscience Canada **23**:213–216.

Molau, U. 1997. Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. Global Change Biology **3**:97–107.

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

Nelson, F. E., O. A. Ansimov, and N. I. Shiklomanov. 2001. Subsidence risk from thawing permafrost. Nature **40**:889–890.

Nyholm, E. 1954–1969. The illustrated moss flora of Fennoscandia. II. Musci Fascicle 1–6. Swedish Natural Science Research Council, Stockholm, Sweden.

Osterkamp, T. E., and V. E. Romanovsky. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes **10**:17–37.

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

Overpeck, J., et al. 1997. Arctic environmental change of the last four centuries. Science **278**:1251–1256.

Parker, R. E. 1979. Introductory statistics for biology. Edward Arnold, London, UK.

Peterson, K. M., and W. D. Billings. 1980. Tundra vegetational patterns and succession in relation to microtopography near Atkasook, Alaska. Arctic and Alpine Research **12**:473–482.

Péwé, T. R. 1966. Ice-wedges in Alaska: classification, distribution and climate significance. Pages 76–81 *in* Proceedings, International Conference on Permafrost. National Academy of Sciences and National Research Council, Washington, D.C., USA.

Robinson, C. H., P. A. Wookey, J. A. Lee, T. V. Callaghan, and M. C. Press. 1998. Plant community responses to simulated environmental change at a high arctic polar semi-desert. Ecology **79**:856–866.

Robinson, C. H., P. A. Wookey, A. N. Parsons, J. A. Potter, T. V. Callaghan, J. A. Lee, M. C. Press, and J. M. Welker. 1995. Responses of plant litter decomposition and nitrogen mineralisation to simulated environmental change in a high Arctic polar semi-desert and a subArctic dwarf shrub heath. Oikos **74**:503–512.

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

Schaefer, J. A., and F. Messier. 1994. Composition and spatial structure of plant communities on southeastern Victoria Island, Arctic Canada. Canadian Journal of Botany **72**: 1264–1272.

Shaver, G. R., and F. S. Chapin. 1991. Production: biomass relationships and element cycling in contrasting Arctic vegetation types. Ecological Monographs **6**:1–31.

Sheard, J. W., and D. W. Geale. 1983. Vegetation studies at Polar Bear Pass, Bathurst Island, N.W.T. I. Classification of plant communities. Canadian Journal of Botany **61**: 1618–1636.

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

Slack, N. G., D. H. Vitt, and D. G. Horton. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. Canadian Journal of Botany **58**:330–350.

Steere, W. C. 1976. Ecology, phytogeography and floristics of Arctic Alaskan bryophytes. Journal of the Hattori Botanical Laboratory **41**:47–72.

Steere, W. C. 1978. Floristics, phytogeography, and ecology of Arctic Alaskan bryophytes. Pages 141–167 *in* L. L. Tieszen, editor. Vegetation and production ecology of an Alaskan Arctic tundra. Springer-Verlag, Berlin, Germany.

Stuiver, M., G. S. Burr, K. A. Hughen, B. Kromer, G. McCormac, J. Van der Plicht, M. Spurk, P. J. Reimer, E. Bard, and J. W. Beck. 1998. INTCAL98 radiocarbon age calibration, 24 000–0 cal 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.

Ter Braak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. Advances in Ecological Research **18**: 271–317.

Vardy, S. R., B. G. Warner, and R. Aravena, R. 1997. Holocene climate effects on the development of a peatland on the Tuktoyaktut Peninsula, Northwest Territories. Quaternary Research **47**:90–104.

Vitt, D. H., P. Achuff, and R. E. Andrus. 1975. The vegetation and chemical properties of patterned fens in the Swan Hills, north central Alberta. Canadian Journal of Botany **53**: 2776–2795.

Vitt, D. H., and W.-L. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio **89**:87–106.

Vitt, D. H., and P. Pakarinen. 1977. The bryophyte vegetation, production and organic components of Truelove Lowland. Pages 225–244 *in* L. C. Bliss, editor. Truelove lowland, Devon Island, Canada: a High Arctic ecosystem. University of Alberta Press, Edmonton, Alberta, Canada.

Vourtilis, G. L., and W. C. Oechel. 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.

Woo, M.-K., and Z. Xia. 1996. Effects of hydrology on the thermal conditions of the active layer. Nordic Hydrology **27**:129–142.

Wookey, P. A., A. N. Parsons, J. M. Welker, J. A. Potter, T. V. Callaghan, J. A. Lee, and M. C. Press. 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. Oikos **67**:490–502.

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

Young, K. L., M-K. Woo, and S. A. Edlund. 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., K. J. McCormick, and G. W. Scotter. 1983. A natural resource survey of Bylot Island and adjacent Baffin Island, Northwest Territories. Parks Canada, Ottawa, Canada.

Zoltai, S. C., and C. Tarnocai. 1975. Perennially frozen peatlands in the western Arctic and Sub-Arctic of Canada. Canadian Journal of Earth Sciences **12**:28–43.