THE CHANGING TUNDRA – PALAEOECOLOGY IN THE HIGH ARCTIC

Christopher Ellis

Arctic terrestrial ecosystems have been an important theme in the development of global change biology. Given the expectation of pronounced climate warming in arctic regions, ecological studies during the last two decades have sought to understand the effect of human-induced change on the structure and function of tundra habitats. Perhaps the most well-known of these recent studies is the International Tundra Experiment (ITEX), which comprised the collaboration of ecologists from 12 countries working at 27 high-latitude circumpolar stations (www.itex-science.net). The ITEX approach sought to simulate climate change across these sites, and thereby understand the ecosystem response amongst contrasting vegetation-types. The simulation-experiment adopted by ITEX is a method used widely by research groups. Experiments have manipulated local factors that will change with climate, *i.e.*, temperature, soil moisture and levels of limiting nutrient, to demonstrate the direct effect of these interacting variables on the tundra vegetation (for a recent review see Wookey and Robinson, 1997).

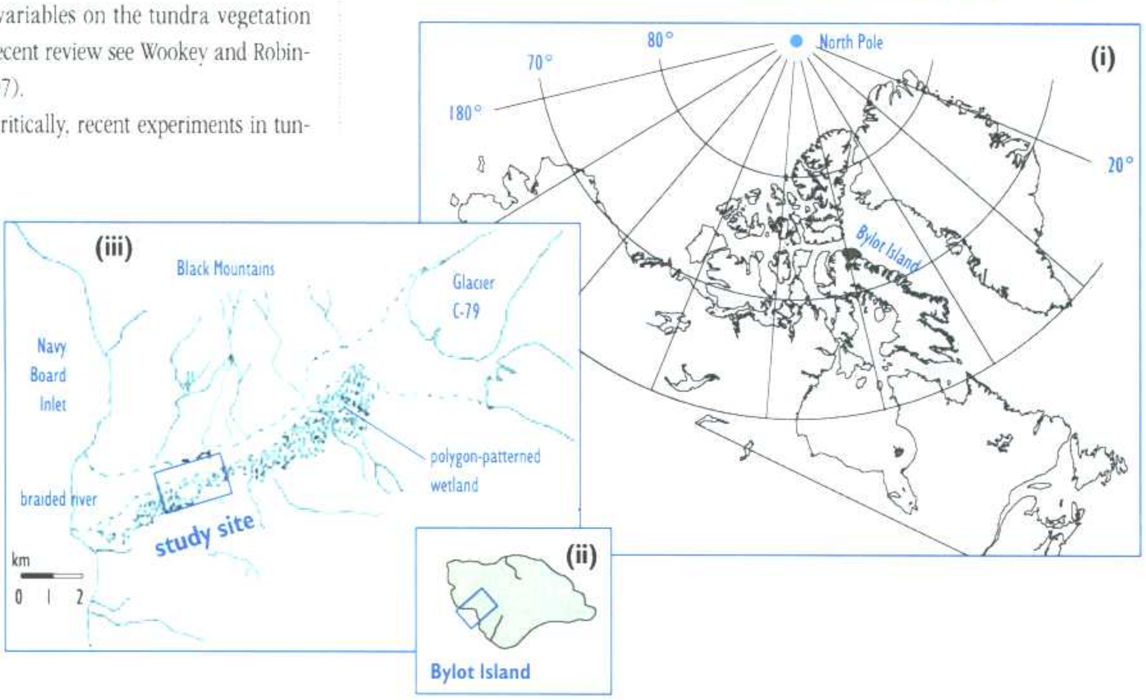
Critically, recent experiments in tundra ecology are limited to relatively short time-scales, normally less than ten years. An experiment would be considered lengthy if it had continued for twenty years, though the vegetation-soil complex may respond over centuries. Consequently, attention has turned to the "scaling-up" of these short-term experiments, to understand how predicted climate change may affect tundra ecosystems over several decades or even centuries. An important part of this scaling-up process should utilise the palaeoecological record as a source of information about the long-term dynamics of an ecosystem. Palaeoecology has played a central role in confirming or refuting short-term observations over longer time-periods in lower-latitude ecosystems (*e.g.*, mires and forests in Temperate zones). Such research could be similarly used at high-latitudes, to establish whether the climatic sensitivity described by short-term studies may also control the development of tundra habitats over the long-term (*i.e.*, 100s–1000s of years). At present very little palaeoecological data is relevant to terrestrial tundra habitats, with the High Arctic particularly lacking. The sensitivity of tundra vegetation to climate warming, demonstrated by short-term experiments, therefore lacks essential long-term context. This article reports on of one of only very few studies to examine the palaeoecology of a High Arctic terrestrial ecosystem.

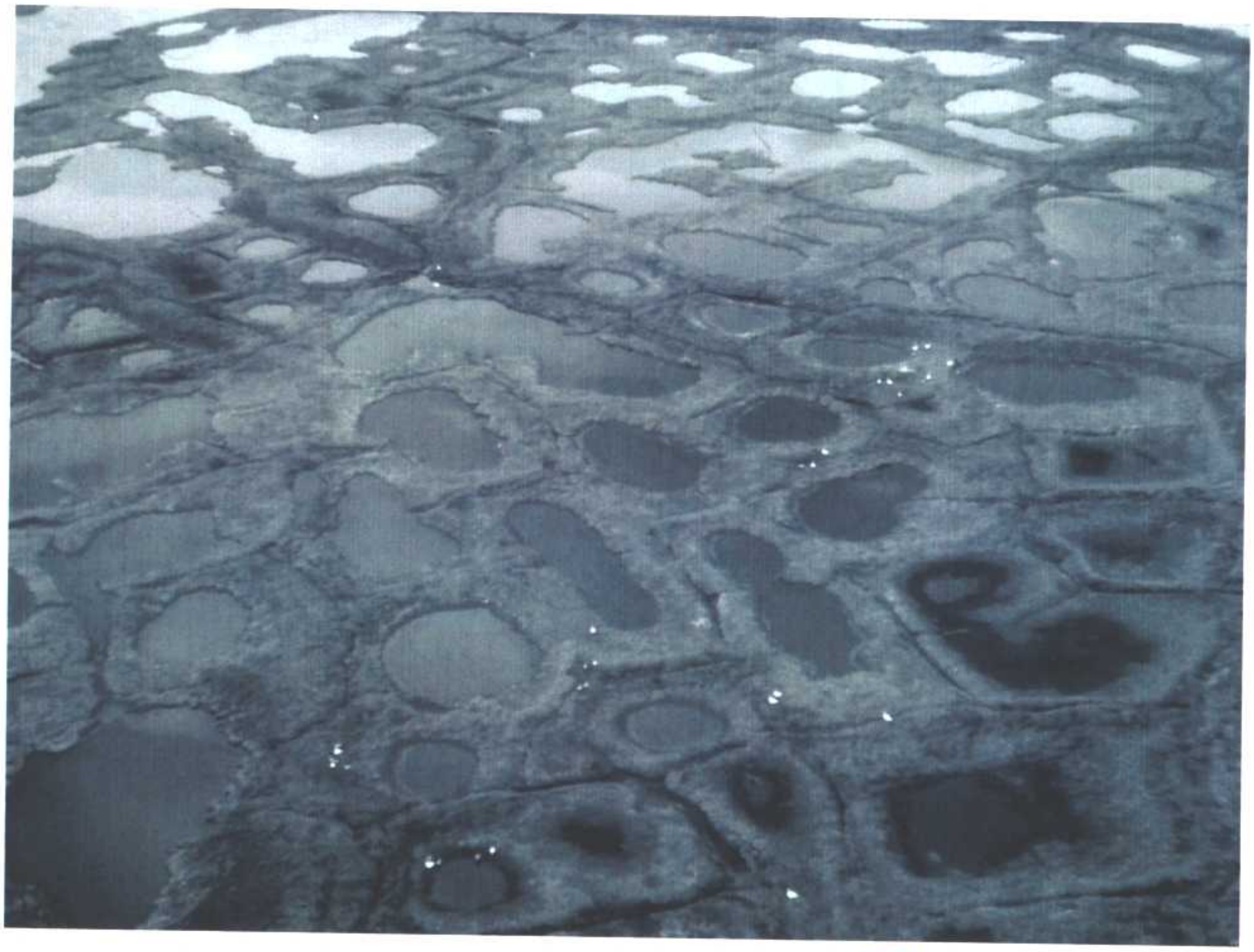
BYLOT ISLAND AND THE WETLAND STUDY SITE

The study was carried out on Bylot Island (*ca.* 73°N, 80°W), which lies to the north-east of Baffin Island, within the Sirmilik

Figure 1

The position (i) of Bylot Island in the Canadian Arctic Archipelago, (ii) the Qunguliqtut Valley in western Bylot Island and (iii) the study site in the polygon-patterned wetland to the south of Qunguliqtut Valley.





National Park (Figure 1). Bylot Island comprises *ca.* 11,000 km^2, of which the majority is mountainous terrain (up to *ca.* 1600m), covered by a central ice cap and with radiating glaciers. The margin of the island includes a series of plateaux with sparsely vegetated polar desert. As the plateaux drop towards the sea the vegetation cover becomes more consistent, and at lower elevations is dominated by heath-tussock tundra. Wetlands develop in areas where spring melt-water accumulates. These wetlands are generally isolated patches on the lower plateaux, though in the glacial valley bottoms they form extensive ecosystems. Fed seasonally by water and nutrients from the surrounding higher ground and adjacent river systems, the lowland wetlands are "minerotrophic" mires, relatively productive and biologically diverse. The vegetation of such mires is dominated on Bylot Island 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.), and they form essential summer habitat for migratory water-fowl. Beause of this richness they have been dubbed "polar oases".

Our study examined the long-term development of one such High Arctic wetland in the Qunguliqtut Valley, on western Bylot Island (Figure 1). The study site comprised a system of large terraces to the south of valley, raised above the channel of the adjacent river. The terraces are building through the accretion of aeolian sands and silts and the concurrent deposition of peat (Allard, 1996). A network of ice-wedges is developing during aggradation of the terraces, forming a complex polygon-patterned wetland (Figure 2). The development of these ice-wedges is critical to our methodology and the interpretation of results.

Figure 2

A low-centre-polygon complex inundated with spring melt-water. Notice that some low-centre polygons are wetter (mid-photograph) compared to others (drier polygons to the lower right). Difference in the wetness of adjacent low-centre polygons is a feature of the polygon complex.

POLYGON-DEVELOPMENT AND PALAEOECOLOGICAL RECONSTRUCTION

The initiation of ice-wedges occurs where ground newly exposed to severe winter temperatures undergoes thermal contraction, cracking into a series of polygonal fissures

(Figure 3a). Melt-water entering the fissures during spring and summer thaw will subsequently refreeze, forming veins of ice (Figure 3b). Perennial cracking of the same ice veins, their inundation by melt-water and subsequent refreezing and fracture cause incremental addition and growth to form wedge shaped bodies of ground-ice. The progressive expansion of ice-wedges displaces surrounding cryosols (frozen soils), causing with the thermal expansion of adjacent ground the development of dry ridges, which thus surround lower and wetter polygon-centres – *i.e.*, low-centre polygons (Figure 3c). In depositional environments 'syngenetic' ice-wedges grow vertically as the permafrost table (*i.e.*, the top of the permafrost layer) rises with the accretion of sediments. Growth of syngenetic wedges is enabled by the long-term aggradation of peat-rich sediment, occurring under limiting conditions of slow, continuous sedimentation and repeated frost-cracking (Figure 3d and 3e). Thus, low-centre polygons at the Qunguliqtut study site will have developed upwards via syngentic ice-wedge growth as the sediments forming the terraces accumulated.

Our study examined the long-term development of five separate low-centre polygons. We extracted peat cores from the frozen centres of polygons using a machine driven corer (Figures 3e and 4). The collected sediment was examined to ensure that it was horizontally bedded and not disturbed by cryoturbation (mixing). Cores from the polygon surface to the mineral base of the sediment were between two and three metres deep. They comprised a mixture of undecomposed plant remains and aeolian silts, deposited over time as the polygons developed upwards. It was thought possible to reconstruct vegetation change during polygon development, by analysing undecomposed plant remains (mostly mosses), preserved in layer upon layer of the cored sediments (*cf.*, Figure 3e). The cores were

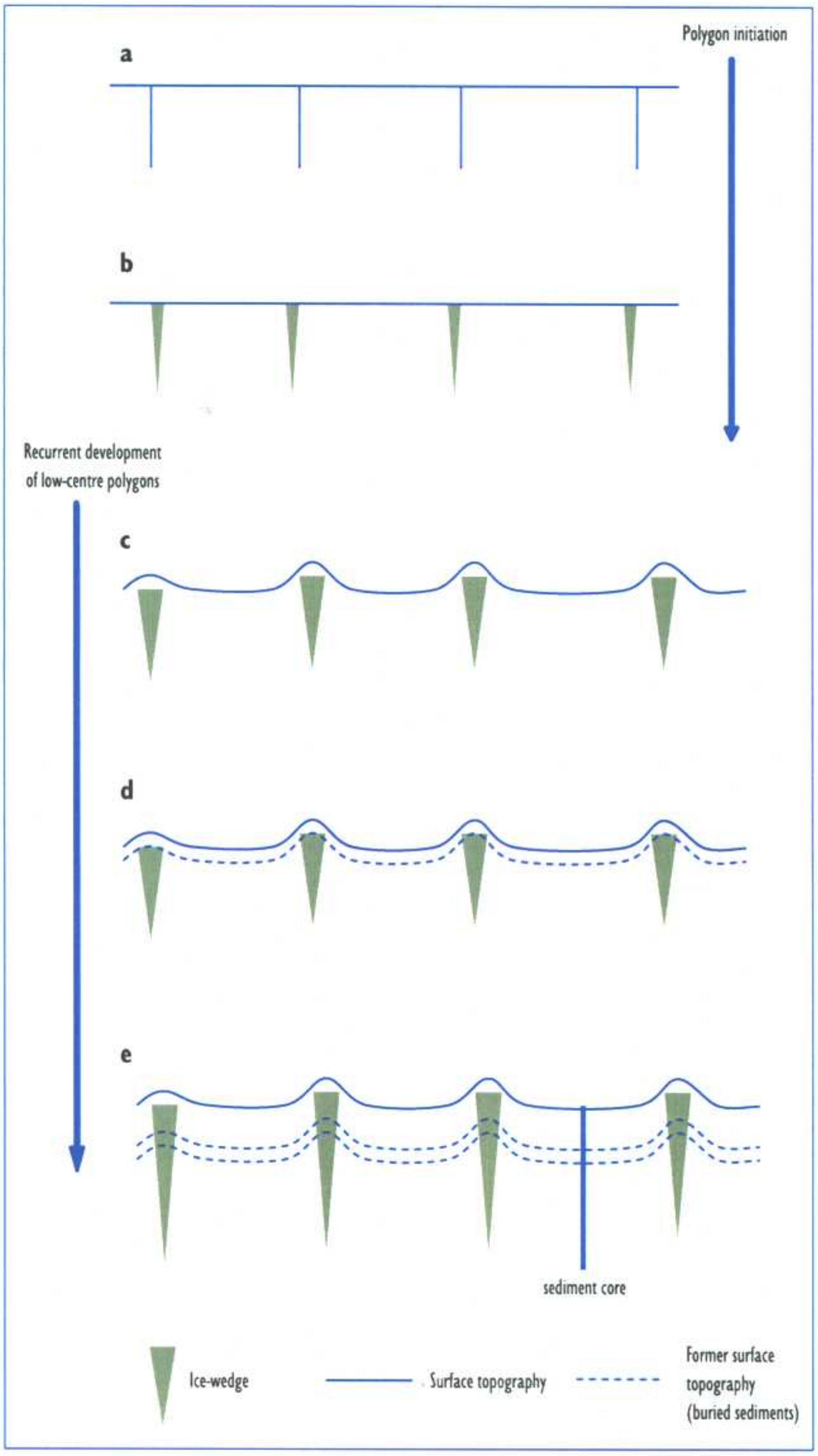


Figure 3
Scheme to summarise the initiation and recurrent development of low-centre polygons (see text, Polygon-development and palaeoecological reconstruction, for a process description).

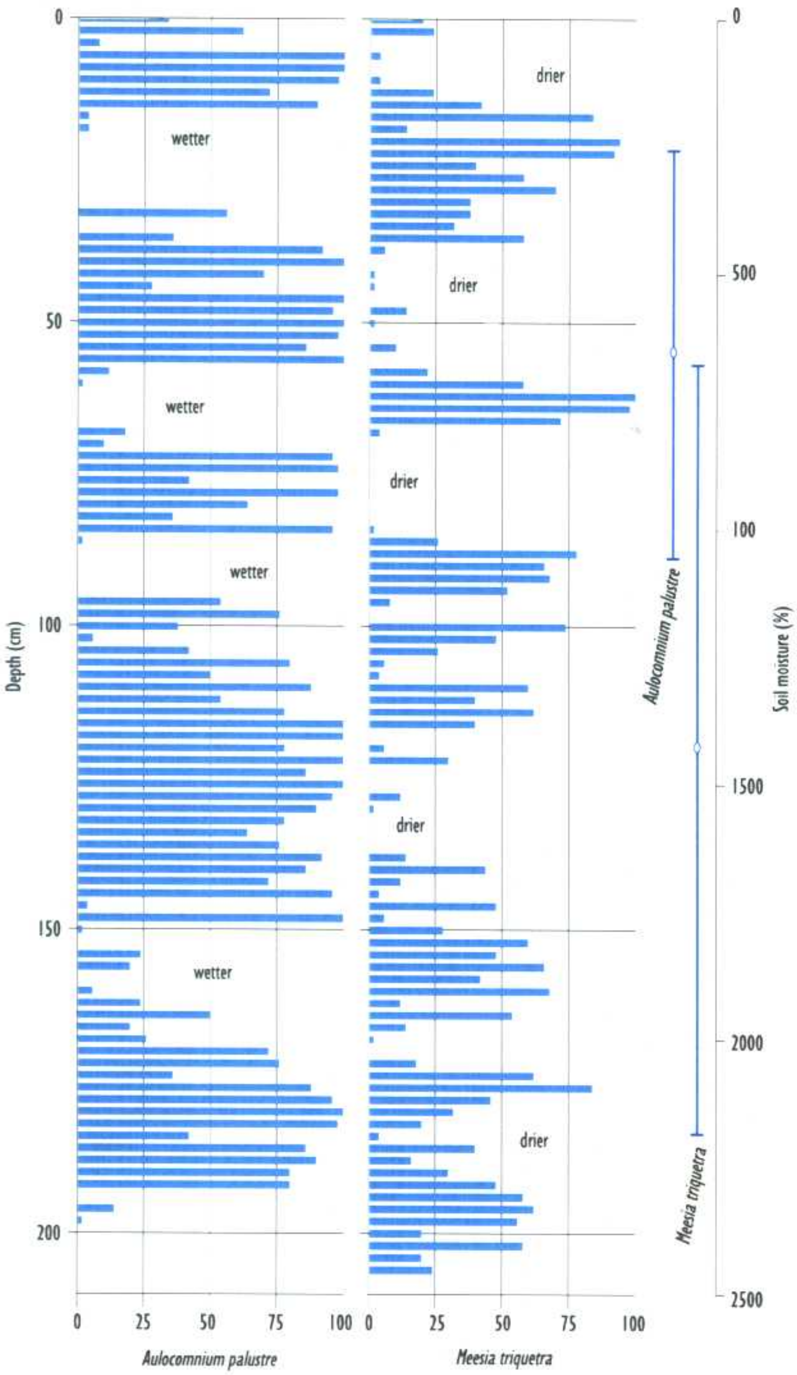


Figure 4

Summary palaeoecological record for two contrasting moss species: *Aulocomnium palustre* and *Meesia triquetra*. Ecological analysis demonstrated a clear difference in the soil moisture optima and tolerance range of each species. This information can be used to infer past changes in soil moisture during polygon development, *i.e.*, as sediments accumulated.

cut into 2cm slices and moss-remains were extracted and analysed from each slice (horizon). Small samples of moss were collected from different horizons and radiocarbon-dated, providing a time-frame for polygon development.

VEGETATION CHANGE DURING POLYGON DEVELOPMENT

The record of moss-remains demonstrated a striking variation in past vegetation during polygon development (Figure 4). The palaeoecological record was combined with ecological research to examine environmental factors controlling the distribution of mosses in the present-day polygon-complex. The ecological study demonstrated clear and predictable differences *spatially,* between moss species growing in communities representative of drier conditions (mesic species) and moss species growing in communities representative of wetter conditions (hydric species). However, the palaeoecological record suggested that for a site in the centre of an individual polygon, equivalent ecological differences had occurred *temporally,* during polygon development (Figure 4). Thus, the differences in moss species preserved in the sediments indicated recurrent shifts in polygon hydrology over time, as the polygon developed upwards and sediment accumulated.

CLIMATIC EFFECTS ON POLYGON DEVELOPMENT

We explored the possible effect of climate on polygon development by comparing the radiocarbon-dated vegetation record to independent palaeoclimatic proxies for the Eastern Arctic Archipelago (Bradley, 1990): five-year average values of percent melt in the stratigraphy of the Agassiz-84 ice core, Ellesmere Island (Koerner and Fisher, 1990) and five-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). These provide proxies for past summer temperature (percent melt) and regional average annual temperature ($\delta^{18}O$).

We found that during one period only, leading up to and including the Little Ice Age (*ca.* 530–300 year BP), reconstructed vegetation and soil moisture change was pronounced and consistent across all the polygons examined, and correlated closely with ice core records of both percent melt and $\delta^{18}O$ (Ellis and Rochefort, 2004; Ellis and Rochefort, in press). In contrast, over the majority of the developmental period examined vegetation change was either (i) inconsistently related to proxy climate values or (ii) entirely unrelated to proxy climate values (Figure 6).

Figure 5
Collecting a permafrost sediment core. The corer was custom built by Michel Allard (Université Laval), supervising (left), and is being operated by Daniel Fortier (to left) and Isabelle Duclos (to right). Photo: C. Ellis.

Figure 6
The strength of climate signals in the polygon palaeoecological records (compared to independent palaeoclimatic proxies; percent melt and $\delta^{18}O$). See Ellis and Rochefort (in press) for a complete analysis.

Strength of the climate signal	*Temporal occurrence across all cores*	*Period*
Shifts to drier or wetter palaeoecological conditions consistent across all polygon cores, associated with significantly higher/lower values of percent melt/d18O, respectively	6% of the palaeoecological record (*ca.* 225 years)	Little Ice Age
Shifts to drier or wetter palaeoecological conditions not consistent across polygon cores, though associated with significantly higher or lower values of percent melt and d18O	44% of the palaeoecological record (*ca.* 1710 years)	
No association between any of the polygon cores and the palaeoclimatic records	50% of the palaeoecological record (*ca.* 1950 years)	

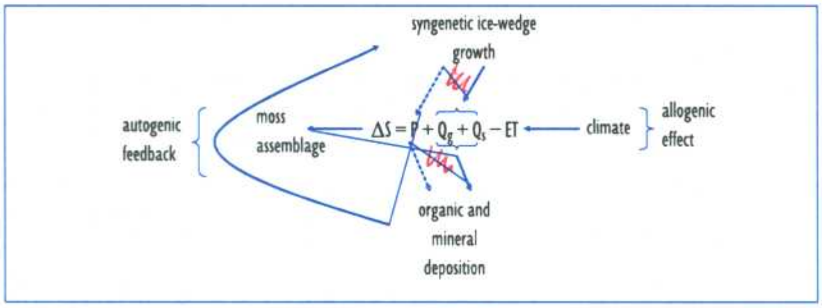


Figure 7

Diagram to show the effect of climate and geomorphology on the soil moisture of a plot within a wetland polygon. The hypothesised autogenic feedback effect between ice-wedge growth and sediment deposition is highlighted.

PERIGLACIAL GEOMORPHOLOGY AND POLYGON DEVELOPMENT

Periodic changes in reconstructed vegetation and soil moisture can be explained in the absence of a climatic influence (*ca.* 50% of the palaeoecological record [Figure 6]) by invoking the known mechanisms of periglacial geomorphology. Accordingly, the water balance (ΔS) of a plot within the centre of a given polygon can be approximated as:

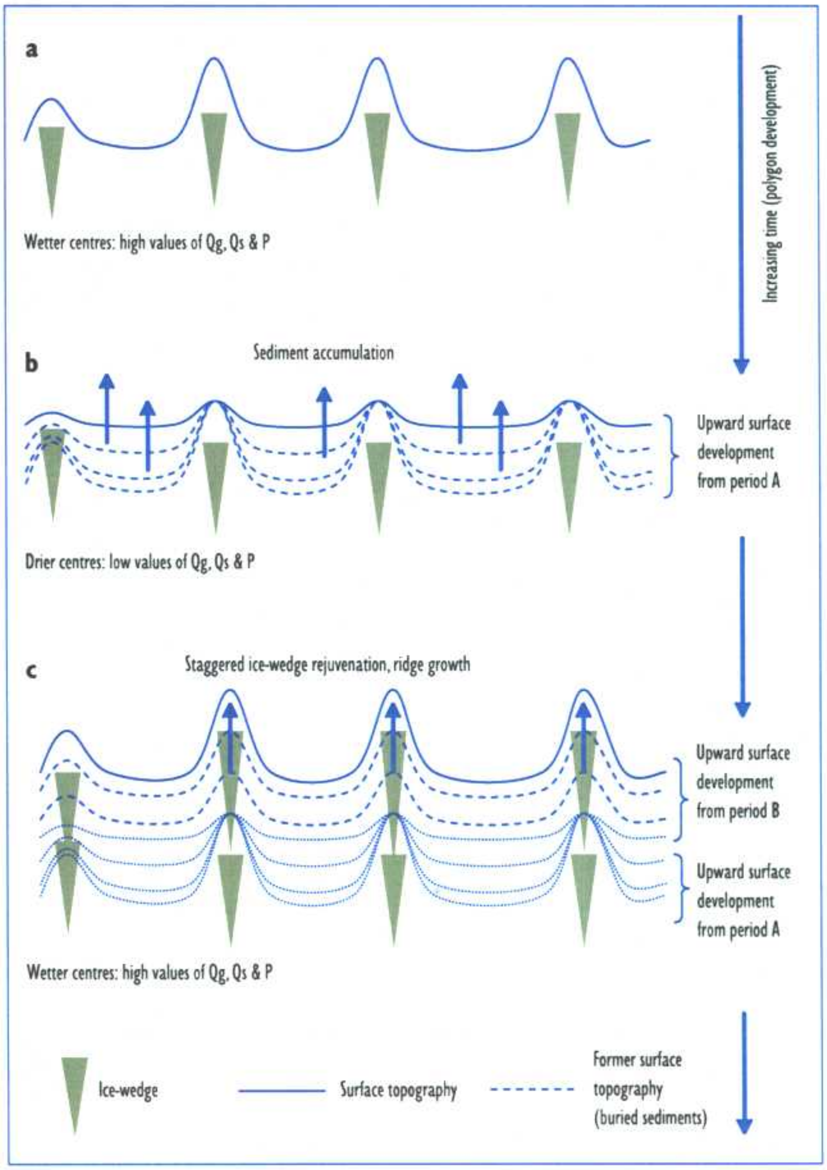
$$\Delta S = P + Qg + Qs - ET \qquad (1)$$

attributable to the dual mechanisms of climatic control and/or geomorphology (Figure 7). Climatic effects include precipitation (P) and evapotranspiration (ET). Geomorphology (*i.e.*, polygon topography) will control groundwater and surface-water input & output (Qg and Qs) and modify inputs from precipitation (P) as deeper low-centre polygons will accumulate more snow in winter and shallower polygons will be blown clear (Rovansek *et al.*, 1996; Young *et al.*, 1997). However, climatic control may also be indirect, through the effect on topography of ice-wedge growth (Kasper and Allard, 2001) which will in turn affect soil moisture (P, Qg and Qs) (Rovansek *et al.*, 1996; Young *et al.*, 1997).

Alternating wetter and drier conditions during polygon development can be explained if the topography of a polygon changes during its development, comprising periods during which it is deeper (higher ridges and lower centre) and, therefore wetter, intercalated by periods during which it is shallower (lower ridges and higher centre) and drier. These changes can 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 (Figures 7 and 8). If wetter conditions correspond to periods when the amplitude

Figure 8

Scheme to demonstrate how a feedback between ice-wedge growth and sedimentation may explain periodic changes in polygon soil moisture, independently of a climatic influence.



between a polygon's ridges and centre is relatively large (higher values for *Qg*, *Qs* and *P*) the upward growth of the syngenetic ice-wedges, and the continued development of ridges, will be limited during these wet periods by their height above the surrounding sediments (Figure 8a). Upward growth of ridges may slow or cease at a threshold height above the surrounding sediments, being rejuvenated only after a period during which sediments sufficient for continued ice-wedge growth have accumulated in the polygon centre. This intervening period of sediment accumulation will lower the amplitude between polygon ridges and centre, and, therefore, values of *Qg*, *Qs* and *P*, causing a shift to drier soil moisture conditions evident in the palaeoecological record as a dry moss community (Figure 8b). A process of staggered ice-wedge formation resulting in a chevron pattern of ice-wedge growth (demonstrated by field studies) might therefore explain recurrent shifts between wetter and drier conditions during the long-term development of low-centre polygons (Ellis and Rochefort, 2004).

CLIMATIC RESPONSE MODIFIED BY LOCAL GEOMORPHOLOGY

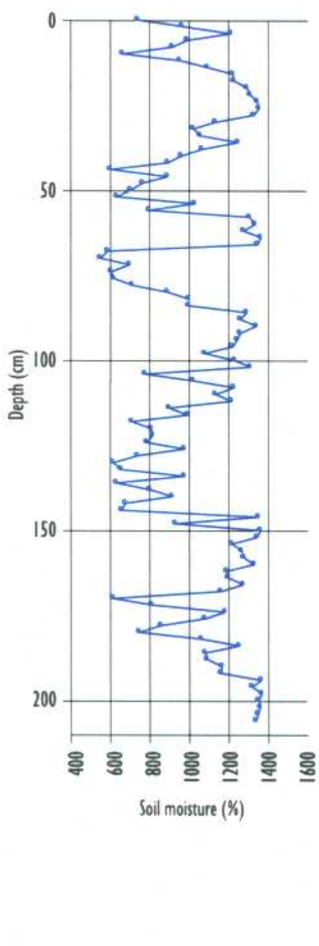
Shifts to drier or wetter palaeoecological conditions are inconsistent between polygon cores over ca 44% of the palaeoecological record (Figure 4). During these periods wetter or drier conditions may be associated with contrasting higher or lower values of percent melt and $\delta^{18}O$ in adjacent polygons. Where a correspondence between palaeoecological and proxy-climatic records is contrasting across several cores it must be considered equivocal. Nevertheless, such a response may represent the modification of a regional climatic effect by local geomorphologic conditions. It is important to remember that past changes in soil moisture (dry-wet) explaining the periodic changes in moss communities (mesic-hydric) can be considered specific to individual polygons, *i.e.*, the ridges surrounding lower-centres are underlain by ice-wedges and act as a water-shed and barrier between adjacent polygons. Hence, if one polygon was in a dry state (*e.g.*, polygon b [Figure 8b] with lower ridges relative to and surrounding the polygon centre and low values of *Qg*, *Qs* and *P*) and one in a wet state (*e.g.*, polygon a [Figure 8a] with higher ridges relative to and surrounding the polygon centre and higher values of *Qg*, *Qs* and *P*) a shift to a wetter and cooler climate may be registered in polygon b though not in Polygon a, and *vice versa*. Thus, wetter and drier conditions in the palaeoecological record of soil moisture, which correspond between polygon cores to contrasting higher and lower palaeoclimatic proxy values, may point to an underlying long-term climatic influence, though modified where registered in individual cores by local geomorphologic conditions.

CONSEQUENCES OF PAST VEGETATION-HYDROLOGIC CHANGE

Several possible mechanisms have been presented to explain the observed changes in soil moisture during polygon development. Confirmation or refutation of these mechanisms, to establish their relative importance, is dependent on further palaeoecological study. However, regardless of the exact mechanism, there is little doubt that soil moisture conditions have changed dramatically during the development of the polygons, over decadal- to centennial-scales (Figure 9). These changes are important because soil moisture exerts a control on tundra ecophysiology through production, decomposition and nutrient cycling, regulating therefore the balance of CO_2 input and output. 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 of soils from net C-input to C-output accompanies the recent drying of tundra habitats (Oechel *et al.*, 1993 and 1995; Weller *et al.*, 1995). 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, with a subsequent positive feedback effect on CO_2-induced global warming. The magnitude of change in reconstructed soil moisture during the development of the polygons is sufficient to infer variation in the functional role (CO_2 flux) of the wetland during its long-term development (Figure 9).

Figure 9

Soil moisture change during the development of a wetland polygon. The reconstruction is based on a weighted average regression of the moisture optima for 14 moss species (core BY-A, cf. Ellis and Rochefort 2004, in press).



CONCLUSIONS

Two major points are warranted by the results of our study:

1. Models to predict long-term change in the ecosystem function of terrestrial tundra habitats (including the effects of future global warming) may need to account for inherent variability during ecosystem development. Peat-rich soils associated with arctic wetlands have contributed a net sink for carbon during the Holocene and are estimated to store >97% of the tundra carbon reserve comprising *ca.* 180–190 × 1015g of soil-C (Post *et al.*, 1982; Oechel and Vourtilis, 1994). Greater understanding of natural variability within and amongst arctic wetlands is essential to policy management of global carbon pools.
2. The mechanisms controlling soil moisture variation during polygon development, suggested by this study, should be confirmed or refuted. Our results suggest that short-term experiments may have neglected the important role of periglacial geomorphology in modifying the regional effect of climate at local scales. This is unusual, because vegetation patterns strongly related to geomorphology are an apparent feature of the tundra landscape. However, we also suggest that long-term polygon development may have been periodically impacted upon by pronounced climatic variability (*i.e.*, during the Little Ice Age). The corollary is that, given the expected magnitude of human-induced climate warming, even High Arctic ecosystems will be sensitive to future climate change. Nevertheless, predicting the effect of climate warming on High Arctic wetlands may require a greater understanding of the interaction between the vegetation-soil system and periglacial processes.

Christopher Ellis's main research interest is the structure and dynamics of ecological communities (especially mosses and lichens). Now based at Royal Botanic Garden Edinburgh (UK), Chris maintains close ties with Dr. Line Rochefort and her research group at Université Laval, Quebec.

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