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Authors: Breen, Katie, and Lévesque, Esther

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The Influence of Biological Soil Crusts on Soil Characteristics along a High Arctic Glacier Foreland, Nunavut, Canada

*Katie Breen**† and
*Esther Lévesque**†‡

*Département de chimie-biologie, Université du Québec à Trois-Rivières, Trois-Rivières, Québec, G9A 5H7, Canada
†Centre d'études nordiques, Université Laval, Québec, Québec, G1V 0A6, Canada
‡Corresponding author: Esther.Levesque@uqtr.ca

Abstract

This study explores the physical, chemical and microclimatological properties of soils along a High Arctic glacier foreland and adjacent moraine in relation to the development of biological soil crusts. We examine various edaphic properties: soil temperature, volumetric water content, organic carbon content, and texture in surface samples (~1 cm) with and without a cover of biological soil crust as well as changes in nitrogen, phosphorus, potassium, organic carbon, pH, volumetric water content, bulk density, and texture in crusted surfaces (<1 cm) and soil cores (5 cm) along a chronosequence following deglaciation. Soil crusts developed within four years of deglaciation and subsequent peaks in crust cover and thickness coincided with an accumulation of nitrogen and organic carbon in the crust. Crusted surfaces had significantly higher volumetric water content, organic carbon, a greater silt and clay fraction, and lower temperature compared to uncrusted soils. A steady supply of water from glacier melt promoted rapid development of biological soil crusts, creating an edaphic environment with enhanced moisture and nutrient properties which contributed to the high rate of vascular plant succession previously observed on this foreland. Results presented in this study are compared with edaphic conditions at other circumpolar sites and glacier forelands.

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Introduction

The retreat of glaciers over much of the High Arctic due to climate warming since the end of the Little Ice Age (LIA), ca. 1850 (Dowdeswell, 1995; ACIA, 2005), has resulted in the exposure of new land surfaces to biotic colonization. Primary succession in the strictest sense occurs on land that is completely devoid of life, and while it is often assumed to be guided by vascular plants, this is rarely the case as microorganisms rapidly colonize even the most extreme terrestrial environments and precede the arrival of most plant colonists (Belnap and Lange, 2001). Although early proglacial environments are generally nutrient-poor, nutrients may be obtained through eolian, terrestrial, and fluvial deposition, from subglacial (Skidmore et al., 2000) or supraglacial (Mueller et al., 2001) microbial communities, or from relict soil and plant material released from the ablating fronts of some polar glaciers (Bergsma et al., 1984).

Pioneering microorganisms such as cyanobacteria, green algae, lichens, mosses, fungi, and heterotrophic bacteria are typically the first organisms to colonize the surface and subsurface of new terrain and can coalesce over time to form a visible organic matrix on the soil surface known as a biological soil crust (Evans and Johansen, 1999; Belnap and Lange, 2001). Crusts may contain some or all of these organisms, the composition of which varies due to many factors including climate and terrain age (Belnap and Lange, 2001). In polar deserts or recently deglaciated areas devoid of higher plants, soil crust constituents can be the only primary producers and thus represent the trophic base of the developing ecosystem on which heterotrophic components depend (Elster et al., 1999). The early microbial members of a community therefore form a precursor for future soil crust development and are believed to be crucial in laying the foundation of an organic and nutrient-enriched medium in which more complex organisms may become established (Smith, 1991; Wynn-Williams, 1993).

Biological soil crusts can occur in all arid and semiarid regions but their ecological significance has been studied most extensively in temperate and warm desert ecosystems around the world. The largest arid regions within Canada are the polar deserts and semideserts of the High Arctic, which represent 95% of its ice-free terrain (Bliss et al., 1973) and where crusts have been recognized as important contributors to High Arctic ecosystems (Sohlberg and Bliss, 1984; Gold and Bliss, 1995; Anderson and Bliss, 1998; Gold, 1998; Bliss and Gold, 1999; Dickson, 2000; Breen and Lévesque, 2006). Crusts are well adapted to the severe conditions of polar terrestrial environments and are able to survive freezing and thawing, desiccation, and rehydration as well as continuous summer solar radiation (Elster, 2002). It is also suggested that the predominance of a darker, rougher soil surface can reduce albedo and substantially elevate arctic soil and surface temperatures (Gold and Bliss, 1995; Gold, 1998).

Arid regions of the world generally lack substantial vegetation cover and soil-stabilizing roots; therefore, crusts perform a key role in stabilizing otherwise mobile surfaces and protecting soil from erosion and cryoturbation (Wynn-Williams, 1993; Gold and Bliss, 1995; Evans and Johansen, 1999), of particular importance in the Arctic where soil cover is thin, undeveloped, and overlies thick permafrost. The adhesive, mucilaginous properties of several cyanobacterial genera, combined with the rhizoids of mosses and fungal hyphae of lichens further promote consolidation and stability by aggregating soil particles (Belnap and Lange, 2001). Many of the organisms in biological soil crusts enhance soil water retention and nutrients and have been found in temperate deserts to increase plant uptake of certain bioessential elements (Harper and Marble, 1988; Harper and Pendleton, 1993;

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FIGURE 1. Photograph of the north-facing Teardrop Glacier with arrow indicating the study area and map of Sverdrup Pass in central Ellesmere Island (79°10′N, 79°45′W), Nunavut. The lighter colored terrain visible in the photograph to the left of the glacier shows the lichen 'trim line' and the extent of glacier melt since the end of the last Little Ice Age.

Harper and Belnap, 2001). In terrestrial arctic environments plant growth is limited by low nitrogen levels (Henry et al., 1986; Archibold, 1995) and the primary source of nitrogen is that fixed by free-living cyanobacteria in soil crusts (Alexander, 1974). As a result, small changes in soil nitrogen can be critical to plant community development.

Vegetation community analysis undertaken during the summer of 2004 demonstrated that the Teardrop Glacier foreland in Sverdrup Pass, Ellesmere Island, Nunavut, supports a very productive community of vascular plants and biological soil crust relative to other High Arctic glacier forelands (Breen and Lévesque, 2006). Multivariate analyses in that study found that the distance from the glacier and the cover of biological soil crust were the two most important variables explaining vegetation distribution on the foreland. Since constituents of soil crusts are recognized as facilitators of subsequent vascular plant development, the objective of the present study was to further our knowledge of the edaphic properties of soils colonized by biological soil crusts and to quantify environmental modifications brought about by their development along a chronosequence. We examine the physical, chemical, and microclimatological properties of surface samples (~1 cm deep) with and without a cover of biological soil crust at four sites. We also examine the changes occurring in crusted substrate with time since deglaciation at 18 sites in order to evaluate the hypothesis that crusts modify the edaphic environment in such a way as to enhance conditions for vascular plant succession.

Material and Methods

STUDY SITE

The field work for this study was undertaken during the summer of 2004 in the Canadian High Arctic on the granite-gneiss based 'Teardrop Glacier' foreland (79°10′N, 79°45′W), 330 m a.s.l. The Teardrop Glacier is a north-facing outflow glacier of the Prince of Wales Icefield, located at the drainage divide of Sverdrup Pass, a deglaciated valley running east-west across central Ellesmere Island (Fig. 1). Ellesmere Island is classified in the polar desert vegetation zone (Edlund and Alt, 1989) and lies within the northwestern arctic climate zone, with a mean July temperature of 3–5°C and less than 150 mm of precipitation per year (Maxwell, 1981). The vegetation of Sverdrup Pass has been previously described by Bergeron and Svoboda (1989) and Maycock and Fahselt (1992), and a survey of the diversity and abundance of soil algae was undertaken by Elster et al. (1999). Jones and Henry (2003) and Breen and Lévesque (2006) described the emerging vascular plant communities on the Teardrop Glacier foreland.

The Teardrop Glacier foreland supports a well-developed community of vascular plants with greater species richness, cover, and density compared to other glacier foreland vegetation communities previously investigated on Ellesmere Island (Breen and Lévesque, 2006). The abundance of vegetation on the foreland was attributed in part to the consistent and moderate supply of glacier meltwater feeding the foreland and the subsequent growth and development of rich biological soil crust communities. Biological soil crusts were composed primarily of dark, cyanobacteria-dominated crusts across most of the foreland with moss-dominated crusts found in later succession, in areas of standing water.

The boulder-strewn foreland is clearly delineated between the glacier's current position and the position of a terminal moraine, marking the maximum advance of the glacier during the LIA (Figs. 2c and 3). The use of air photos and *in situ* measurements allowed Fahselt et al. (1988) to estimate a rate of glacier retreat of 1.6 m y^{-1} ± 0.3 SE between 1959 and 1986. *In situ* measurements in 2004 determined that the rate of retreat had increased to 2.01 m y^{-1} ± 0.13 SE from 1992 to 2004. Retreat rates were used to calculate approximate terrain ages as seen in Figure 3.

SAMPLING DESIGN

A 200-m-wide subsection of the ~1.2-km-wide foreland was chosen for its gentle slope, continuous vegetation, and lack of disruptive physical features, such as kames, steep ravines, or proglacial lakes that might inhibit the continuous growth of soil crusts or plants along the foreland. Within this subsection, a reference point was established at the glacier terminus on 29 June 2004, from which all distances referred to in this study were measured. The study area spans the entire foreland length along a north-south transect from the glacier to the terminal moraine (190 m) and extends beyond it to include an area on older moraines deglaciated at some point prior to the LIA, up to 212 m from the glacier.

Sites (40 m × 5 m) were marked every 6 m along the transect for the first 60 m and every 20 m thereafter, resulting in 17 sites

FIGURE 2. Photographs of the glacier foreland at various distances and the associated dominant vascular plant species in percent cover and frequency; (a) 5–10 m from the glacier, scattered individuals of *Alopecurus borealis*, *Papaver radicatum*, *Saxifraga cernua*, *Saxifraga rivularis*, and *Draba oblongata*; (b) 25–30 m from the glacier, *Luzula confusa*, *Saxifraga oppositifolia*, *Stellaria longipes*, *Alopecurus borealis*, and *Saxifraga cernua*; (c) 170 m from the glacier, *Salix arctica*, *Saxifraga oppositifolia*, *Luzula confusa*, *Luzula arctica*, and *Dryas integrifolia*. The end of the boulder field and foreland at 190 m is visible to the right of Figure 2c.

along the foreland with an additional 3 sites beyond the terminal moraine, leading to a total of 20 sites (Fig. 2). To avoid spatial bias, sites were established at random distances up to 100 m alternating to the east and west of the north-south transect line.

SOIL MICROCLIMATE MEASUREMENTS IN AND OUT OF CRUST

A microclimate station was established ~40 m from the glacier in order to monitor soil microclimate variables from crusted and uncrusted surfaces at four sites at 20, 40, 48, and 56 m from the terminus of the glacier ('Met' in Fig. 3). Each of the microclimate sites was chosen for its availability of both crusted and uncrusted substrate and its proximity to the microclimate station in order to accommodate a fixed length of cable. A CR10X datalogger and AM416 multiplexer (Campbell Scientific) were used to log hourly and daily averages, temperature minima and maxima, and water content in crusted and uncrusted substrate from 3 July to 7 August 2004. Temperature was measured at all four sites using a soil temperature probe (Model 107B, Campbell Scientific, accuracy ±0.2°C). Volumetric water content (VWC) was measured at two of the sites (20 and 56 m from the glacier), using a Time Domain Reflectometer (TDR) (CS616, Campbell Scientific, accuracy ±2.5% VWC). Instruments were inserted horizontally, ~1–2 cm below the soil surface, in both crusted and uncrusted surface at each site. The 'in crust' measurements were in fact directly beneath the crusted surface, given that the actual crust is generally less than 2 mm and instrument thickness would not allow for a more shallow measurement; nonetheless the physical properties of crusts are understood to be relevant within the ~1–2 cm region below the surface. Data on ambient air and soil temperature were also collected directly at the microclimate station at 1.5 m and 10 cm above the crusted soil surface and 1 cm below the crusted soil surface using copper-constantan thermocouples.

SURFACE AND SOIL CORE SAMPLING

The soil sampling on the Teardrop Glacier foreland was undertaken by distinguishing between 'crusted' and 'uncrusted' surfaces. Crusted surfaces were covered in a visible biological soil crust, usually black, of variable texture, and less than 2 mm thick. Uncrusted surfaces consisted of coarse-textured, gray, glaciofluvial sediment, referred to in this study as 'glacial soil,' which is more characteristic of arctic forelands (Fig. 4). A third surface category 'paleo material' is a dark-colored, organic substrate comprised of dead but intact, relict plant and organic soil matter released from the retreating ice margin of some cold-based glaciers (see Bergsma et al., 1984). Exposure to weathering leads to the disintegration of most paleo material on the soil surface and

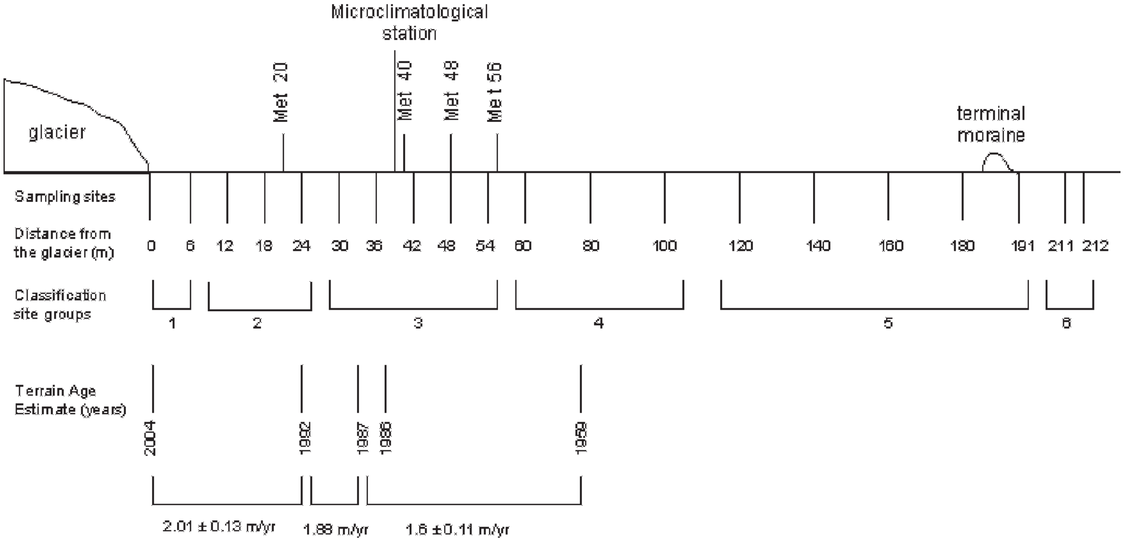

FIGURE 3. Location of the microclimate (Met) and sampling sites, the classification groups derived from divisive classification analysis of the vascular plant cover, and approximate terrain ages along the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut. Modified from Breen and Lévesque (2006).

FIGURE 4. Samples of biological soil crust (left) and glacial soil (right) from the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut.

therefore it appears to exist only within the first few meters of the glacier; however, soil pits dug across the foreland show that paleo material subsists in a patchy network below the surface substrate.

Surface samples (~1 cm deep) were collected in order to undertake comparative analyses of texture and organic carbon in and out of crust at each of the four microclimate sites. At each of these sites, samples in and out of crust were collected on 7 and 10 August 2004 and consisted of one surface layer (one ~15 × 15 × 1 cm deep block [225 cm^3 total sample]). The uncrusted substrate at these sites was glacial soil, as described above.

The analysis of changing characteristics in crusted soil with distance from the glacier was undertaken using crusted surface samples (<1 cm) and soil cores (5 cm) collected on 9 and 10 August 2004 at a total of 18 sites, including all but the first two sampling sites at 0 m and 6 m from the glacier where crusts were undeveloped or nonexistent and therefore not included in the analyses. Surface samples and soil cores were collected randomly within unvegetated areas of each site in order to undertake comparative analyses of edaphic properties within crust among distances from the glacier. One surface sample was obtained as a composite sample of five 0.7-cm-deep samples collected using half of an 8.8-cm-diameter Petri dish (213 cm^3 total sample). Three soil cores were collected, each a composite sample of three randomly collected 5-cm-deep, 6-cm-diameter soil cores (1272 cm^3 total sample).

Surface samples and soil cores were weighed wet to 0.01 g, frozen and shipped at −10°C after which they were air-dried to constant weight. Samples were then sieved and the nutrient and granulometric analyses of the <2 mm fraction were performed at the Forestry Soil Science Laboratory, Université Laval, Québec City, Canada. The surface samples collected in and out of crust at the microclimate sites were analyzed for texture and soil organic carbon (n = 1 in each substrate at each site). A summary of surface sample variables collected at the microclimatological sites is presented in Table 2. The soil (n = 3 per site) and surface samples (n = 1 per site) of crusts from 20 sites with distance from the glacier were analyzed for texture, pH, organic carbon, total nitrogen, exchangeable potassium, available phosphorus, volumetric water content, and bulk density. Granulometric analysis (% sand, loam, and clay) was determined by the hydrometer method (Bouyoucos, 1962), soil pH was determined using $CaCl_2$ (McKeague, 1978), organic soil carbon was determined using methods outlined in Yeomans and Bremner (1988), total soil nitrogen was extracted by the Kjeldahl method, and exchangeable potassium and available phosphorus were determined using the methods in Mehlich (1984).

The percent cover of biological soil crust was previously determined in the field using vertical projection to ground level within a minimum of 20 quadrats (50 × 50 cm) placed randomly in each of the 40 × 5 m site areas to determine a mean per site (Breen and Lévesque, 2006). The physical development of crusts was considered from field measurements of the thickness of ten randomly chosen crusts at each site with the mean of the five largest values used to estimate a maximum thickness per site.

DATA ANALYSES

At each of the four microclimate sites, paired *t*-tests using Sigma Stat 3.1 (Systat Software Inc., Point Richmond, California) were performed on data to test for differences in and out of crust for temperature and volumetric water content from logged data over the summer, and *t*-tests were used to test for differences in texture and organic carbon content of surface samples collected in and out of crust.

The 18 sites sampled for along the chronosequence were classified into groups based on classification analysis (TWINSPAN) of the vascular plant cover previously surveyed at each site (Breen and Lévesque, 2006). These groupings represent distance from the glacier and were used as factors in analyses in lieu of the 18 sites (Fig. 3), therefore the average value from each site is used as a replicate within a group. In addition, since sites at 0 m and 6 m (group 1 of the original classification analysis) were excluded from soil sampling due to a lack of crust, we used only five of the six classification groups in our analyses. Multiple one-way ANOVAs were then performed on surface samples and soil cores to test for the effect of distance from the glacier on pH, organic carbon, nitrogen, phosphorous, potassium, volumetric water content, bulk density, texture, crust cover, and crust thickness.

In all analyses, when data did not meet the assumptions of normality or equal variance, data were either rank transformed or an equivalent non-parametric test was used (Zar, 1999). Multiple comparison tests following ANOVAs were used to determine significant differences between classification groups. The Tukey test was used for parametric data and Dunn's test was used for non-parametric data using Sigma Stat 3.1. Data are presented graphically in relation to classification groups but site values are occasionally noted in the text in order to emphasize maximum or minimum observed values.

Results

CLIMATE AND THAWING DEGREE-DAYS

The valley of Sverdrup Pass has climatic conditions comparable to the nearby climate station in Eureka, Nunavut (79°58′N, 85°55′W), ~150 km northwest of Sverdrup Pass. Over the course of the measurement period from 3 July–7 August 2004, the mean daily ambient temperature on the foreland, measured 1.5 m above ground, was 5.7°C and ranged from 2 to 13°C (Fig. 5). This was slightly higher than the daily mean July 2004 temperature in Eureka (4.5°C) but equivalent to July climate normals in Eureka from 1971 to 2000 (Environment Canada, 1971–2000, 2004). Temperature 10 cm above the soil and 1 cm under the soil (with a cover of crust) were warmer on average than air temperature, with daily means and ranges of 6.7°C (0.2 to 16.7°C) and 5.9°C (0.4 to 17.4°C), respectively (Fig. 5). July thawing degree-days (TDD) (sum of all daily mean temperatures above 0°C), calculated from 3 July–3 August data, reflect this trend with the greatest number of

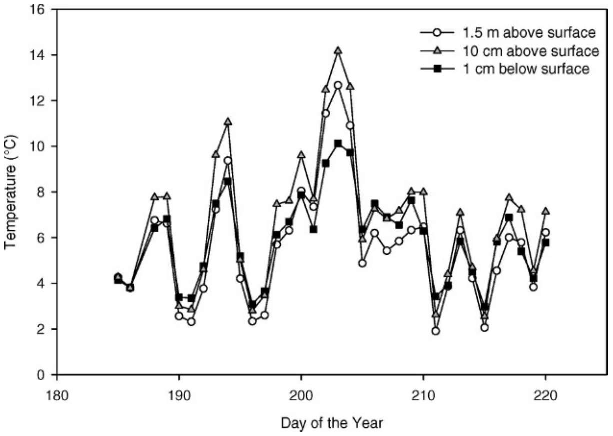

FIGURE 5. Daily mean temperatures of ambient air (1.5 m above surface), boundary air layer (10 cm above surface) and soil surface (1 cm below surface) at the microclimate station, 40 m from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut from 3 July to 7 August 2004.

TDD calculated 10 cm above ground (216), followed by 1 cm below ground (190), and 1.5 m above ground (182). These values are comparatively similar to the mean 216 TDD from 1989 to 1993 July data in the Sverdrup Pass valley 1.5 m above ground (Lévesque et al., 1997) and the mean TDD values from Eureka (178) from 1971 to 2000 (Environment Canada, 1971–2000). Although not recorded at Sverdrup Pass, mean July 2004 precipitation recorded in Eureka was 22.2 mm, almost double the 1971–2000 climate normal of 12.5 mm (Environment Canada, 1971–2000, 2004).

SUBSTRATE DIFFERENCES IN AND OUT OF CRUST

Data logged from instruments placed in and out of crust at each of the four microclimate sites showed that average daily soil temperatures were significantly lower ($p < 0.001$) in crust than outside of crust, ranging from 3.3 to 12.9°C in crust and 3.6 to 15.3°C out of crust (Fig. 6). As such, noncrusted surfaces had, on average, a greater number of TDD in July (282 TDD) as opposed to crusted surfaces (248 TDD; Table 1). The volumetric water content measured by TDR at two microclimate sites was significantly greater (up to four times) in crust ($p < 0.001$), with average values of 13.7% ± 0.5 SE in crust and 9.6% ± 0.5 SE out of crust (Fig. 7).

Granulometric analyses of the ~1 cm surface samples revealed that soils covered in crust had a greater quantity of silt and clay and were classified as loamy sand while the uncrusted glacial soil was primarily sand, or in the case of one sample, sandy loam (Table 2). Organic carbon content in the ~1 cm surface samples was significantly greater in crust than out of crust, by an average of 25 times (Table 2).

CHANGES WITH DISTANCE FROM THE GLACIER

Biological soil crust cover reached a maximum of 37% within approximately 20 years of glacier retreat and once established, maintained a thickness of between 1.4 and 1.8 mm (Fig. 8). After reaching a maximum in cover early in succession, crust cover declined slightly over the rest of the foreland, yet still represented the majority of substrate available for plant establishment, given that pebbles, cobbles, and boulders dominate the landscape (up to 44% cover) and increasing vascular plant growth reduced available terrain for crust establishment. Despite apparent changes in crust cover and thickness, neither were statistically different across classification groups 2–6.

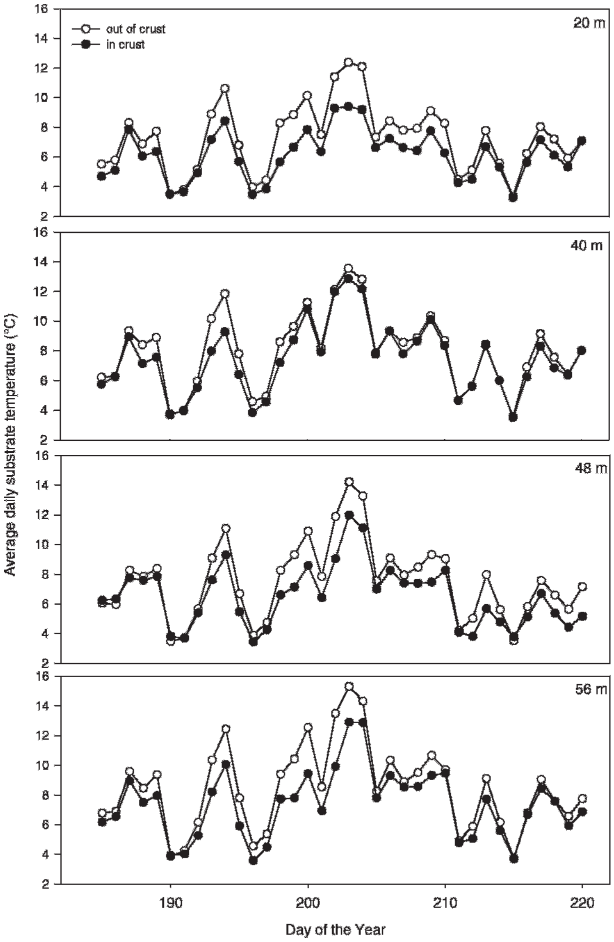

FIGURE 6. Daily mean temperature (°C) of crusted and uncrusted surfaces (~1 cm deep) at each of the four microclimate sites at 20, 40, 48 and 56 m from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut from 3 July to 7 August 2004.

The average volumetric water content was generally higher in the surface samples rather than soil cores but there was no significant difference in water content in either across the classification groups (Fig. 9a). In addition to higher water content, surface samples had a lower bulk density than soil cores (Fig. 9b), and both soil cores and surface samples showed a significant difference in mean bulk density across classification groups ($p =$

TABLE 1

Thawing degree-days (TDD) in and out of crusted soil surfaces (~1 cm deep) in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island. July TDD are calculated from 3 July to 3 August 2004.

	July TDD (d > 0°C)	
Distance from the glacier (m)	In crust	Out of crust
20	221	262
40	269	288
48	235	271
56	266	305
mean	*248*	*282*

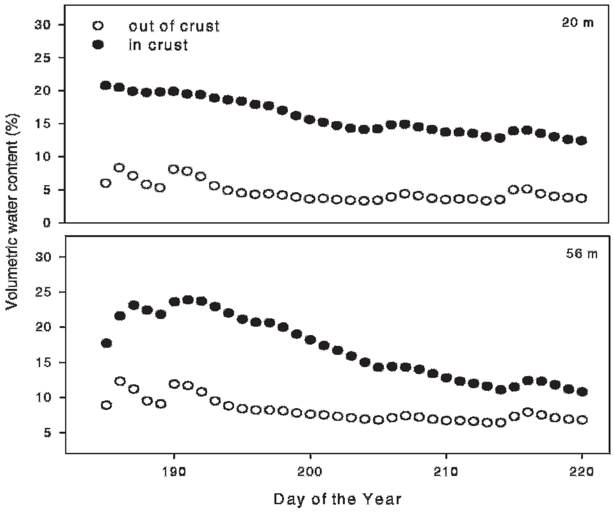

FIGURE 7. Daily mean percent volumetric water content (from TDR) in and out of crust (~1 cm deep) at two microclimate sites at 20 and 56 m from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut, from 3 July to 7 August 2004.

0.004 and 0.003). Surface samples contained on average a greater proportion of silt and less clay and sand than the soil cores, with surface sample values ranging from 68 to 74% sand, 16 to 22% silt, and 7 to 12% clay and in soil cores from 74 to 79% sand, 11 to 14% silt, and 10 to 14% clay. Soil and surface texture was relatively homogeneous; only clay varied significantly across the classification groups in the surface samples ($p = 0.024$).

Soil pH and nutrient concentrations changed to varying degrees across the foreland and moraine but were generally higher in the surface samples than in soil cores, with the exception of phosphorus (Fig. 10). Nitrogen, phosphorus, potassium, organic carbon, and pH all differed significantly in the surface samples across the classification groups. In soil cores, all variables except phosphorus and organic carbon were significantly different across the groups. The location of significantly different groups is noted in Figure 10.

Previous sampling of the <2 mm fraction of soil from granitic polar desert sites in Sverdrup Pass (Lévesque, 1997; Lévesque et al., 1997) differed in core depth (10 cm) and altitude (347–727 m a.s.l.) and provided only a limited quantity (approximately 5%) of fine fraction soil due to the coarse, rocky substrate, but nonetheless offers the only regional comparative soil values and are thus displayed in Figure 10. In general, nutrient values in the surface samples are higher than those obtained by Lévesque (1997) and in the soil cores the differences are less pronounced but are evidently higher for phosphorus and organic carbon (Fig. 10). The surface samples and soil cores on the Teardrop foreland generally had a higher proportion of clay and less sand than the surrounding polar desert (Lévesque, 1997).

Discussion

SUBSTRATE DIFFERENCES IN AND OUT OF CRUST

The results presented here highlight the ability of biological soil crusts, in comparison with uncrusted glacial soil, to alter microclimatological, textural, and nutrient regimes, which in turn create favorable conditions for plant growth. Crusted surfaces would be expected to reduce water stress to plants as a result of increased volumetric water content and organic carbon. Crusted surfaces retained a greater quantity of silt and clay than uncrusted surfaces, which can further contribute to water retention and increase soil fertility since fine, negatively charged clay particles are better able to stick to the mucilaginous sheaths of crusts and subsequently bind with positively charged plant nutrients (Belnap et al., 2001).

The only unexpected result in our analyses in and out of crust came from soil temperature, which was lower in crust, contrary to the results of Gold (1998), and supported on average, fewer thawing degree-days than uncrusted glacial soil. Surface crusts are generally dark in color and are therefore expected to have a low albedo, absorb radiant energy better than neighboring uncrusted glacial soil, and thus support higher soil temperatures and TDD. Although depth of measurement differed from our study, Gold (1998) found that mean daily soil temperatures 5 cm below crusted surfaces at Truelove Lowland on Devon Island (75°33′N, 84°40′W) were generally 1–3°C higher than soil below uncrusted surfaces during sunny periods, yet during cloudy conditions the difference was negligible. Studies of the water content at that site showed that differences in water content between crusted and uncrusted surfaces was generally less than 5% (Gold and Bliss, 1995), whereas the difference in water content in the crusted and uncrusted soils on the Teardrop foreland were greater, as was the maximum water content (Fig. 7). The summer of 2004 was unusually overcast and rainy in Sverdrup Pass, as evident from the higher than normal precipitation recorded in Eureka in July 2004 (Environment Canada, 2004). It is possible that the increased precipitation, combined with predominantly overcast days, increased the water content of crusts and prevented them from receiving sufficient radiation to increase temperatures above those in the adjacent, drier glacial soil. The presence of liquid water in the crusts acts as a buffer to temperature change due to the specific heat capacity of water, thus stabilizing soil temperatures. Our results show that crusts may not always provide the warmest substrate for plant establishment and that year-to-year and even

TABLE 2

Soil characteristics (mean ± SE) of variables from surface samples (~1 cm deep) collected in and out of crust at each of the four microclimate sites in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Significance of difference in and out of crust * $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Samples are analyzed from the fine soil fraction (<2 mm).

Variables	Surface samples (~1 cm)		Significance
	In crust	Out of crust	
Texture			
% sand	74 ± 1.4	90.3 ± 1.4	***
% silt	16.5 ± 1.8	3.25 ± 0.9	*
% clay	9.5 ± 0.65	6.5 ± 0.5	*
Textural class	sandy loam	sand or loamy sand	—
Organic carbon (%)	4.6 ± 0.9	0.18 ± 0.04	*

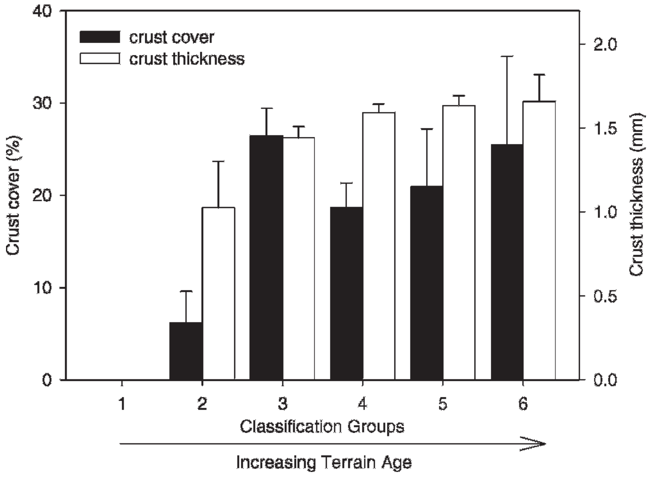

FIGURE 8. Mean crust cover (%) ± SE and thickness (mean ± SE of the five thickest crusts) for each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Classification groups are averaged from 18 site values in sequential order: Group 2 ($n = 3$), 3 ($n = 5$), 4 ($n = 3$), 5 ($n = 5$), 6 ($n = 2$).

daily variations can be weather dependent, as was noted by Gold (1998). However, high soil surface temperatures of up to 30°C in the High Arctic (Gold, 1998) can actually be a source of severe physiological stress to plants in a polar desert environment, especially if water is limiting, as in the dry glacial soils where water content was less than 10% for most of the summer. Despite fewer thawing degree-days, the lower temperatures observed in crust were sufficient for summer growth and may in fact have protected plants from desiccation caused by increased surface temperatures and water deficit.

CHANGES WITH DISTANCE FROM THE GLACIER

Direct comparisons of nutrient concentrations on other forelands are difficult due to dissimilarities between environments, sampling strategies, and analyses used. Generalizations regarding soil development abound but commonly suggest that organic matter and nitrogen accumulate and phosphorus, cation concentrations, and pH decrease with time since deglaciation (see Walker and del Moral, 2003). The Teardrop Glacier foreland follows some but not all of these trends due to the distinctive nature of the site. Results presented here show that the development of soils in extreme arctic environments is not necessarily confined to physical and chemical processes, as biological soil crusts have a substantial effect on the nutrient regime. The subtleties observed in the upper 1 cm due to the growth of biological soil crusts would have been lost with the analysis of 5 cm cores alone.

PHYSICAL AND CHEMICAL CHANGES

Differences between surface samples and soil cores reveal the capacity of crusts to retain water due to increased organic matter and the hydrophilic nature of certain crust constituents. The higher clay fraction seen in the Teardrop foreland and old moraine soils as compared to soils from the surrounding polar desert (Lévesque, 1997) may have led to preferential colonization by crust-forming microorganisms (Kaštovská et al., 2005) and increased overall soil fertility.

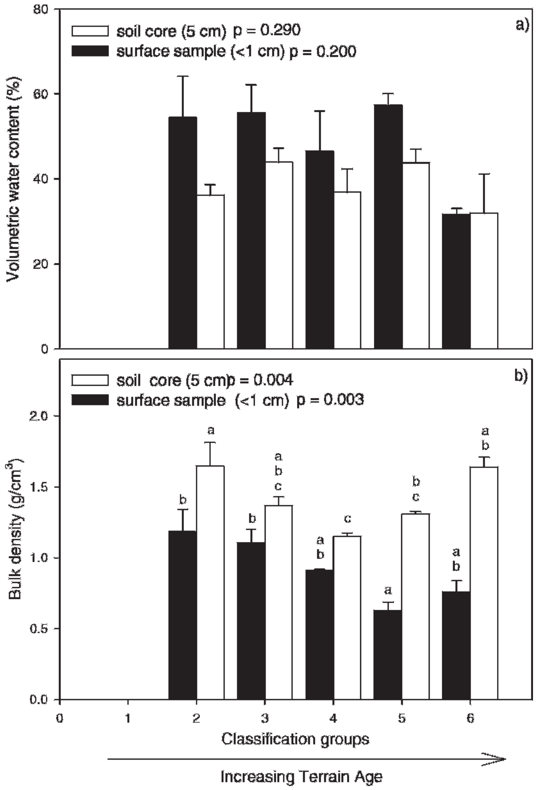

FIGURE 9. (a) Volumetric water content and (b) bulk density of crusted surface samples (0.7 cm deep) and soil cores (5 cm deep) for each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Classification Groups are averaged from 18 site values in sequential order: Group 2 ($n = 3$), 3 ($n = 5$), 4 ($n = 3$), 5 ($n = 5$), 6 ($n = 2$). p-values note significance across classification groups. Letters denote results of multiple comparison tests. Groups with the same letters were not significantly different from each other.

A decline in pH with time is assumed to be a universal characteristic of glacier foreland chronosequences (Matthews, 1992), with the increasingly acidic compounds linked to increasing biological activity. The increase in pH on this foreland is likely attributable to wind-blown dolomitic dust driven onto the granitic foreland from the northern side of Sverdrup Pass valley (Lévesque et al., 1997). However, the growth of crusts along the foreland may also have contributed to the increase in pH, particularly in the surface samples, as the presence of photosynthetic crustal organisms have been shown to significantly increase the pH of surrounding media (Garcia-Pichel and Belnap, 1996; Belnap et al., 2001).

Colonization by biological soil crusts generally served to increase nutrients in the crust, where the greatest concentration of nutrients were measured; however, individual nutrients exhibited varying trends, not only along the chronosequence but with depth of sampling. Although most nutrient concentrations were higher in the surface samples than in the soil cores, the beneficial effects of organisms found within the top few millimeters of crust (such as increased N fixed by cyanobacteria) can eventually be transferred down through soil profiles to provide an overall improvement to soil fertility (Elster et al., 1999). Decreases in certain nutrients in later succession, as seen in the soil cores, may be attributed to the uptake and retention of nutrients by vegetation, in particular for limiting nutrients such as nitrogen. Since most roots are established below the crust layer, in certain cases a loss of nutrients might be observed in the 5 cm core but not in the upper surface sample where nutrients are generally more tightly bound in the presence of a crust (Harper and Belnap, 2001). The roots of

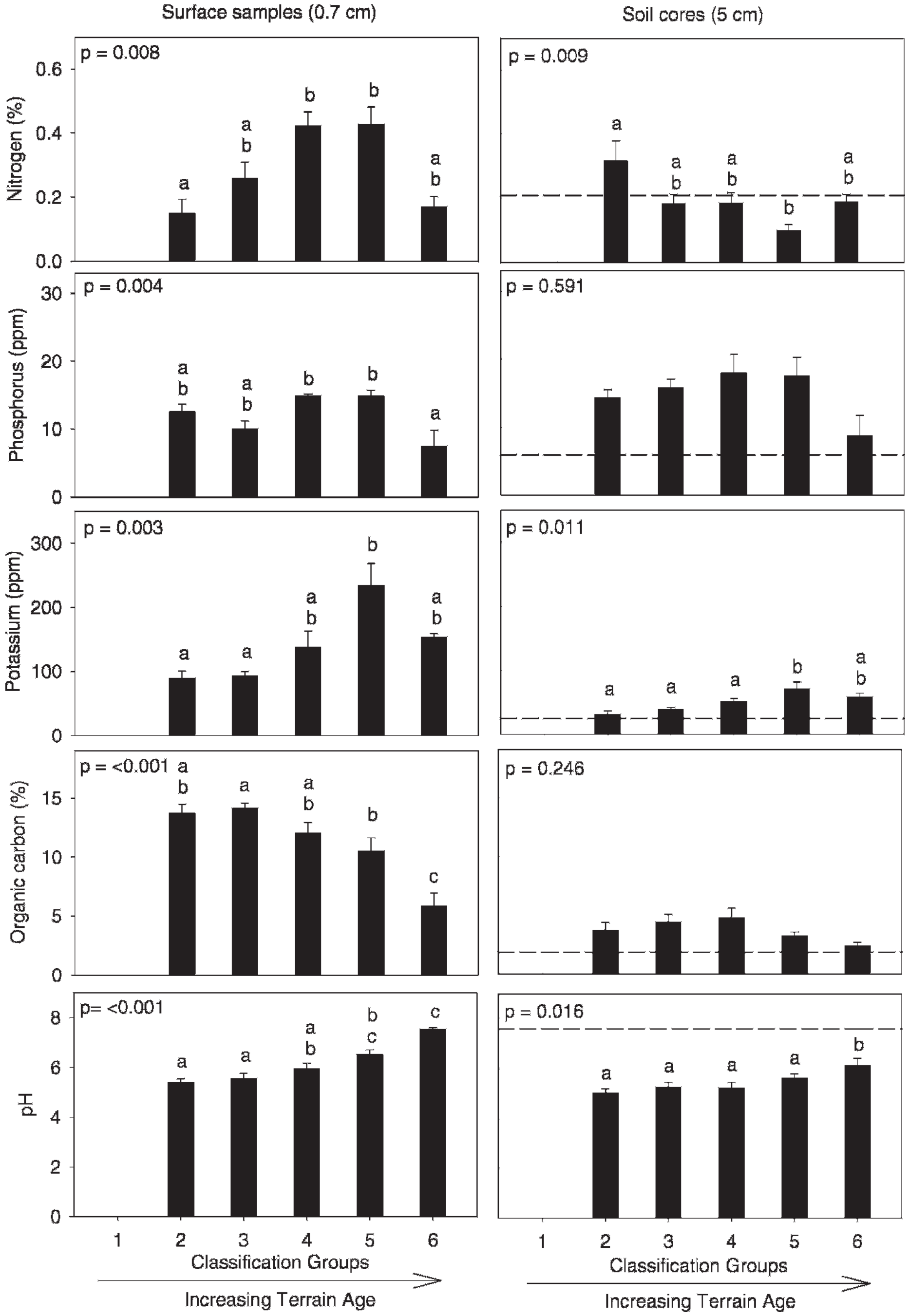

FIGURE 10. Mean nutrient concentrations and pH values of the <2 mm soil fraction from surface samples (0.7 cm deep) and soil cores (5 cm deep) for each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. The dashed horizontal lines are mean values from Lévesque (1997) and Lévesque et al. (1997). Classification Groups are averaged from 18 site values in sequential order: Group 2 ($n = 3$), 3 ($n = 5$), 4 ($n = 3$), 5 ($n = 5$), 6 ($n = 2$). p-values note significance across classification groups. Letters denote results of multiple comparison tests. Groups with the same letters were not significantly different from each other.

various plant species occupy different soil layers and will therefore vary in their capacity to utilize resources from the crust. Harper and Belnap (2001) noted that temperate desert plants with the greatest mineral uptake were those with shallow feeder roots lying within the portions of the soil profile that were influenced by biological soil crusts. Arctic species have relatively shallow root systems due to a thin active layer (Billings, 1987), suggesting that most species would be able to acquire nutrients leached from the crusts.

NITROGEN

Most successional studies show a consistent increase in nitrogen concentration through time following deglaciation with a relatively rapid rise in the early stages of succession and a leveling off or slight decrease at a maximum value on older terrain (Matthews, 1992). As the growth of crust proceeded, N in surface samples quickly reached a maximum, coinciding approximately with peaks in crust cover and thickness and then leveled off and remained high over the rest of the foreland (up to group 5). The decrease in N in the last two old moraine sites (group 6; Fig. 10) is likely linked with the decrease in water content in these sites, which is essential for maintaining high N_2 fixation rates (Dickson, 2000). The discrepancy between N values in surface samples and soil cores suggests that most of the N is derived from N_2 fixation by cyanobacteria in the developing crusts. In temperate deserts, between 5 and 88% of N_2 fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris, 1954; Silvester et al., 1996; Belnap et al., 1997) and it is likely that some of the N in lower surface layers was leached from the crusts.

At Glacier Bay, Alaska (58°58′N, 136°04′W), a temperate glacier foreland, both Crocker and Major (1955) and Bormann and Sidle (1990) documented a peak in the soil N content in pioneer successional stages and a marked decline in later succession, which was attributed to vegetation uptake. They suggest that the rapid initial accumulation appeared to result from N_2 fixation primarily by *Alnus sinuata* and *Dryas drummondii* on the youngest surfaces which, when decomposed, was taken up by the succeeding *Picea* stand. Crusts likely played a similar facilitative role in early succession due to N_2 fixation and the decrease in N seen in soil cores in later succession suggests that it may have been progressively taken up by the increasing vegetation cover (Breen and Lévesque, 2006).

Values from comparative arctic and alpine sites suggest that the N concentration and rate of accumulation on the Teardrop Glacier foreland are relatively high. Typical, noncrusted soils of the polar deserts have extremely low concentrations of total soil nitrogen (0.04%), whereas crusted soils can have more than twice this amount (Gold and Bliss, 1995). Nitrogen concentration in the top 5–10 cm on granitic plateaus above the nearby polar oasis at Alexandra Fiord (78°53′N, 75°55′W) and Truelove Lowland on Devon Island both had means of 0.01% (Bliss et al., 1994), while Lévesque (1997) reported an average of 0.21% in the fine soil fraction from granitic polar desert sites in Sverdrup Pass. On the Robson Glacier foreland in British Columbia (53°07′N, 119°09′W), mean total nitrogen content reached a temporary steady state at 0.4% in less than two centuries within the uppermost 15 cm (Sondheim and Standish, 1983), whereas values from 5 cm cores on the Teardrop Glacier foreland reached a mean value of almost 0.4% in a little over 10 years.

PHOSPHORUS

Data on soil phosphorus content on glacier forelands is limited and the information available points to a variety of patterns and processes (Matthews, 1992). Decreases in P concentration have been noted on other forelands at Glacier Bay, Alaska (Bormann and Sidle, 1990) and Alexandra Fiord, Ellesmere Island (Jones and Henry, 2003) and are generally attributed to weathering of the mineral soil over time, uptake by increasingly prevalent plants in later succession, or the formation of organic complexes that are unavailable to plants at richer, more productive sites. Muc et al. (1994) linked low P availability (1–7 ppm) with the high organic content of soils, having observed higher phosphorus values in soils of sparsely vegetated polar deserts (up to 64 ppm). Lévesque and Svoboda (1999) also noted a similar trend of lower P availability in sites with comparatively higher plant cover. This might explain the slightly lower phosphorus values in the organic-rich surfaces as compared to the soil cores, which likely contained a greater proportion of mineral-rich glacial soil under the crust. The P values did not exhibit a clear pattern across the foreland but were generally higher (up to 32 ppm in 5 cm soil cores) than those on the Twin Glacier foreland at Alexandra Fiord, which had mean values of approximately 5 ppm from 5 cm soil cores (Jones and Henry, 2003). The Teardrop foreland values were also higher than the 5.9 ppm determined from 10 cm soil cores in the granitic polar desert soils of Sverdrup Pass (Lévesque et al., 1997) and Alexandra Fiord, which ranged between 3 and 14 ppm (Lévesque and Svoboda, 1999).

POTASSIUM

Potassium is generally not considered a limiting factor to plant growth in undisturbed natural ecosystems as it can be leached from dead and living tissues (Brady and Weil, 1999). Potassium levels rose steadily across the foreland within both soil cores and surface samples but crusts appear to enhance the accumulation of exchangeable K as the surface cores reached a maximum of almost 350 ppm in one site, approximately three times higher than the maximum soil core values. The concentration of K on the foreland was considerably higher than the maximum of 60 ppm in 5 cm soil cores on the Twin Glacier foreland at Alexandra Fiord (Jones and Henry, 2003) and the mean of 24.8 ppm in the granitic polar deserts in Sverdrup Pass (Lévesque et al., 1997).

ORGANIC CARBON

Richly vegetated areas with soils high in organic carbon are extremely rare and erratically distributed on Ellesmere Island (Tedrow, 1977). Although the organic carbon in soil cores did not show a clear trend with distance from the glacier, the high concentration and subsequent decline of organic carbon in the surface samples coincides with peaks in crust cover and suggests that much of this carbon is derived from crusts. All crust components secrete extracellular carbon within a few days of acquisition, and in cyanobacteria these secretions can represent up to 50% of total fixed carbon (Lewin, 1956; Fogg, 1966). The organic carbon in both soil cores and surface samples surpassed the mean value found by Lévesque (1997) in the polar deserts surrounding Sverdrup Pass (Fig. 10) as well as that found on alpine moraines in front of the Robson Glacier, British Columbia, which had a maximum of 0.87% at 15 cm depth after 100 years (Sondheim and Standish, 1983).

In temperate deserts, studies have shown that crusts appear to consistently enhance plant nutrients such as N, K, and several micronutrients and to occasionally reduce other essential elements such as P (Harper and Belnap, 2001). A greater understanding of arctic biological soil crusts is necessary to determine whether these patterns might occur in polar environments. Future studies in the field and laboratory are needed to determine the rates at which limiting nutrients present in crust can be acquired by vascular plants and incorporated into their tissues.

ADDITIONAL ORGANIC INPUTS

The influence of paleo material on modern plant community mineralization and decomposition rates has yet to be explored, but Jones and Henry (2003) highlighted their importance in dictating plant distribution patterns in early succession. In Sverdrup Pass, paleo material was only evident intermittently within the first 30 m of the glacier, after which time it was either buried by glacial soil and debris or degraded by exposure to sun, wind, or glacial runoff. However soil pits dug across the foreland and on the older moraine beyond the foreland clearly showed patchy but distinct layers of paleo material that have likely been contributing to the surrounding nutrient and organic matter pool since initial Little Ice Age deglaciation. The high concentration of nitrogen and organic carbon close to the glacier also suggests the input of nutrients from organically rich paleo plants and soils. Paleo material likely provides nutrients to microorganisms and plants throughout succession; however, a more detailed analysis of past deposition layers would be required to quantify its precise contribution. Other sources of nutrients on this foreland include feces from numerous animals, including musk ox, lemming, fox, and ermine as well as several bird species such as snow buntings, ptarmigan, jaegers, and gyrfalcon. Multivariate analyses of above-ground cover did not find feces to be a significant determinant of vegetation distribution (Breen and Lévesque, 2006), yet it likely contributes to surrounding nutrient pools. Researchers of temperate desert crusts have raised the possibility that plants grown on crusts provide better quality forage for grazing animals (Robbins, 1983; Harper and Belnap, 2001), an idea which merits consideration in the Arctic, in particular due to the high grazing pressure by musk ox in Sverdrup Pass (Raillard, 1992).

Conclusion

Most arctic glacier forelands experience fluctuating water availability from glacial discharge leading to alternating periods of drought and flood. The melt pattern of the Teardrop Glacier is unique in that it supports over 100 small melt water channels evenly distributed across its Teardrop-shaped terminus. As a result, water is discharged relatively evenly, providing the foreland with a persistent supply of water, often carrying glacial soil, paleo-material, and nutrients that encourage the colonization of soil crust microbiota (Elster et al., 1999). Prolonged surface water flow provides favorable conditions for the proliferation of crust constituents, especially nitrogen-fixing cyanobacteria (Dickson, 2000), which are often the only significant source of nitrogen in extreme polar environments and one of the most limiting nutrients for plant production and community development (Henry et al., 1986). The importance of biological soil crust growth and N_2 fixation was emphasized in previous multivariate analyses on this foreland (Breen and Lévesque, 2006), which showed that the nitrogen concentration and percent cover of crusts were highly significant in explaining the vegetation distribution across the foreland. The further contribution of crusts to the physical environment and soil nutrient regime likely led to the increased vascular plant cover, richness and density as well as the increased rate of succession observed on this foreland as compared to others in the High Arctic (Breen and Lévesque, 2006). As global warming increases glacial melt in the High Arctic (ACIA, 2005), glacier forelands will become increasingly important constituents of polar nutrient regimes and those that promote the colonization and growth of biological soil crusts may be better able to support rich biotic communities despite rigorous surrounding environments.

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